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The Genera of Phyllomedusine Frogs (Anura: Hylidae)

BY

✓ WILLIAM E. DUELLMAN

UNIVERSITY OF KANSAS
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1968

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The Genera of Phyllomedusine Frogs
(Anura: Hylidae)

NOV 13 1968

BY

WILLIAM E. DUELLMAN

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One of the most distinctive phyletic lines among the diverse Neotropical hylid frogs is composed of a group of 40 species placed in the genus *Phyllomedusa* (Funkhouser, 1957) or in two or three different genera (Goin, 1961; Lutz, 1966). These species differ from all other Neotropical hylids by possessing a vertical, instead of horizontal, pupil. The only other hylids having a vertical pupil belong to the Papuan genus *Nyctimystes*. Goin (1961) erroneously stated that *Nyctimantis* and *Tripurion* have vertical pupils.

Although limited information is available on the cytotaxonomy of hylids, the data show that phyllomedusine species have $n = 13$ ($2n = 26$) chromosomes. *Acris* has $n = 11$ ($2n = 22$) (Cole, 1966). Members of the *Hyla leucophyllata*, *microcephala*, and *parviceps* groups have $n = 15$ ($2n = 30$), *Gastrotheca ceratophrys* has a haploid number of 14, the Papuan hylid genus *Nyctimystes* and all but one of the Australo-Papuan *Hyla* for which the numbers are known have a haploid number of 13, and all other New World hylids studied have $n = 12$ ($2n = 24$) (Duellman and Cole, 1965; Duellman, 1967).

Cei (1963) and Cei and Erspamer (1966) noted that phyllomedusine frogs differ notably from other Neotropical hylids on the basis of the amines and polypeptides in the skin. All species of phyllomedusines deposit their eggs in a gelatinous mass on leaves or branches above water. Although this type of egg deposition is characteristic of some rhacophorines and apparently all centrolenids, it is known among hylids only in the phyllomedusines and in two species of *Hyla*.

The distinctive combination of morphological, physiological, chromosomal, and behavioral characteristics is strongly suggestive that these frogs represent an early phyletic divergence within the Hylidae. Günther (1859) proposed the familial name Phyllomedusidae for *Phyllomedusa bicolor* (Boddaert). I suggest the recognition of the group as a subfamily. The following classification of

the phyllomedusines is based on my own knowledge of the Middle American and some South American species and on evidence from the literature on those South American species with which I am not personally familiar.

Subfamily Phyllomedusinae Günther, 1859

Phyllomedusidae Günther 1859 [Type genus, *Phyllomedusa* Wagler, 1830].

Definition.—Moderately small to large hylids having vertical pupils, $n = 13$ ($2n = 26$) chromosomes, skin containing large amounts of powerful bradykinin-like and physalaemin-like polypeptides, eggs suspended from vegetation above water, and tadpoles have a ventral spiracle sinistral to midline.

Range.—Low and moderate elevations in South and Middle America, including Trinidad, from northern Argentina and northwestern Ecuador to Veracruz and southern Sonora, México.

Content.—Three genera, one of which probably is composite.

Genus *Agalychnis* Cope, 1864.

Agalychnis Cope, 1864 [Type species, *Hyla moreletii* Duméril, 1853, by subsequent designation].

Definition.—Fingers and toes at least half webbed; terminal discs large; first toe shorter than second and not opposable to others; skin smooth, lacking osteoderms; parotoid glands, if present, poorly developed and diffuse; palpebral membrane reticulate (except in *A. calcarifer*); iris red or yellow; skull shallow, depth less than 40 per cent of length; nasals large; frontoparietal fontanelle large; quadratojugals reduced; prevomerine teeth present.

Range.—Central Veracruz and northern Oaxaca, México, south-eastward through Central America to northwestern Ecuador; one species disjunct in Amazonian Ecuador.

Content.—Eight species [synonyms in brackets]: *annae* (Duellman, 1963); *calcarifer* Boulenger, 1902; *callidryas* (Cope, 1862) [*helenae* Cope, 1885; *callidryas taylori* (Funkhouser, 1957)]; *craspedopus* (Funkhouser, 1957); *litodryas* (Duellman and Trueb, 1967); *moreleti* (Duméril, 1853) [*holochroa* (Salvin, 1861)]; *saltator* Taylor, 1955; *spurrelli* Boulenger, 1913.

Remarks.—Savage and Heyer (1967) provided evidence that *A. callidryas taylori* (Funkhouser) and *A. helenae* Cope were junior synonyms of *A. callidryas* (Cope).

Genus *Pachymedusa*, new genus

Type species, *Agalychnis dacnicolor* Cope, 1864.

Definition.—Fingers and toes having basal webs and lateral fringes; terminal discs large; first toe shorter than second and not opposable to others; skin smooth or shagreened, lacking osteoderms; paratoid glands present, diffuse; palpebral membrane reticulate; iris golden yellow with black reticulations; skull deep, depth more than 50 per cent of length; nasals large; frontoparietal fontanelle moderately large; quadratojugal robust; prevomerine teeth present.

Range.—Pacific slopes and lowlands from southern Sonora to the Isthmus of Tehuantepec, México.

Content.—Monotypic: *dacnicolor* Cope, 1864 [*alcorni* Taylor, 1952].

Remarks.—The generic name is derived from the Greek *pachy* meaning thick and the Greek *Medousa* (Latin, *Medusa*) in reference to *Phyllomedusa*; the sense implied is the heavy body of *Pachymedusa dacnicolor*.

Genus *Phyllomedusa* Wagler, 1830

Phyllomedusa Wagler, 1830 [Type species, *Rana bicolor* Boddaert, 1772].

Pithecopus Cope, 1866 [Type species, *Phyllomedusa azurea* Cope, 1862 (= *Phyllomedusa hypochondrialis* Daudin, 1803), by original designation].

Hylomantis Peters, 1872 [Type species *Hylomantis aspera* Peters, 1872, by monotypy].

Phrynomedusa Miranda-Ribeiro, 1923 [Type species, *Phrynomedusa fimbriata* Miranda-Ribeiro, 1923, by subsequent designation].

Bradymedusa Miranda-Ribeiro, 1926 [Type species, *Bradymedusa moschada* Miranda-Ribeiro, 1926 (= *Phyllomedusa rohdei* Mertens, 1926) by subsequent designation].

Definition.—Fingers and toes having greatly reduced webbing or lacking webs; terminal discs small; first toe shorter than, equal to, or longer than second, opposable or not; skin smooth or rugose having osteoderms or not; paratoid glands present, in most species, usually distinct and elevated; palpebral membrane not reticulate; iris uniformly silvery white to orange-bronze with black reticulations; skull moderate to deep, depth more than 38 per cent of length; nasals moderately small; frontoparietal fontanelle present, variable in size; quadratojugal reduced in some species; prevomerine teeth present or absent.

Range.—Low and moderate elevations in South America east of the Andes from the Caribbean (including Trinidad) to northern Argentina; Costa Rica and Panamá in Central America.

Content.—Thirty-one species [synonyms in brackets]: *aspera* (Peters, 1872); *ayeaye* (B. Lutz, 1966); *bahiana* A. Lutz, 1925; *bicolor* (Boddaert, 1772) [*scleroderma* Cope, 1868]; *blombergi* Funkhouser, 1957; *boliviana* Boulenger, 1902; *buckleyi* Boulenger, 1882; *burmeisteri burmeisteri* Boulenger, 1882; *burmeisteri distincta* B. Lutz, 1950; *centralis* Bokermann, 1965; *cochranae* Bokermann, 1966; *coelestis* (Cope, 1874); *edentula* Andersson, 1945; *feltoni* Shreve, 1935; *fimbriata* (Miranda-Ribeiro, 1923) [*appendiculata* A. Lutz, 1925]; *guttata* A. Lutz, 1925; *hypochondrialis* (Daudin, 1803) [*azurea* Cope, 1862; *megacephala* (Miranda-Ribeiro, 1926)]; *iheringi* Boulenger, 1885; *lemur* Boulenger, 1882; *loris* Boulenger, 1912; *medinae* Funkhouser, 1962; *nicefori* Barbour, 1926; *orceci* Funkhouser, 1957; *pailona* Shreve, 1959; *perlata* Boulenger, 1882; *rohdei* Mertens, 1926 [*moschada* (Miranda-Ribeiro, 1926)]; *sauvagei* Boulenger, 1882 [*rickettsii* Günther, 1897]; *tarsius* (Cope, 1868); *tomopterna* (Cope, 1868) [*palliata* Peters, 1872]; *trinitatis* Mertens, 1926, *vaillanti* Boulenger, 1882, *venusta* Duellmann and Trueb, 1967.

Remarks.—*Phyllomedusa* includes 1) a series of large species (*bicolor-burmeisteri*) showing progressive specialization of the feet; 2) a series of small species having grasping feet (*ayeaye*, *centralis*, *cochranae*, *guttata*, *hypochondrialis*, and *rohdei*); 3) a series of small, relatively unspecialized species (*lemur*, *loris*, and *medinae*); and 4) several other species of questionable affinities. Lutz (1966) resurrected Cope's (1866) *Pithecopus* for 12 species (*ayeaye*, *boliviana*, *burmeisteri*, *coelestis*, *hypochondrialis*, *nicefori*, *rohdei*, *sauvagei*, *tarsius*, *tomopterna*, *trinitatis*, and *vaillanti*). Adequate material is not available for detailed study of all South American species; consequently, a firm classification cannot be established at this time. Nevertheless, it is obvious that Lutz's arrangement is unnatural. If subsequent investigations show, as seems likely, that the small specialized phyllomedusines are a natural phyletic unit, the generic name *Pithecopus* is available. However, species such as *boliviana*, *burmeisteri*, *nicefori*, and *trinitatis* do not belong in *Pithecopus*. As noted by Funkhouser (1962), the small, relatively unspecialized species (*lemur*, *loris*, and *medinae*) form a natural group; possibly this group should be accorded generic recognition. Until more evidence on the interspecific relationships is acquired, the maintenance of the current classification is desirable.

DISCUSSION

Noble (1931) considered the species of *Phyllomedusa* having opposable digits, reduced terminal discs, and no webbing to be advanced and such species as *Agalychnis moreleti*, *calcarifer*, and *spurrelli* to be primitive. Funkhouser (1957) followed Noble's suggestion and attempted to explain the evolution of the species of *Phyllomedusa* (*sensu lato*) by assuming that they evolved from an advanced *Hyla*-like ancestor. Therefore, she placed those species having large, fully webbed hands and feet near the base of her phylogenetic scheme and hypothesized that evolutionary sequences involved stages of reduction and eventual loss of webbing, followed by the development of grasping toes. Such an evolutionary history is highly unlikely. The *Agalychnis* phyletic line has one kind of specialization for an arboreal existence. It is contrary to evolutionary theory that a specialized group would evolve into a generalized form and then evolve new kinds of specializations to meet the needs imposed by the same environmental conditions affecting the earlier specialized group. A more reasonable hypothesis is that the evolution of opposable digits took place in a phyletic line that had as its ancestral stock a frog with generalized hands and feet. If this assumption is correct, *Phyllomedusa* and *Agalychnis* represent different phyletic lines; each exhibits divergent modes of adaptation for arboreal habits, whereas *Pachymedusa* probably remains relatively little changed from the basic phyllomedusine stock.

On the basis of modern distribution and areas of diversification alone (no fossils are known), it is evident that *Phyllomedusa* underwent its adaptive radiation in South America, *Agalychnis* evolved in Central America, and *Pachymedusa* ended up in western México. If we follow the Matthewsian concepts of the American herpetofauna outlined by Dunn (1931) and modified by Schmidt (1943) and Stuart (1950), *Pachymedusa* represents a "hanging-relict" of a group that moved southward. According to Savage's (1966) interpretation of the origins and history of the American herpetofauna, *Agalychnis* and *Pachymedusa* are members of the Mesoamerican fauna, and *Phyllomedusa* is part of the Neotropical fauna. Perhaps the phyllomedusines arose in South America; from there a primitive stock spread northward and survived as *Pachymedusa* in México, whereas the stock in Central America and South America evolved into *Agalychnis* and *Phyllomedusa*, respectively.

Evidently the primitive phyllomedusines evolved the habit of arboreal egg deposition and a walking gait; the latter is best developed in the small, highly specialized species of *Phyllomedusa* (Lutz, 1966). Probably the other divergent arboreal adaptations resulted from environmental stresses and competition. The generalized *Pachymedusa* inhabits relatively dry areas characterized by low forest. Throughout its range it coexists with no more than five other arboreal hylids. The species of *Agalychnis* live in rain forests and humid montane forests. In any given area one species of *Agalychnis* occurs sympatrically with no more than a dozen other arboreal hylids. With few exceptions the species of *Agalychnis* are more arboreal in their habits than are other hylids. The species of *Phyllomedusa* live in the same kinds of habitats as do those of *Agalychnis*, but throughout the ranges of most of the species of *Phyllomedusa* the diversity of arboreal hylids is much greater than in Central America. In the upper Amazon Basin as many as 35 hylids occur sympatrically. Many groups of *Hyla* in this area (for example, the *Hyla boans* and *Hyla marmorata* groups) are equally as arboreal in their habits as are the species of *Agalychnis* in Central America. Conceivably, competition within this array of tree frogs resulted in selection for modification of the extremities, thereby bringing about a different mode of climbing in *Phyllomedusa*. The walking gait already present in phyllomedusines provided a source for further modification, which resulted in the development of opposable digits and the associated lemuroid manner of climbing.

The known life histories of most species of *Phyllomedusa*, all species of *Agalychnis*, and that of *Pachymedusa* are similar. Characteristically the tadpoles are generalized pelagic types that develop in ponds, but at least some of the small specialized *Phyllomedusa* in southeastern Brazil have stream-adapted tadpoles with funnel-shaped mouths (Cochran, 1955; Bokermann, 1966). Knowledge of the life histories of the other species of *Phyllomedusa* should aid in the interpretation of the phylogenetic relationships of the several groups of frogs now assigned to that genus.

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Cranial Osteology of the Hylid Frog,
Smilisca baudini

BY

LINDA TRUEB

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Cranial Osteology of the Hylid Frog, *Smilisca baudini*

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LINDA TRUEB

HARVARD
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INTRODUCTION

The paucity of descriptive cranial anatomical work dealing with hylid frogs was pointed out by Trueb (1966) in her paper describing the cranial osteology of *Hyla septentrionalis*. Comparative studies on the cranial osteology of the genus *Smilisca* (Duellman and Trueb, 1966), along with other more brief descriptions, reveal variation among cranial characters of hylids. Since these external characters have been useful in defining species, species groups, and genera, it seems worthwhile to pursue correlated studies on internal cranial structure. The following account dealing with the Neotropical tree frog, *Smilisca baudini* Duméril and Bibron, 1841, is the first published description of the internal cranial anatomy of a hylid frog, and supplements the recent account (Duellman and Trueb, 1966) of external cranial osteology of the same species. Comparative studies of hylid skulls are expected to yield information of taxonomic importance.

I am grateful to Richard J. Baldauf of Texas A & M University and William E. Duellman of the University of Kansas for critically reading the manuscript and offering helpful suggestions. The findings reported here result from research on Middle American hylids supported by a grant from the National Science Foundation (GB-1441) to William E. Duellman.

Materials and Methods

The serial sections illustrated beyond are from an adult male of *Smilisca baudini* (KU 89924) having a snout-vent length of 53.0 mm. and a head width (measured at angle of jaws) of 17.0 mm. The specimen was collected 5.2 kilometers east-southeast of Córdoba, Veracruz, México. Transverse sections were cut at thicknesses of 10 and 15 microns on a rotary microtome and stained according to the technique described by Baldauf (1958). Cleared and stained specimens and dried skeletons also were used. Figure 1 is based on KU 68183-4 and Fig. 9 on KU 55614. All other draw-

ings are made from KU 89924. In all cross-sectional figures, bone is represented by solid black, cartilage by stippling, and connective tissue by cross-hatching. Unless otherwise noted all descriptions are given in an anterior-posterior sequence.

Commonly accepted English terms are used. For example, dentary is used in preference to dentale and maxillary process instead of processus maxillaris. If no commonly accepted English term is available for a given structure, the Latin name is retained. For example, the cartilaginous plate separating the cavum principale from the cavum medium is termed the lamina superior.

DESCRIPTION OF INTERNAL CRANIAL OSTEOLOGY

Olfactory Region

Alary cartilage.—The anterior end of the alary cartilage (*al. c.*, Figs. 2-5) lies within the posterior concavity of the alary process

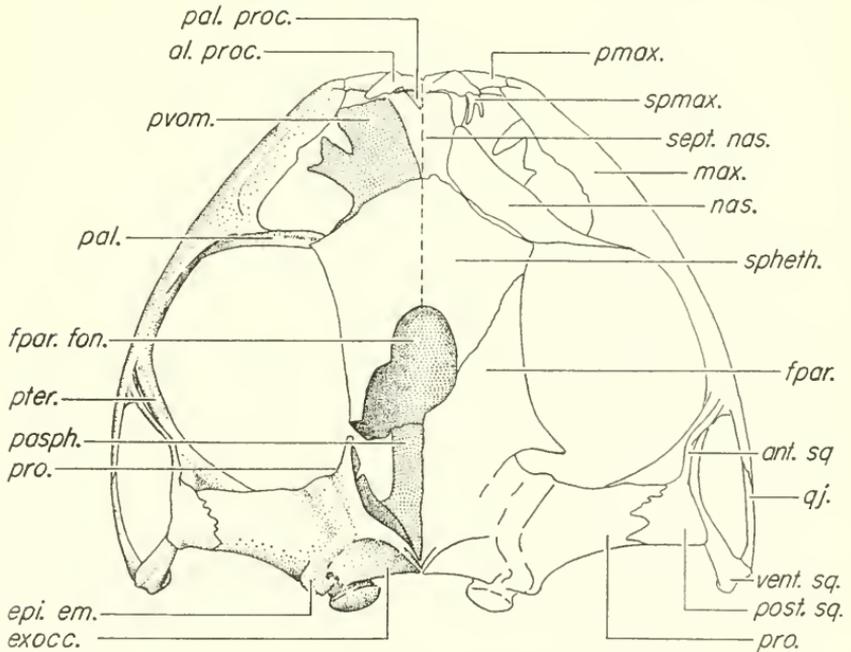


FIG. 1. Partially disarticulated skull (left frontoparietal and nasal removed) of *Smilisca baudini*, KU 68183, ♀. $\times 4$. Abbreviations: *al. proc.*, alary process of premaxillary; *ant. sq.*, anterior arm of squamosal; *epi. em.*, epiotic eminence; *exocc.*, exoccipital; *fpar.*, frontoparietal; *fpar. fon.*, frontoparietal fontanelle; *max.*, maxillary; *nas.*, nasal; *pal.*, palatine; *pal. proc.*, palatine process; *posph.*, parasphenoid; *pmax.*, premaxillary; *pvom.*, prevomer; *post. sq.*, posterior arm of squamosal; *pro.*, prootic; *pter.*, pterygoid; *qj.*, quadratojugal; *spmax.*, septo-maxillary; *sept. nas.*, septum nasi; *spheth.*, sphenethmoid; *vent. sq.*, ventral arm of squamosal.

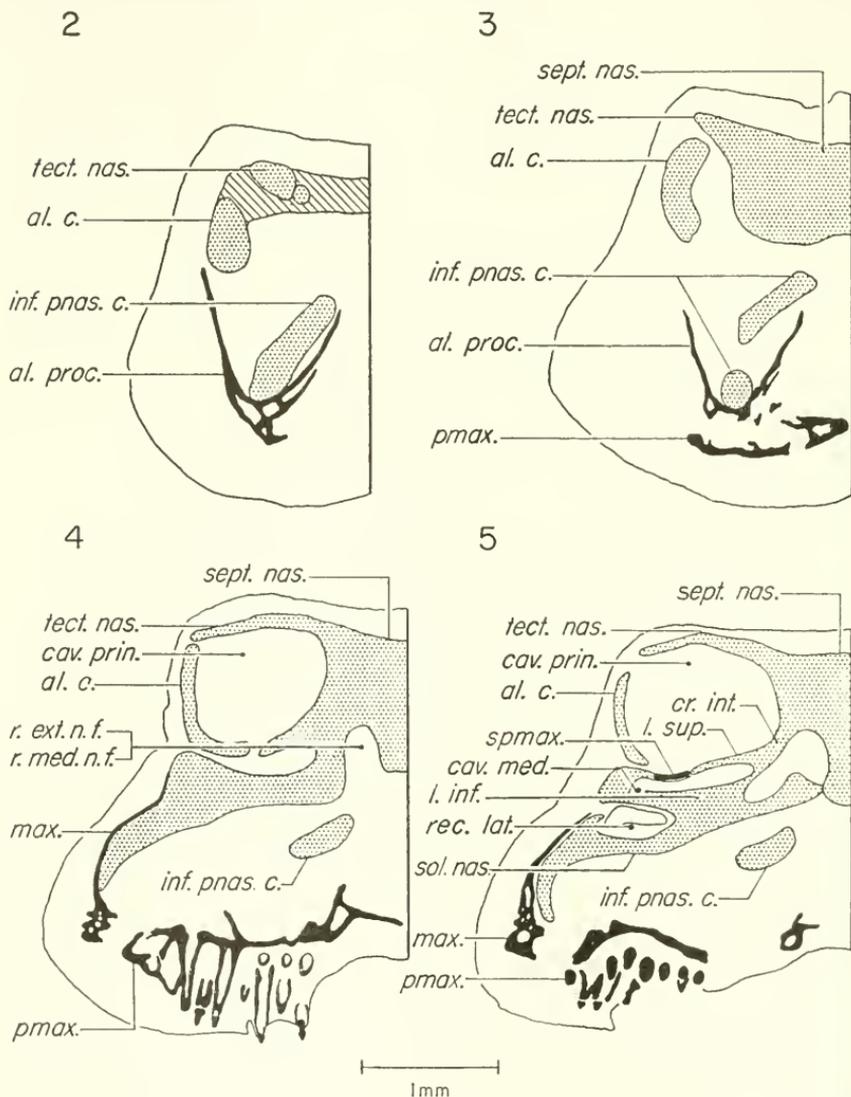
(*al. proc.*, Figs. 1-3) of the premaxillary (*pmax.*). In posterior sections the cartilage assumes a dorsolateral position (Fig. 3), ventral and slightly lateral to the tectum nasi. The alary cartilage remains narrowly separated from the tectum nasi but fuses ventromedially with the septum nasi and forms a nearly complete cartilaginous capsule around the anterior end of the cavum principale. Posterior to the anterior end of the cavum medium and the lamina superior, the alary cartilage separates ventrally from the lamina. In subsequent posterior sections, the cartilage, arcuate in cross section, becomes progressively smaller and terminates at the level of the union of the medial and lateral recesses of the cavum inferior.

Prenasal cartilages.—The superior prenasal cartilage is small; it lies adjacent to the posterodorsal surface of the alary process of the premaxillary, and anterior to the alary cartilage. The inferior prenasal cartilage (*inf. pmas. c.*, Figs. 2-6, and 8) appears posterior to the appearance of the alary cartilage. The anterior terminus lies at the base of the alary process; the cartilage extends dorsally (Fig. 3) along the posterior surface of the alary process and then curves posterodorsally and joins the solum nasi medioventral to the posterior end of the septomaxillary (Fig. 8d).

Tectum nasi.—The anterolateral corner of the tectum nasi (*tect. nas.*, Fig. 2) appears just posterior and dorsomedial to the anterior end of the alary cartilage. The anterior process is short; it fuses medially with the septum nasi forming a complete roof to the cavum principale (Figs. 3 and 4). The oblique cartilage (*obl. c.*) diverges laterally from the tectum nasi just posterior to the terminus of the alary cartilage (Fig. 6). Medially, the tectum nasi persists, overlaid by the nasal bone laterally.

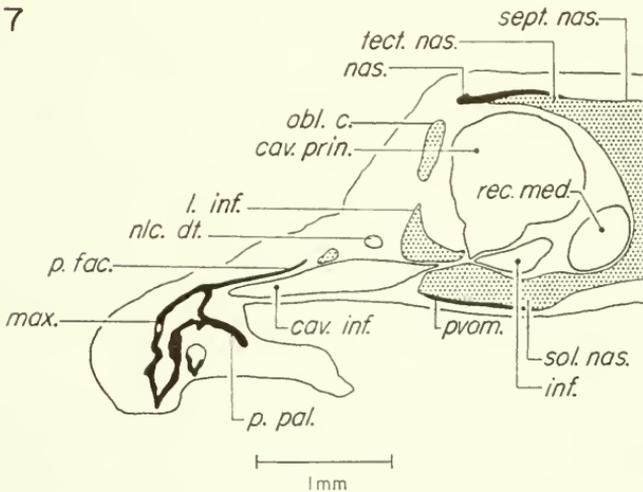
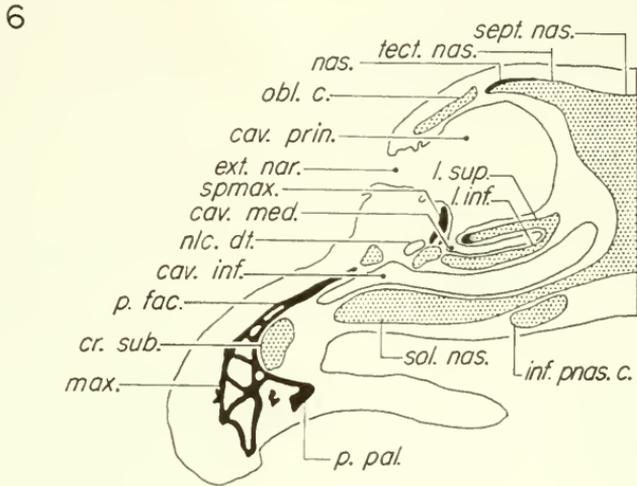
Septum nasi.—Posterior to the appearance of the septum nasi (*sept. nas.*) and its union with the tectum nasi (Fig. 3), the septum abruptly expands across the width of the skull medial to the alary cartilage. The septum is entirely cartilaginous posterior to the level of the olfactory eminence, except for a small amount of secondary membranous ossification dorsomedially at a level anterior to the nasal bones. Perichondral ossification commences in the dorsal part of the septum nasi at the level of the olfactory eminence. Endochondral ossification first appears dorsally in the vertical part of the septum at the level of the internal nares. Ossification of dorsal parts of the septum precedes ossification of ventral parts. Perichondral ossification of the ventral part of the septum nasi is first noted at the level of transition between the planum antorbitale

and solum nasi. Perichondral ossification gradually gives way to endochondral ossification posteriorly.



FIGS. 2-5. Transverse sections through anterior end of skull: 2) anterior level of inferior prenasal cartilage; 3) anterior level of internasal septum; 4) olfactory capsule at anterior level of cavum principale; 5) olfactory capsule at anterior level of cavum inferius. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *cr. int.*, crista intermedia; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *pmax.*, premaxillary; *r. ext. n. f.*, ramus externus narium foramen; *r. med. n. f.*, ramus medialis narium foramen; *rec. lat.*, recessus lateralis; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spx.*, septomaxilla; *tect. nas.*, tectum nasi.

Nasal cavities and associated structures.—The cavum principale (*cav. prin.*, Fig. 4) is the most anterior of the nasal cavities. It first appears within the capsule bordered dorsally by the tectum nasi, medially and ventrally by the septum nasi, and laterally by



FIGS. 6-7. Transverse sections through olfactory capsule: 6) posterior level of cavum medium; 7) anterior level of prevomer. Abbreviations: *cav. inf.*, cavum inferius; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *cr. sub.*, crista subnasalis; *ext. nar.*, external nares; *inf.*, infundibulum; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *nas.*, nasal; *nlc. dt.*, nasolacrimal duct; *obl. c.*, oblique cartilage; *p. fac.*, pars facialis; *p. pal.*, pars palatina; *pvom.*, prevomer; *rec. med.*, recessus medialis; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spmax.*, septomaxillary; *tect. nas.*, tectum nasi.

the alary cartilage. The cavity extends posteriorly within recesses of the sphenethmoid to the level at which the septum nasi terminates.

The cavum medium (*cav. med.*, Fig. 5) lies ventral and slightly posterior to the anterior end of the cavum principale. It appears slightly anterior to the septomaxillary at the level of the foramen ramus externus narium and ramus medialis narium. The appearance of the cavum medium within the ventrolateral extension of the septum nasi divides the latter into an upper component, the lamina superior (*l. sup.*) lying between the cavum principale and cavum medium, and a lower part, the lamina inferior (*l. inf.*) lying ventral to the cavum medium. As the cavum medium increases in width in posterior sections, the lamina superior and lamina inferior lose their lateral connection. The lateral part of the cavum medium diverges in the region of the external nares as the nasolacrimal duct (*ncl. dt.*) and the cavum medium becomes confluent with the cavum principale (Fig. 6). The posterior end of the cavum medium lies at the level of the posterior terminus of the septomaxillary.

Slightly posterior to the anterior end of the cavum medium the foramen for the ramus externus narium (*r. ext. n. f.*) and ramus medialis narium (*r. med. n. f.*) opens ventromedially into the floor of the septum nasi (Fig. 4). The ventral closure of the floor of the foramen completes the solum nasi, marks the anterior end of the recessus medialis of the cavum inferior, and differentiates the roof of the recess, the crista intermedia (*cr. int.*), from the solum (Fig. 5). The crista intermedia joins the laminae superior and inferior and joins them for a short distance to the septum nasi medially. The anterolateral part of the cavum inferior (*cav. inf.*) lies ventrolateral to the cavum medium, and extends medially to join the medial recess. The fusion of the two recesses of the cavum inferior completely separates the lamina inferior from the solum nasi (Fig. 6).

Near the level of the union of the recessus lateralis and recessus medialis of the cavum inferior, the crista intermedia separates from the septum nasi, and the lamina superior diverges at its mid-width to accommodate the septomaxillary (*spmax.*) (Figs. 5 and 6). The lateral remnant of the lamina superior and transition zone between the lamina superior and lamina inferior is short and is quickly replaced by connective tissue. Slightly posterior, the distal edge of the lamina inferior diverges laterally as a small process, which lies dorsal to the pars facialis (*p. fac.*) of the maxillary. This part

of the lamina inferior terminates posteriorly at the level of confluence between the cavum principale and lateral recess of the cavum inferior.

Slightly posterior to the divergence of the crista intermedia from the septum nasi, the crista terminates, thereby separating the lamina superior and the lamina inferior from one another (Figs. 6 and 8). The lamina superior terminates at the level of the infundibulum (*inf.*, Fig. 7), whereas the lamina inferior extends posterolaterally, increases greatly in depth and joins the laterally ascending oblique cartilage (*obl. c.*) to form the planum terminale (*pla. ter.*, Fig. 10).

The crista subnasalis (*cr. sub.*, Fig. 6) differentiates from the lateral edge of solum nasi adjacent to the maxillary in sections just posterior to the confluence of the recessus medialis and the recessus lateralis. The crista persists as a rod of cartilage which gradually diminishes in size and terminates at the posterior level of the septomaxillary.

The septomaxillary.—The septomaxillary (*spmax.*, Fig. 9a-c) is a triradiate bone. The anterior terminus is a thin sliver of bone oriented horizontally between the cavum principale and cavum medium and lateral to the lamina superior (Figs. 5 and 8a). This anterior ramus of the septomaxillary increases in size posteriorly and diverges medially into a medial ramus (*med. r. spmax.*) and lateral ramus (*lat. r. spmax.*, Fig. 9a-b) to accommodate the confluence of the cavum principale and cavum medium (Figs. 6 and 8b-c). The small medial ramus is associated with the distal end of the lamina superior whereas the lateral ramus lies dorsal to the lateral margin of the cavum medium. Just anterior to the anterior end of the nasolacrimal duct, the ventral ramus of the septomaxillary (*vent. r. spmax.*, Fig. 9c) is present in cross-sections ventral to the cavum medium. The ventral ramus joins the horizontal and dorsal rami of the septomaxillary at the anterior end of the nasolacrimal duct. The medial branch terminates posteriorly at the level at which the cavum principale joins the cavum inferior. The lateral ramus of the septomaxillary terminates posteriorly at the level at which the recessus medialis diverges from the recessus lateralis posteriorly and cavum principale and recessus lateralis are confluent.

Planum terminale.—Posterior to the infundibulum the lamina inferior and oblique cartilage join to form the planum terminale (*pla. term.*) which lies lateral to the cavum principale (Fig. 10). The lamina inferior diverges ventrally from the planum terminale anterior to the olfactory eminence. The planum terminale is re-

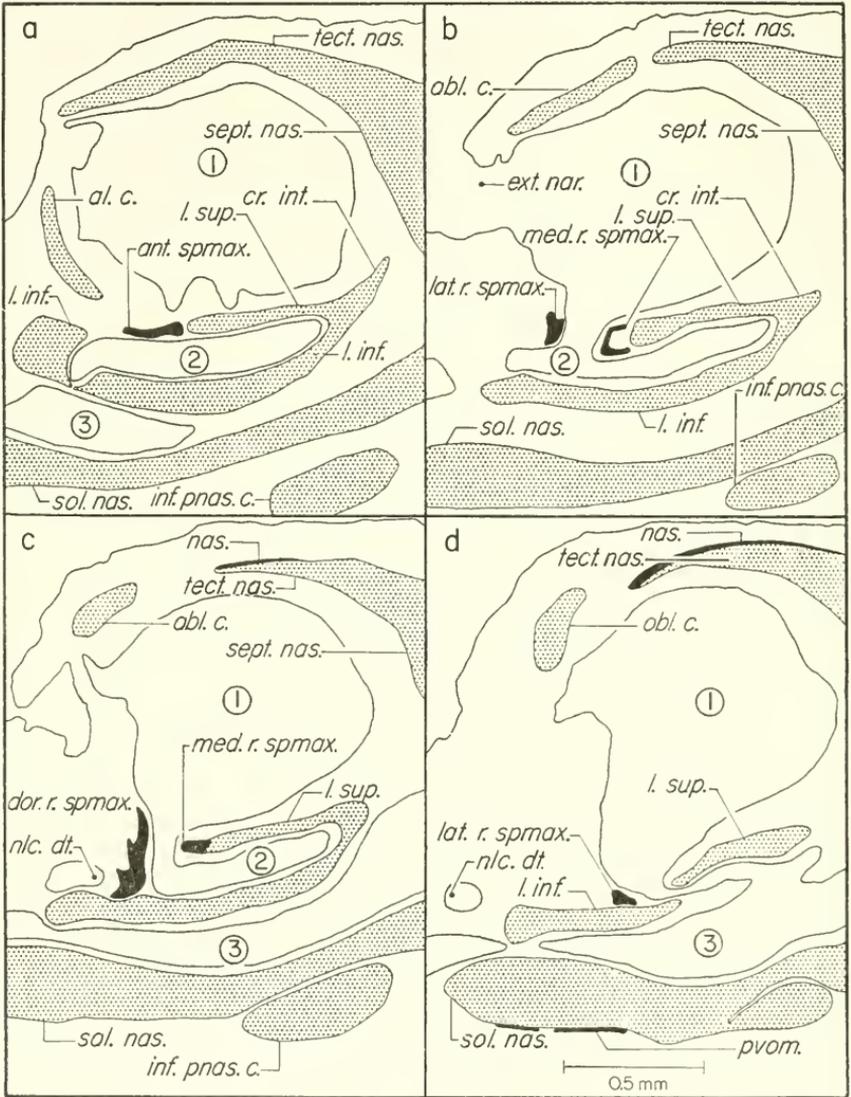


FIG. 8. Transverse sections through olfactory capsule in region of septomaxillary: a) anterior terminus of septomaxillary; b) medial divergence of septomaxillary; c) dorsal ramus of septomaxillary; d) posterolateral terminus of septomaxillary. Encircled numbers represent the nasal cavities as follows: 1) cavum principale; 2) cavum medium; and 3) cavum inferius. Abbreviations: *al. c.*, alary cartilage; *ant. spmax.*, anterior end of septomaxillary; *cr. int.*, crista intermedia; *dor. r. spmax.*, dorsal ramus of septomaxillary; *ext. nar.*, external nares; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *lat. r. spmax.*, lateral ramus of septomaxillary; *med. r. spmax.*, medial ramus of septomaxillary; *nas.*, nasal; *nlc. dt.*, nasolacrimal duct; *obl. c.*, oblique cartilage; *pvom.*, prevomer; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spmax.*, septomaxillary; *tect. nas.*, tectum nasi.

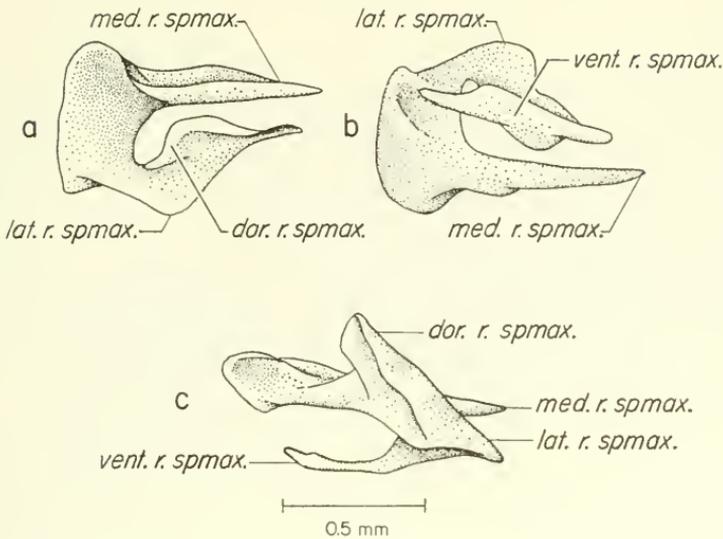


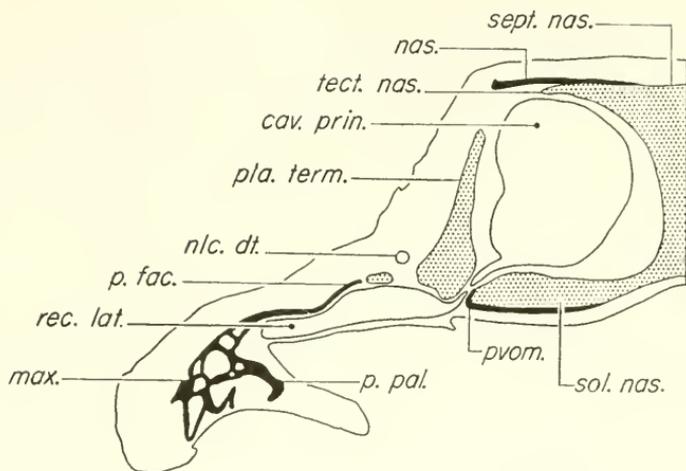
FIG. 9. Septomaxillary drawn from cleared and stained specimen of *Smilisca baudini*, KU 55614: a) dorsal; b) ventral; c) lateral. In each example, the anterior end lies to the left. Abbreviations: *dor. r. spmax.*, dorsal ramus of septomaxillary; *lat. r. spmax.*, lateral ramus of septomaxillary; *med. r. spmax.*, medial ramus of septomaxillary; *vent. r. spmax.*, ventral ramus of septomaxillary.

stricted ventrally and terminates at the level of the olfactory eminence (*olf. em.*, Fig. 11).

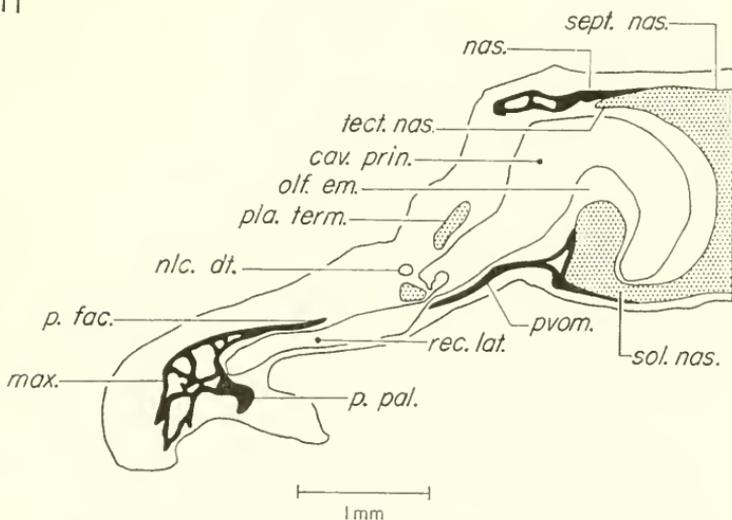
Anterior and posterior maxillary processes.—The anterior end of the anterior maxillary process (*ant. max. proc.*) lies within the maxillary at the level of the posterior terminus of the planum terminale. The anterior maxillary process diverges medially from the maxillary (Fig. 13) and expands dorsally along the medial face of the pars facialis to meet the planum antorbitale just anterior to the transition zone between the latter and the solum nasi. Posterior to the transition zone, the planum antorbitale disappears and the posterior maxillary process is restricted ventrally along the pars facialis of the maxillary. Posteriorly the cartilage is associated with the pterygoid, where it is known as the pterygoid process (*pter. proc.*, Fig. 14).

Planum antorbitale.—The anterior terminus of the planum antorbitale (*pla. ant.*) lies medial to the ventrolateral part of the nasal and lateral to the internal nares (Fig. 12). It abruptly expands dorsally along the medial face of the nasal to join the tectum nasi dorsolaterally; somewhat posteriorly the planum antorbitale joins

10



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FIGS. 10-11. Transverse sections through posterior part of olfactory capsule: 10) region of planum terminale; 11) anterior region of olfactory eminence. Abbreviations: *cav. p.*, cavum principale; *max.*, maxillary; *nas.*, nasal; *nlc. dt.*, nasolacrimal duct; *olf. em.*, olfactory eminence; *p. fac.*, pars facialis; *p. pal.*, pars palatina; *pla. ter.*, planum terminale; *pvom.*, prevomer; *rec. lat.*, recessus lateralis; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *tect. nas.*, tectum nasi.

the anterior maxillary process ventrally at the posterior margin of the internal nares.

External dermal bones associated with the olfactory region.—The association of the premaxillary (*pmax.*) to the nasal cartilages is

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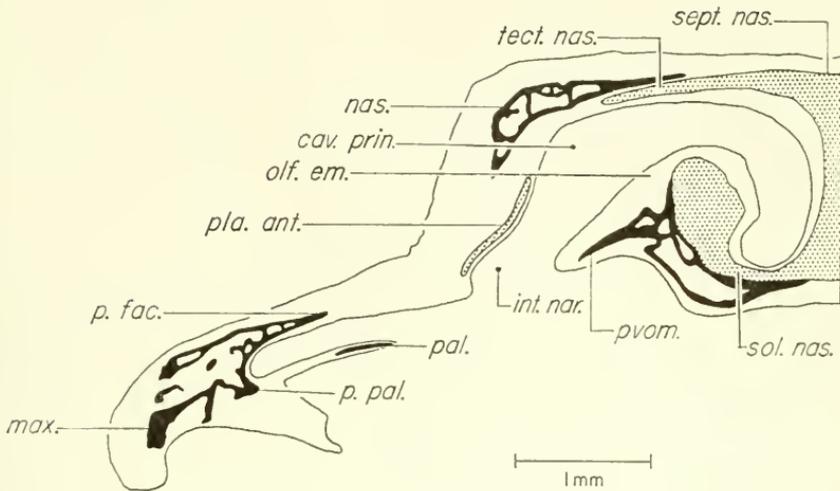


FIG. 12. Transverse section through the olfactory capsule in region of planum antorbitale. Abbreviations: *cav. prin.*, cavum principale; *int. nar.*, internal nares; *max.*, maxillary; *nas.*, nasal; *olf. em.*, olfactory eminence; *p. fac.*, pars facialis; *p. pal.*, pars palatina; *pal.*, palatine; *pla. ant.*, planum antorbitale; *pvom.*, prevomer; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *tect. nas.*, tectum nasi.

described in preceding sections. The premaxillaries are separated from each other medially and from the maxillaries laterally by dense connective tissue. Anteriorly, the maxillary (*max.*) bears a small palatine process (*pal. proc.*, Fig. 1) and a long, delicate pars facialis (*p. fac.*, Fig. 6), which terminates dorsally at the level of the lamina inferior. Posterior to the transition zone between the planum antorbitale and solum nasi the pars facialis is greatly reduced. The pars palatina (*p. pal.*, Fig. 6) persists to the posterior part of the orbit.

The anterior end of the prevomer (*pvom.*, Fig. 1) is associated with the venter of the solum nasi at the level of the infundibulum just posterior to the incorporation of the inferior prenasal cartilage into the solum (Fig. 7). The prevomer expands dorsally around the distal end of the solum to provide a bony lateral support for the olfactory eminence (Figs. 10 and 11). A distal wing of the prevomer forms the bony anterior and medial margins of the internal nares.

The palatine (*pal.*, Figs. 1 and 12) lies in connective tissue medial and adjacent to the pars facialis. At its maximum size the palatine forms the bony posterior margin of the internal nares and extends

dorsomedially from the pars palatina to the distal part of the solum nasi.

The nasal (*nas.*, Fig. 1) is a thin bone overlying the tectum nasi anteriorly (Fig. 7). It expands laterally to form a complete roof over the cavum principale (Fig. 10). In the region of the internal nares, the nasal forms the lateral wall of the cavum principale (Fig. 12).

Sphenethmoid Region

Posterior to the transition zone between the planum antorbitale and solum nasi, the sphenethmoid (*spheth.*, Fig. 1) is fully ossified medially, the lateral parts of the bone at this level are only ossified perichondrally. The septum nasi persists at the anterior level of the orbit and terminates just anterior to the orbitonasal foramen (*orbnas. f.*) and the anterior end of the parasphenoid (*pasph.*, Fig. 13). The orbitonasal foramen is moderately large, has a complete bony margin, and is located at the dorsolateral corner of the braincase.

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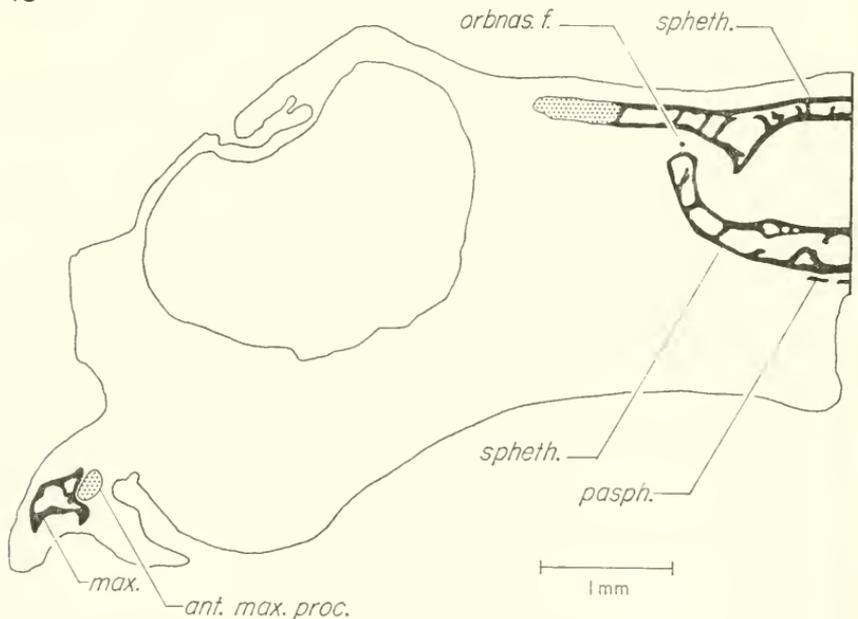


FIG. 13. Transverse section through sphenethmoid region at level of orbitonasal foramen. Abbreviations: *ant. max. proc.*, anterior maxillary process; *max.*, maxillary; *orbnas. f.*, orbitonasal foramen; *pasph.*, parasphenoid; *spheth.*, sphenethmoid.

At the level of the orbitonasal foramen, the sphenethmoid is entirely ossified except for a small dorsolateral extension. This distal extension expands laterally in posterior sections as the braincase is increased to its maximum width at the mid-length of the orbit; the cartilaginous margin is retained throughout the length of the sphenethmoid.

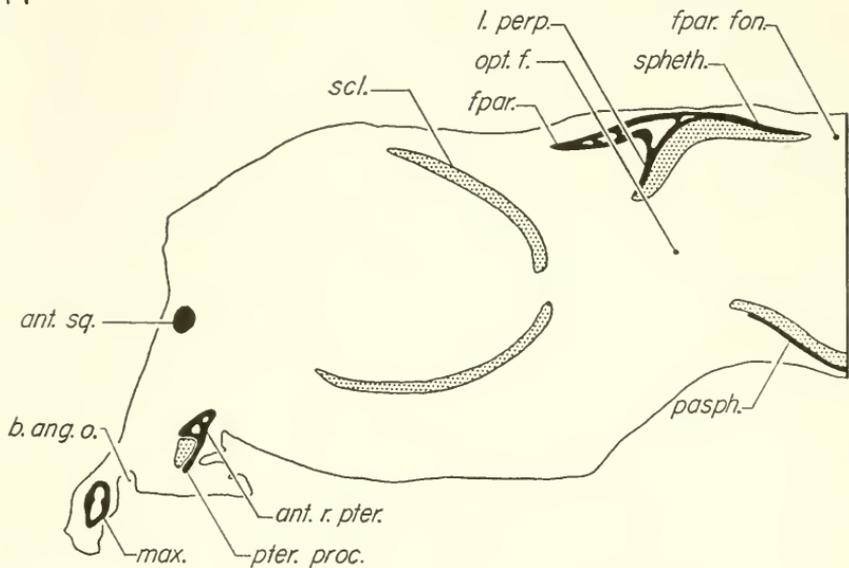
The bony dorsomedial part of the sphenethmoid diverges, forming the anterior border of the frontoparietal fontanelle (*fpar. fon.*, Figs. 1 and 14). The entire fontanelle is covered with a layer of dense connective tissue continuous with that in which marginal bones and cartilage of the sphenethmoid lie, and which is discrete from the lower dermal layer of the overlying skin. At this level the braincase is U-shaped in cross-section. Ossification terminates first in the ventrolateral corners, followed by the lateral and dorsolateral areas. The bony support of the latter area is furnished by the lamina perpendicularis (*lam. perp.*) of the frontoparietal (*fpar.*, Fig. 14). Cartilage appears in the ventral part of the sphenethmoid in postermost sections; at the posterior levels of the orbit the sphenethmoid is entirely cartilaginous.

Orbital, Otic, and Occipital Regions

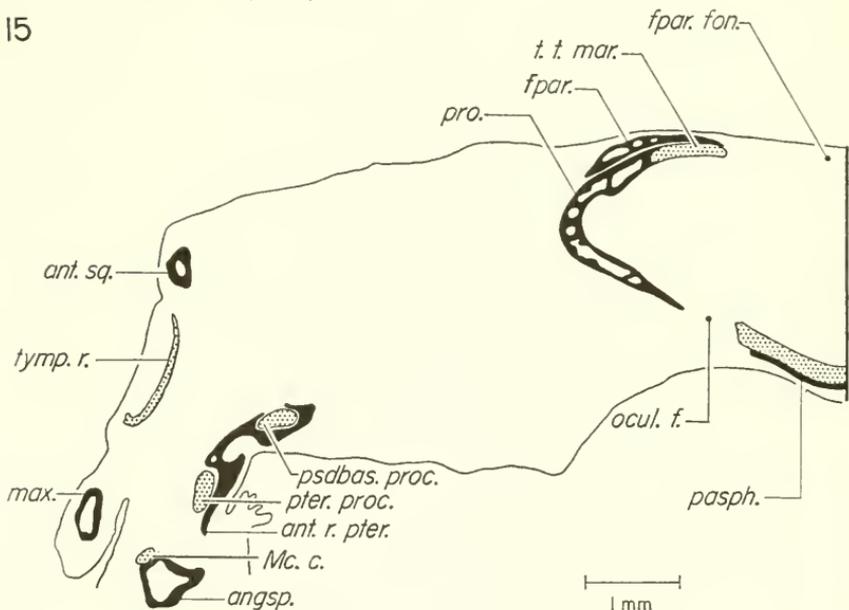
Orbital region.—The sclera (*scl.*, Fig. 14) of the eye is cartilaginous. The optic foramen (*opt. f.*) is large and lies in connective tissue at the posterior limits of the orbit and sphenethmoid. At the posterior levels of the foramen the dorsolateral cranial roof cartilages, taeniecti marginales (*t. t. mar.*) converge medially to form the posterior margin of the frontoparietal fontanelle and the tectum synoticum (*tect. syn.*) of the occipital region. At the posterior levels of the orbit the bursa angularis oris (*b. ang. o.*, Fig. 14) is present adjacent to the maxillary.

Nerve foramina of otic and occipital regions.—The trochlear foramen lies within the bony margins of the optic foramen. The trochlear nerve is located posterodorsal to the optic tract, and separated from the latter by connective tissue. The oculomotor foramen (*ocul. f.*) lies in connective tissue posterior and ventral to the optic foramen (Fig. 15). Anteriorly, dorsally, and ventrally the foramen has a bony margin formed by the prootic (*pro.*); posteriorly, only a thin layer of connective tissue separates the oculomotor from the large prootic foramen (*pro. f.*). The latter is bordered by bone dorsally and by cartilage ventrally (Fig. 16). Posteriorly, bone separates the prootic foramen from the anterior acoustic foramen (*ant. acus.*

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FIGS. 14-15. Transverse sections through skull: 14) at level of optic foramen; 15) at level of oculomotor foramen. Abbreviations: *angspl.*, angulosplennial; *ant. r. pter.*, anterior ramus of pterygoid; *ant. sq.*, anterior arm of squamosal; *b. ang. o.*, bursa angularis oris; *fpar.*, frontoparietal; *fpar. fon.*, frontoparietal fontanelle; *l. perp.*, lamina perpendicularis of frontoparietale; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *pasph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter. proc.*, pterygoid process; *scl.*, sclera; *t. t. mar.*, taenia tecti marginalis; *tym. r.*, tympanic ring.

f.), through which the ramus acusticus anterior and medius pass (Fig. 17). An extremely narrow bridge of cartilage separates the anterior acoustic foramen from the larger posterior acoustic foramen (*post. acus. f.*). The latter has a bony posterior margin and is widely separated from the bony jugular foramen (*jug. f.*) posteriorly (Fig. 19).

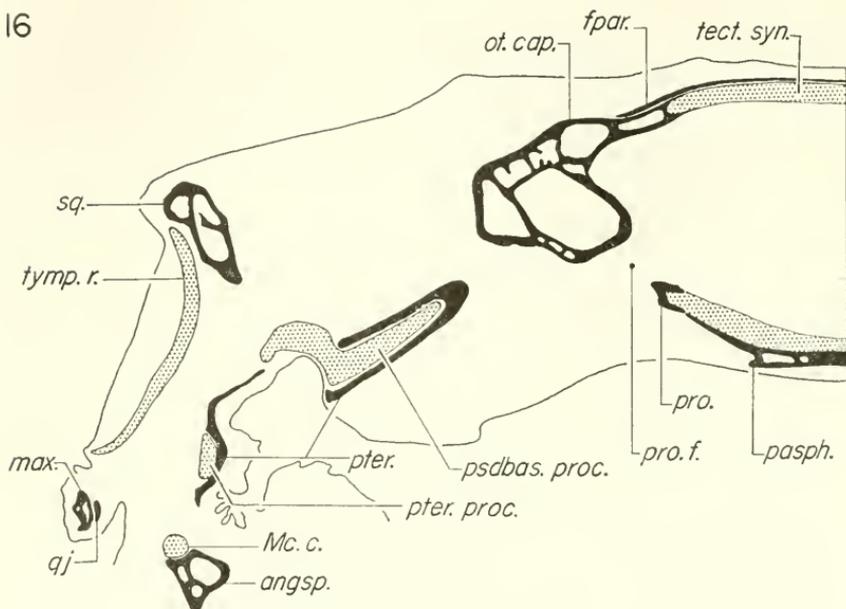
Pterygoid.—The anterior terminus of the pterygoid (*pter.*, Fig. 1) appears at approximately the mid-length of the orbit as a small arcuate bone closely applied to the posterior maxillary process. Farther posteriorly the maxillary decreases in size, and the pterygoid and posterior maxillary process diverge medially from it. Posterior to this point of divergence, the posterior maxillary process is known as the pterygoid process (*pter. proc.*). The anterior terminus of the quadratojugal (*qj.*) lies medial to the maxillary at the level of the oculomotor foramen (Fig. 14).

Otic region.—The anterior end of the otic capsule (*ot. cap.*) is present at the anterior level of the oculomotor foramen. The anterior terminus of the pseudobasal process (*psdbas. proc.*) lies within the medial portion of the pterygoid at the posterior border of the oculomotor foramen (Fig. 15). The pseudobasal process abruptly increases in size. At the level of the prootic foramen (Fig. 16) the medial branch of the pterygoid diverges from the posterior ramus and is closely applied to the medial surface of the pseudobasal process. The otic process extends along the medial surface of the squamosal from the dorsolateral edge of the pseudobasal process, and then expands medially to meet the bony edge of the otic capsule and form the crista parotica. Posterior to the formation of the crista parotica, the ventral part of the otic process splits. The medial part forms the ventrolateral ledge of the otic capsule (*vl. l. ot. c.*, Fig. 20a-f), whereas the lateral part moves ventrad in association with the ventral arm of the squamosal and fuses with the pterygoid process posteriorly.

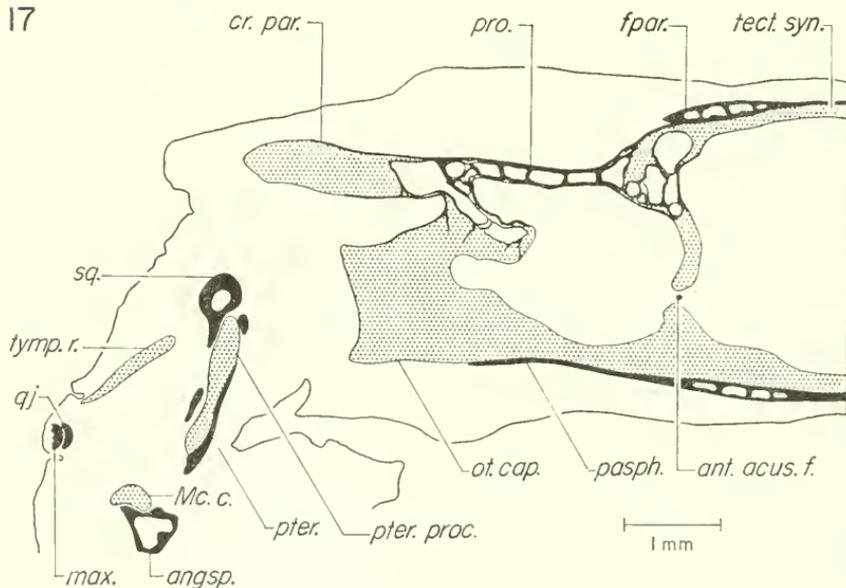
Posterior to the bony closure of the prootic foramen, the ventromedial part of the pseudobasal process joins the prootic and forms the ventrolateral edge of the otic capsule. The posterior terminus of the medial branch of the pterygoid lies ventral to the lateral part of the otic capsule. The posterior branch of the otic process merges with the pterygoid process ventrally.

At the level of the anterior acoustic foramen the cornu principalis of the hyale (*corn. prin.*) appears as a lateral ledge at the ventrolateral corner of the otic capsule (Fig. 20a-b). The cornu principalis

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FIGS. 16-17. Transverse sections through otic region: 16) at level of prootic foramen; 17) at level of anterior acoustic foramen. Abbreviations: *angspl.*, angulosphenial; *ant. acus. f.*, anterior acoustic foramen; *cr. par.*, crista parotica; *fpar.*, frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *ot. cap.*, otic capsule; *pasph.*, parasphenoid; *pro.*, prootic; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

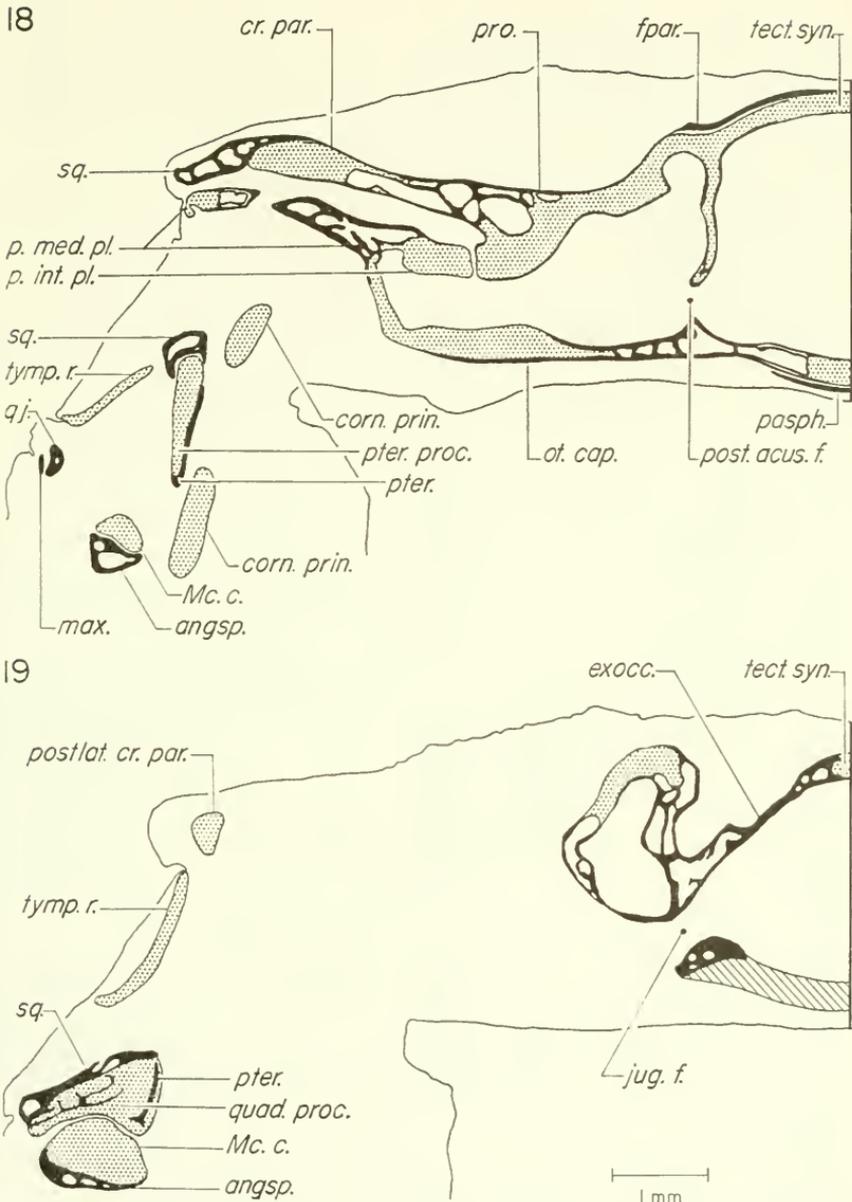


FIG. 18-19. Transverse sections through otic capsule: 18) at level of posterior acoustic foramen; 19) at level of jugular foramen. Abbreviations: *angspl.*, angulosplenial; *corn. prin.*, cornu principalis; *cr. par.*, crista parotica; *exocc.*, exoccipital; *fpar.*, frontoparietal; *jug. f.*, jugular foramen; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *ot. cap.*, otic capsule; *p. ext. pl.*, pars externa plectri; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *pasph.*, parasphenoid; *post. acus. f.*, posterior acoustic foramen; *postlat. cr. par.*, posterolateral edge of crista parotica; *pro.*, prootic; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *quad. proc.*, quadrate process; *qj.*, quadratojugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

diverges from the ledge at the level of the abbreviated bridge between the anterior and posterior acoustic foramina. In posterior sections the cornu lies medial to the squamosal-pterygoid process-ptyergoid complex (Fig. 18). The posterior terminus of the cornu lies at a level with that of the posterior acoustic foramen.

The pars externa plectri (*p. ext. pl.*, Fig. 20a-b) is cartilaginous and first appears dorsal to the ventral arm of the squamosal in association with the tympanic membrane. The pars externa plectri expands dorsomedially and is fused briefly to the crista parotica by the pars ascendens plectri (*p. asc. pl.*, Fig. 20b). The pars interna plectri (*p. int. pl.*, Fig. 20b-f) is cartilaginous and appears medial to the pars media plectri and the ventrolateral ledge of the otic capsule at the level of the anterior acoustic foramen. The pars media plectri (*p. med. pl.*, Fig. 20b-f), a cartilage and bone element, appears proximally at the dorsolateral edge of the otic capsule and distally, ventral to the squamosal at a level between the anterior and posterior acoustic foramina. At the level of the posterior acoustic foramina the pars media plectri is bony, greatly expanded in size, and joined to the pars interna plectri medially.

The operculum (*op.*, Fig. 20d-h) is cartilaginous and lies medial to the lateral edge of the otic capsule between the pars interna plectri and pars media plectri. The anterior end of the operculum (Fig. 20d) lies at a level corresponding to the posterior part of the posterior acoustic foramen. Posteriorly the operculum increases in size, and the pars interna plectri and pars media plectri are reduced (Fig. 20e-f). At a level corresponding to the posterior border of the posterior acoustic foramen the medial portion of the pars interna plectri disappears and leaves a small lateral rod of cartilage surrounded on all but the ventral side by the operculum (Fig. 20f). The operculum expands medially to merge with the main part of the otic capsule (Fig. 20g). The lateral edge of the operculum expands ventrally and then dorsomedially to form a complete tube. Slightly more posteriorly the cartilaginous lateral edge of the otic capsule, lateral to the operculum, dissipates into connective tissue and finally disappears, leaving the posterior end of the operculum as the most distal element of the otic capsule (Fig. 20h).

Ossification in otic and occipital regions.—The otic region of the cranium is largely unossified. At the level of the optic foramen (Fig. 14) the floor of the neurocranium is cartilaginous but completely underlaid by the bony parasphenoid. The taenia tecti

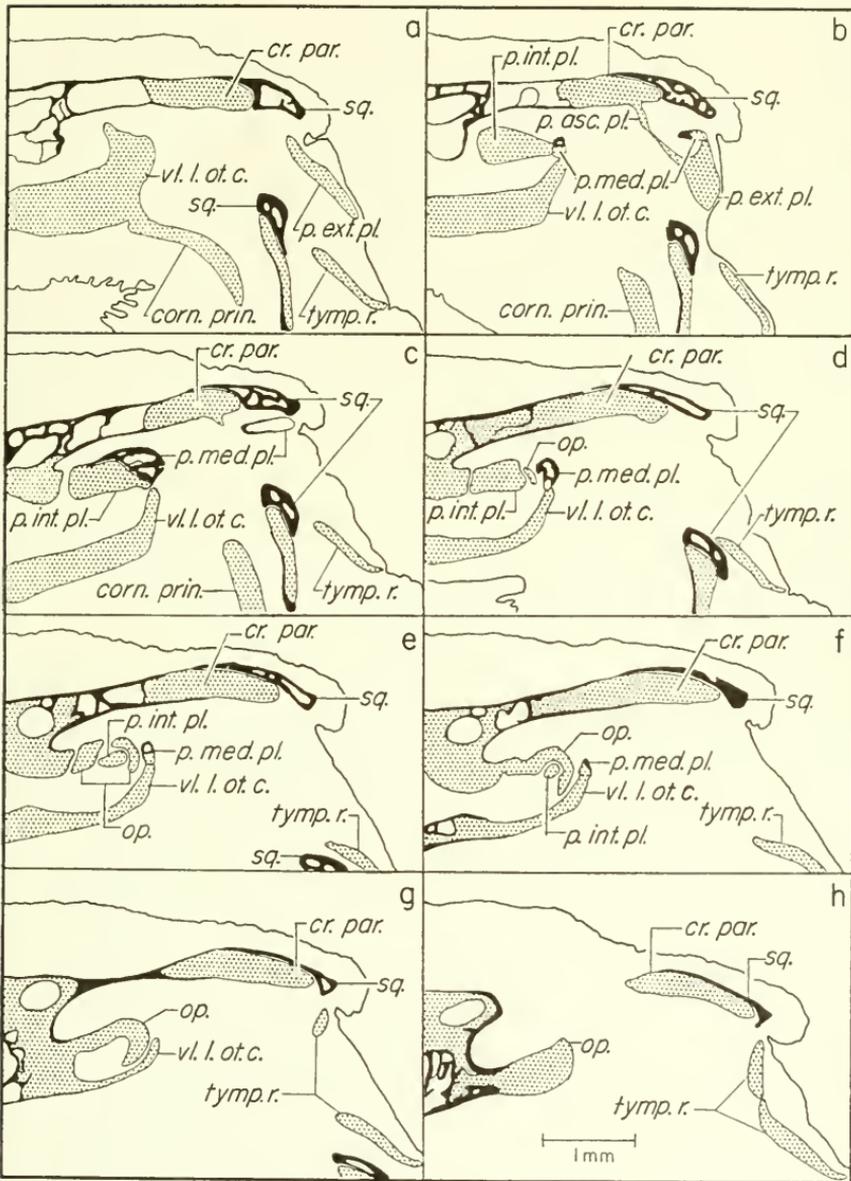


FIG. 20. Transverse sections through otic capsule: a) level of anterior ledge of otic capsule; b) anterior level of pars interna plectri and pars ascendens plectri; c) level of pars media plectri; d-f) successive levels of operculum and pars media plectri; g-h) posterior levels of operculum. Abbreviations: *corn. prin.*, cornu principalis; *cr. par.*, crista parotica; *op.*, operculum; *p. asc. pl.*, pars ascendens plectri; *p. ext. pl.*, pars externa plectri; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *sq.*, squamosal; *tym. r.*, tympanic ring; *vl. l. ot. c.*, ventrolateral ledge of otic capsule.

marginales and the tectum synoticum are covered dorsally and laterally by the frontoparietals. Perichondral ossification representing the prootic bone occurs at the margin of the optic foramen and somewhat posteriorly over part of the floor of the neurocranium. Perichondral and endochondral ossification occurs in the sides of the neurocranium ventral to the lamina perpendicularis. This ossification expands laterally until it meets the crista parotica dorsolaterally and forms the dorsal part of the prootic bone. The anteroventral edge of the otic capsule remains cartilaginous. Posteriorly, at the level of the anterior acoustic foramen, endochondral ossification is meager and restricted to the dorsomedial parts of the otic capsule, plus a small amount in the neurocranial floor; perichondral ossification is restricted to the peripheral areas showing endochondral ossification. Posteriorly, endochondral ossification is restricted in the dorsal part of the otic capsule but somewhat increased in the floor of the capsule. The lateral part of the otic capsule posterior to the terminus of the operculum and the ventromedial and dorso-medial parts of the neurocranium remain unossified.

Articular Region

In the anterior sections (at the level of the oculomotor foramen) the angulosplenic (*angspl.*) is a moderate-sized bone (Fig. 15). Meckel's cartilage (*Mc. c.*) is present as a small ovoid cartilage lying dorsolateral to the angulosplenic. Posteriorly, Meckel's cartilage is dorsal to the angulosplenic. The cartilage increases in size at the level of the posterior acoustic foramen, and the angulosplenic decreases in size posteriorly. At the level of the posterior border of the posterior acoustic foramen, the maxillary terminates and is replaced by the quadratojugal. The quadratojugal, ventral arm of the squamosal, pterygoid process, pterygoid, and Meckel's cartilage converge. At the level of the jugular foramen (*jug. f.*) (Fig. 19) the quadratojugal is incorporated into the squamosal-ptyerygoid process-ptyerygoid complex. The complex is narrowly separated by connective tissue from Meckel's cartilage ventrally. The quadrate process (*quad. proc.*) is represented by the cartilage bordered dorsally by the pterygoid process and the ventral arm of the squamosal, and ventrally by Meckel's cartilage. At the posterior terminus of the skull all bony elements of the articular region terminate, except for a small terminal part of the angulosplenic underlying Meckel's cartilage.

SUMMARY

Since no accounts comparable to the preceding for *Smilisca baudini* are available for other hylid frogs, it is meaningless to attempt any discussion dealing with character significance or variation within the Hylidae. There is considerable literature treating bufonids, leptodactylids, ranids, and various Old World genera (see Baldauf, 1955, for a review of these works). Likewise, a comparison at the familial level based on the study of a single species seems inadequate and premature. By way of summary and synoptic description a list of cranial osteological characters of *Smilisca baudini* is presented. The items selected enable comparison with similar compilations by other workers, and are based in part on my unpublished observations of other hylids.

1. Compared to hylids not having integumentary-cranial co-ossification, the dermal roofing bones of *Smilisca baudini* are extensive, and the skull is well-ossified internally. In contrast to most casque-headed hylids (those having integumentary-cranial co-ossification), the dermal roofing bones are much less extensive, the dermal sphenethmoid (see Trueb, 1966, p. 563) is absent, and internal ossification is less extensive.

2. The solum nasi is not ossified; the septum nasi is ossified only posteriorly, and the olfactory eminence is supported by the cartilaginous solum nasi and the bony prevomer.

3. The lingual process is absent. There is no palatal cartilage isolated between the premaxillaries.

4. The anterior end of the cavum medium lies anterior to the cavum inferius.

5. The septomaxillary is basically a U-shaped structure and has a dorsal, anteriorly curved, ramus on the lateral branch and a longitudinal loop of bone ventrally.

6. A distinct pars nasalis is absent on the maxillary.

7. A cartilaginous sclera is present.

8. The taenia tecta marginalis and the tectum synoticum are the only roofing cartilages present.

9. The external part of the plectral apparatus (columella) is directed anterolaterally. The pars ascendens plectri is fused with the crista parotica.

10. The pseudobasal process is fused to the otic capsule.

11. The cornu principalis of the hyale fuses with the pseudobasal process.

12. Two acoustic foramina are present.

13. The sphenethmoid and prootic are synchondrotically united.
14. The frontoparietal is separate from the prootic and exoccipital.
15. The prootic and exoccipital are fused.
16. A bursa angularis oris is present.

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The Amphibians and Reptiles
of Sinaloa, México

BY

LAURENCE M. HARDY AND ROY W. McDIARMID

UNIVERSITY OF KANSAS
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INTRODUCTION

The Mexican state of Sinaloa supports a varied biota that reflects the intricate nature of the transition between the fluctuating temperate environments of North America and the stable tropical environments of Middle America. For more than 100 years biologists have been interested in the amphibian and reptile fauna of the region. Much recent attention has been due to increased accessibility of a major portion of the state. Mexican Highway 15 and its numerous side roads now extend the entire length of the coastal lowlands, facilitating work by herpetologists on zoogeographic problems posed by the merger of the tropical and temperate biotas. Consequently numerous collections have accumulated, permitting the present report.

The lowlands of Sinaloa were visited first by collectors from European museums early in the nineteenth century. The port of Mazatlán served as a shipping point for specimens from Sinaloa and other areas in northwestern México. Early reports by Wagler (1830) of specimens in the Munich Museum, by Gray (1831, 1855) of specimens in the British Museum, by Weigmann (1834) and Peters (1867) of specimens in the Berlin Museum, by Jan (1863) of specimens in the Leipzig Museum, and by Fischer (1883) of specimens in the Hamburg Museum, reflect the initiative of the early collectors and naturalists, such as F. Deppe.

A collection made at Mazatlán by Ferdinand Bishoff and deposited in the Smithsonian Institution was the subject of papers by Cope (1864, 1868).

In the early 1880's a noteworthy collection was accumulated by Alfonso Forrer from the vicinity of Mazatlán and Presidio. This collection, which includes several type specimens, was sent to the British Museum (Boulenger, 1882, 1883; Günther, 1882, 1885-1902). Evidently part of this collection also was sent to the United States National Museum (Stejneger, 1893).

Collections from Mazatlán made by Gustav Eisen and Frank H. Vaslit, and also by David Starr Jordan, that were deposited in the California Academy of Sciences and the Natural History Museum at Stanford University, were the subject of reports by Van Denburgh (1898) and McLain (1899).

During parts of 1897, 1898, and 1899, E. W. Nelson and Edward A. Goldman traversed the entire west coast of México from near Guaymas, Sonora, southward to San Blas, Nayarit (Goldman, 1951). Many specimens were secured by these men at Culiacán, Mazatlán,

Rosario, and Plomosas, and sent to the United States National Museum.

Two other small collections from near Mazatlán were made about 1920. Specimens collected by J. A. Kusché from "Venodido" (Vena-dillo) were sent to the United States National Museum and reptiles and amphibians collected by Paul D. R. Ruthling were deposited in the American Museum of Natural History.

During the past 30 years herpetologists have shown renewed interest in the herpetofauna of Sinaloa. The variety of species, many at the geographic limits of their distributions, has stimulated the publication of many reports pertaining to reptiles and amphibians from the state. The first work on the herpetofauna of Sinaloa was by Taylor (1938). Although Taylor's paper is limited in scope, it lists the species of amphibians and reptiles known from the state and includes a brief résumé of previous collections. Since Taylor's work, several papers have appeared that deal with various aspects of the herpetofauna—particularly notes on distributions, range extensions, ecology, life history, and taxonomy. Among these are reports by Martin del Campo (1941), Smith and Van Gelder (1955), Lewis and Johnson (1956), Duellman (1957b), Fugler and Dixon (1961), Campbell and Simmons (1962), and Scott (1962). Other reports dealing with one or a few species are mentioned in appropriate accounts beyond. It is important to realize that no author since Taylor has dealt with the total hereptofauna of Sinaloa, or even of large areas within the state; and yet, within the last ten years, increased collecting in Sinaloa has more than tripled the number of herpetological specimens previously available from the state.

For the past 20 years students of Mexican herpetology have relied heavily on the checklists by Smith and Taylor (1945, 1948, 1950b). Anyone interested in the reptiles and amphibians of México recognizes the value of the detailed studies by Bogert and Oliver (1945) on the herpetofauna of Sonora, by Martin (1958) on the herpetofauna of the Gómez Farías region in southern Tamaulipas, by Zweifel (1960) on the herpetofauna of the Tres Mariás Islands, and by Duellman (1960) on the amphibian fauna of the Isthmus of Tehuantepec and on the herpetofauna of Michoacán (1961, 1965).

In the summer of 1962, the second author began a four-month study of the lowland herpetofauna in northwestern México. Data gathered formed the basis for a study of the biogeography and

evolution of the amphibians and reptiles in the Pacific lowlands of western México. The following summer, the first author collected amphibians and reptiles in Sinaloa and made ecologic observations. On the basis of the latter material and preserved specimens in the collection of the University of Kansas, the first author initiated a study of the amphibians and reptiles of Sinaloa. Early in 1964 we started correspondence that pointed up the similarities of our studies, and as a result combined our efforts toward preparation of this publication based primarily on specimens readily available to us.

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University of Illinois, Museum of Natural History; Stanford University Natural History Museum; Robert C. Stebbins, Museum of Vertebrate Zoology, University of California, Berkeley; Charles F. Walker, University of Michigan, Museum of Zoology; Ernest E. Williams, Museum of Comparative Zoology, Harvard University; William H. Woodin and Merritt S. Keasey, Arizona-Sonora Desert Museum, Tucson; Richard G. Zweifel, American Museum of Natural History.

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DESCRIPTION OF THE AREA

Physiography

Sinaloa is a long, narrow state that is situated on the western coast of México between 22°30' and 27°00' north latitude and between 106°25' and 109°30' west longitude; northward from Mazatlán the coastline lies in a direction of approximately 315° from north. The state has an area of 58,092 square kilometers (Encyclo. Brit., 1967, 20:558) and a total relief of 2779 meters. Sinaloa is bounded by Sonora to the north, by Chihuahua and Durango to the east, and by Nayarit to the south.

The Sierra Madre Occidental lies along the entire length (about 560 kilometers) of the state on the east. In the northern part of the state the Sierra Madre Occidental is less rugged and slightly lower than in the southern half. A narrow coastal plain, which consists mainly of mature outwash slopes from the adjacent mountains and broad alluvial valleys associated with the major rivers, extends the entire length of the state. In general the lowlands are uniform except near Culiacán, where six small mountains (less than 900 meters in elevation) are separated from the sierra by lowlands less than 300 meters in elevation. Sinaloa has seven small moun-

tain peaks exceeding 2100 meters in elevation, but only one (east of San Ignacio) exceeds 2700 meters. The Gulf of California and the Pacific Ocean limit the state to the west. The coast is extensively divided into small islands and fringes of land that parallel the mainland (Fig. 1).

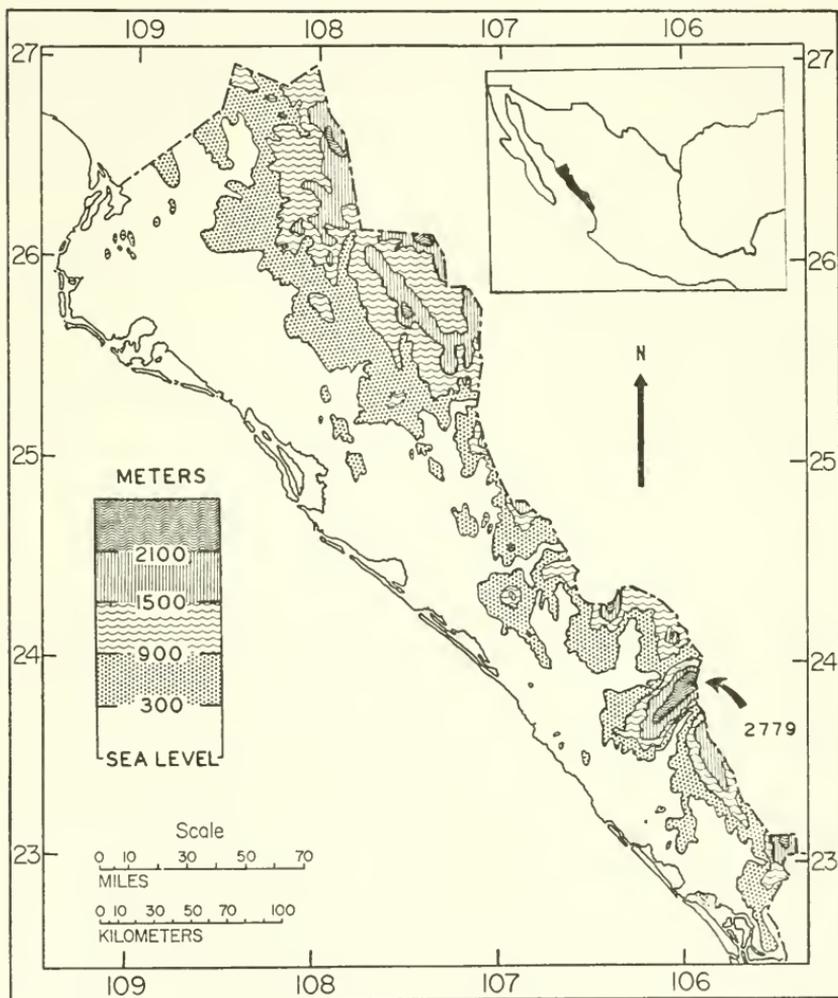


FIG. 1. Physiographic map of Sinaloa, México.

At least ten major rivers, all of which flow into the Gulf of California or the Pacific Ocean, drain the state. The most important rivers from north to south are: Río Fuerte, Río Sinaloa, Río Mocorito, Río Culiacán, Río San Lorenzo, Río Elota, Río Piaxtla, Río

Quelite, Río Presidio, and Río del Baluarte. Two river valleys (Culiacán and San Lorenzo) of less than 300 meters elevation extend into Durango, and another (Fuerte) transects the state in the north. The other rivers and their tributaries penetrate deeply into the mountains.

Climate

The climate of Sinaloa is characterized by marked wet and dry seasons. Three factors are important in controlling this climate. The first factor is the latitude of the state. The second is the temperature of the bordering Gulf of California and Pacific Ocean. The annual range in temperatures of the coastal waters increases from south to north and secondarily influences the annual temperatures on the coastal plain and foothills in the same direction. Another factor influencing the climate in Sinaloa is the direction of the prevailing winds. Winds blow from the northern arid regions of Sonora during the dry season and notably affect the vegetation. In the southern lowlands the winds are cooler because of more open access to the waters of the Pacific Ocean. The cooling effects of wind in local areas, for example Mazatlán, account for lower mean annual temperatures at these locales than in areas only a few miles inland. The velocities and direction of the winds vary with the season, higher velocities occurring during the dry season. At Mazatlán the wind velocities vary from 4.3 m/sec. to 6.1 m/sec. with a yearly average of 5.1 m/sec. The winds are northerly from November through April and southwesterly from May until October (Roden, 1958).

Climatic data (taken from Contreras Arias, 1942) at six localities in Sinaloa are presented graphically, illustrating the mean monthly temperature and mean monthly precipitation at three lowland and three highland sites. A lowland and highland site are compared in northern Sinaloa (Fig. 2), in central Sinaloa (Fig. 3), and in southern Sinaloa (Fig. 4). The three lowland sites of Ahome, Guamúchil, and Mazatlán are compared (Fig. 5), and the three highland sites of Choix, Badiraguato, and Pánuco are compared (Fig. 6).

Temperature

There is less than a degree difference among the mean yearly temperatures at the six sites, with Mazatlán registering the lowest at 23.6°C and Choix and Guamúchil showing the highest at 24.5°C. The hottest mean monthly temperatures in the lowlands occur in

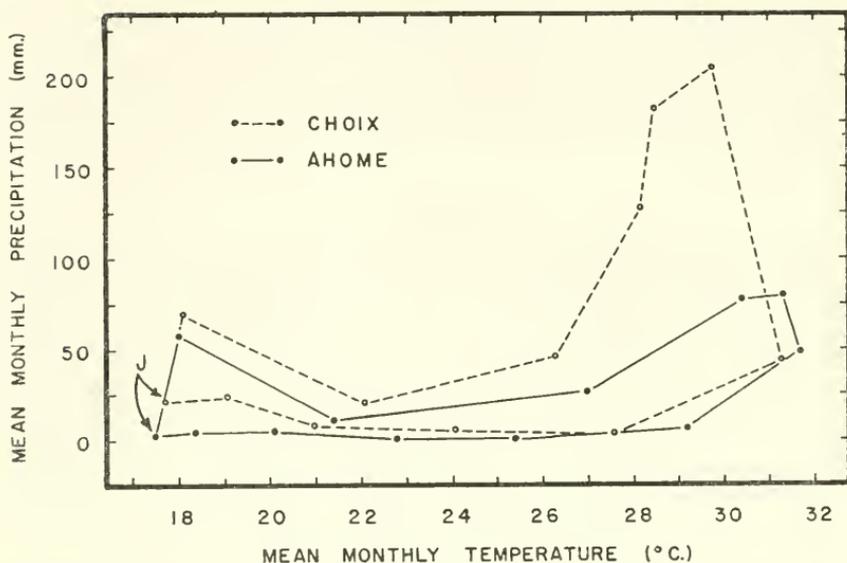


FIG. 2. Temperature-moisture climograph comparing a lowland (Ahome) and highland (Choix) locality in northern Sinaloa, México. Each point represents a month, proceeding counter-clockwise from January (J).

July and August, and decrease from 38.6°C at Ahome to 29.5°C at Mazatlán. In the highlands the warmest months are May and June, and the temperatures decrease southward from 39.1°C in June at Choix to 34.9°C in May at Pánuco. The highest daily temperatures decrease from north to south and usually are recorded in July, September, or October. The lowest mean monthly temperatures in the lowlands was 8.1°C for January at Guamúchil. The lowest lowland temperature recorded, -1.1°C, was also in January at Guamúchil. In the highlands the lowest mean monthly temperature was recorded from central Sinaloa, 6.2°C at Badiraguato. The lowest temperature reported in the state was at Badiraguato in January when the thermometer dipped to -2.5°C.

Temperatures fluctuate between monthly and daily extremes in northern Sinaloa but remain nearly constant in the southern part of the state. For brief periods during the dry season, temperatures in the north may show a daily fluctuation of 20°C. During the months of June to November the daily fluctuations rarely exceed 15°C and commonly remain near 11°C. Stability in temperature is characteristic of the southern limits of the state; at Mazatlán the greatest fluctuation is 5.1°C in April, and at Pánuco the greatest monthly fluctuation is 15.2°C in March. Temperatures are almost continu-

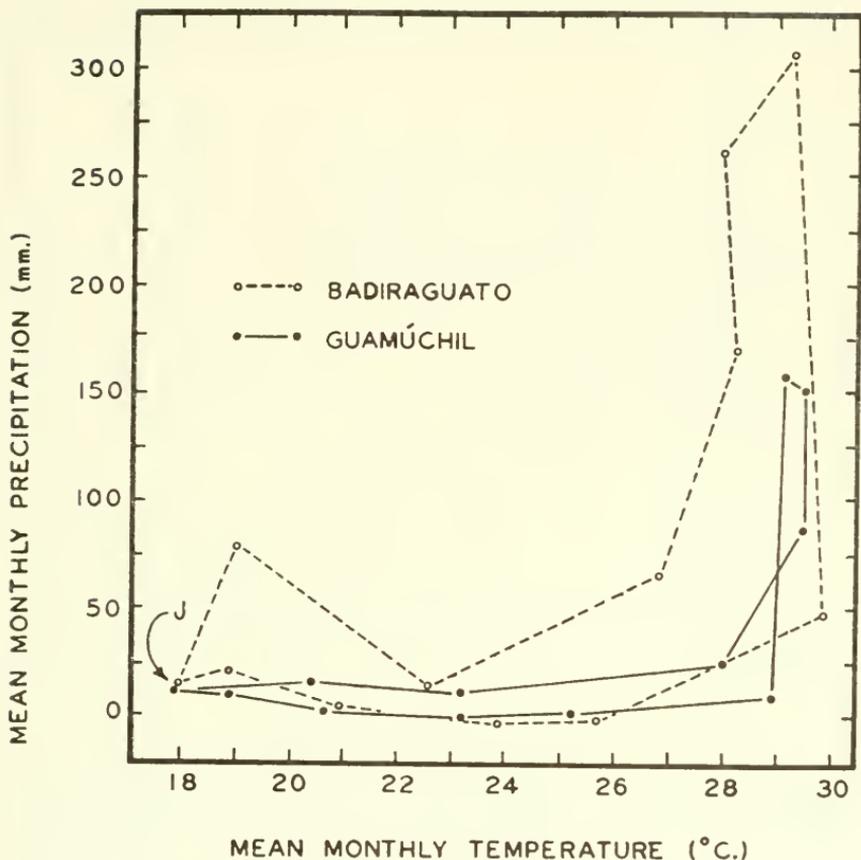


FIG. 3. Temperature-moisture climograph comparing a lowland (Guamúchil) and highland (Badiraguato) locality in central Sinaloa, México. Each point represents a month, proceeding counter-clockwise from January (J).

ously favorable to growth throughout the region, particularly during summer when water is readily available. Frost is not uncommon at higher elevations in the northern and central portions of the state but is unknown in the southern lowlands. Snowfalls are of almost yearly occurrence in January and February at high elevations along the northeastern border (Gentry, 1946b:453).

Rainfall

Annual precipitation increases from north to south. In the lowlands the annual totals increase from 321 mm at Ahome to 478 mm at Guamúchil to 851 mm at Mazatlán. In the highlands the annual rainfall increases from 767 at Choix to 982 at Badiraguato to 1279 at Pánuco. The highland sites receive more rain than comparable

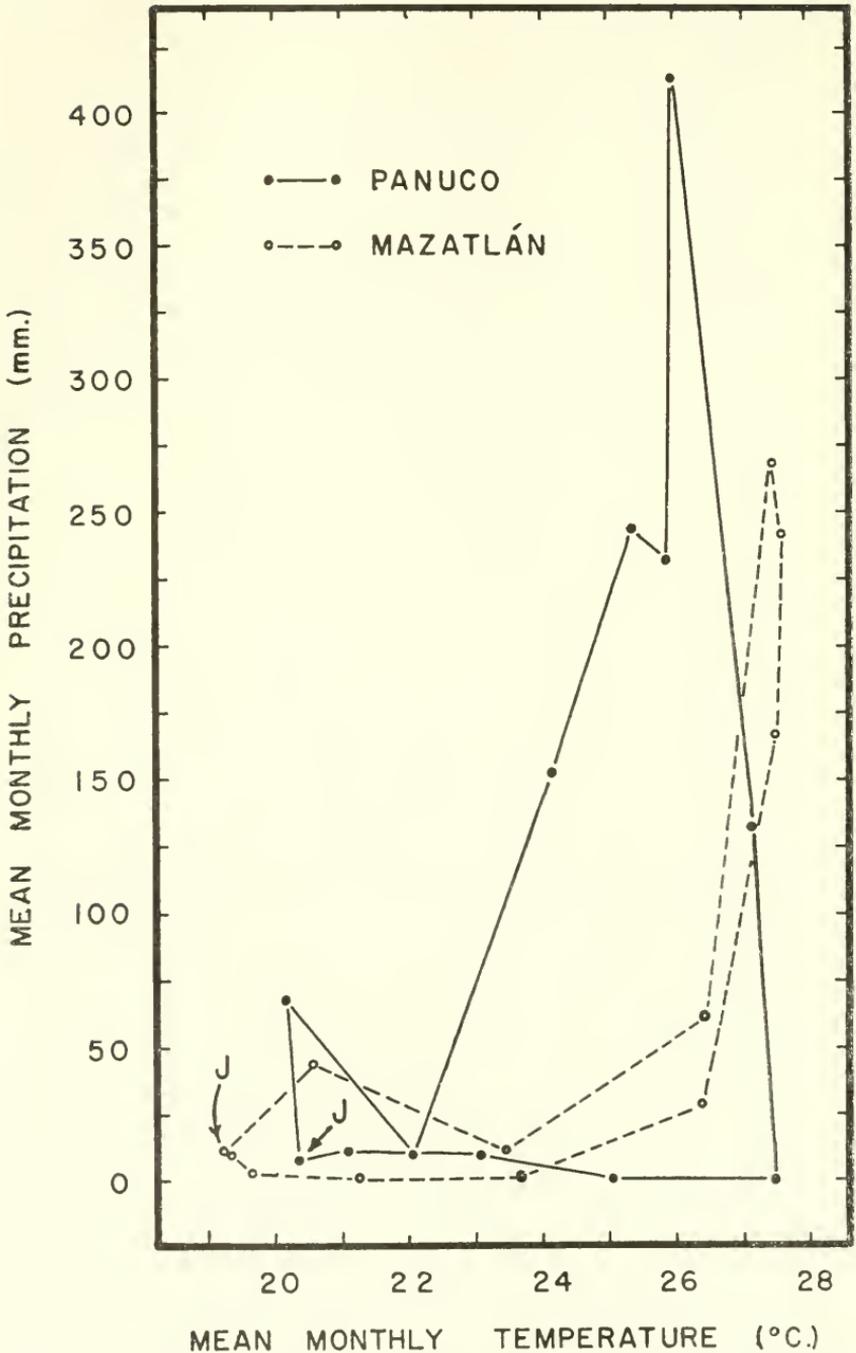


FIG. 4. Temperature-moisture climograph comparing a lowland (Mazatlán) and highland (Pánuco) locality in southern Sinaloa, México. Each point represents a month, proceeding counter-clockwise from January (J).

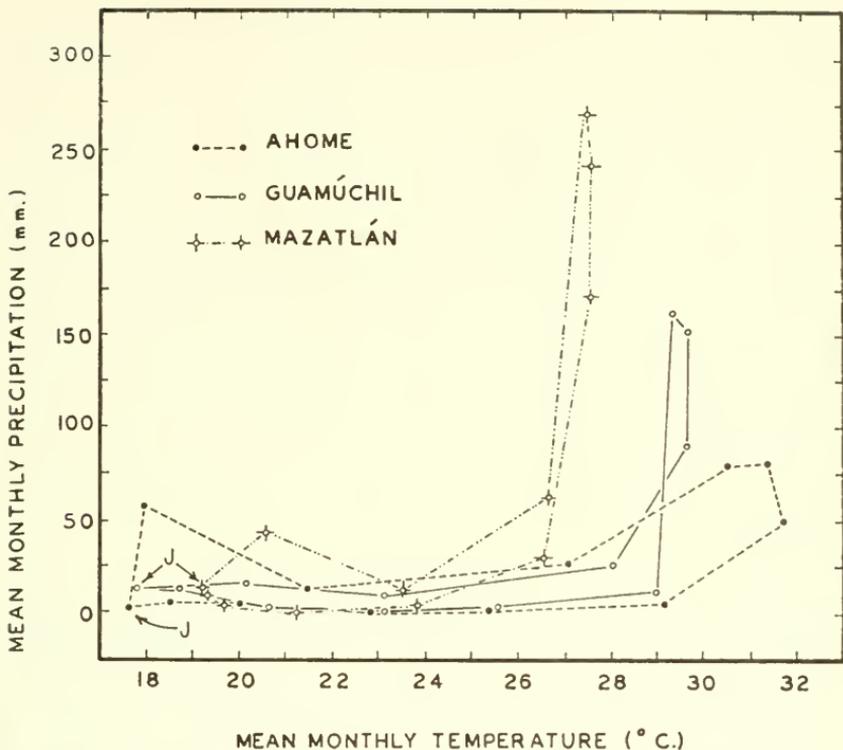


FIG. 5. Temperature-moisture climograph comparing the three lowland localities in northern (Ahome), central (Guamúchil), and southern (Mazatlán) Sinaloa, México. Each point represents a month, proceeding counter-clockwise from January (J).

sites in the lowlands. Precipitation is restricted mainly to the months of July, August, and September. All localities except Guamúchil exhibit a secondary peak of precipitation in December. Vegetative growth is dependent on heavy summer rains. The second author has traveled the length of the state in December and found the vegetation generally inactive and leafless, except along the rivers or in areas where the water table is unusually high, as in the extreme southwest near Teacapán. In making the same trip in July, he found the vegetation in a progressively advanced stage of leaf and general activity the further south he traveled.

The percentage of annual precipitation that falls in July, August, and September, also increases gradually from north to south. The small amount of precipitation that falls from November through June results in a very dry period during the first six months of the year, especially in the northern lowlands (Shreve, 1944:108-09). It

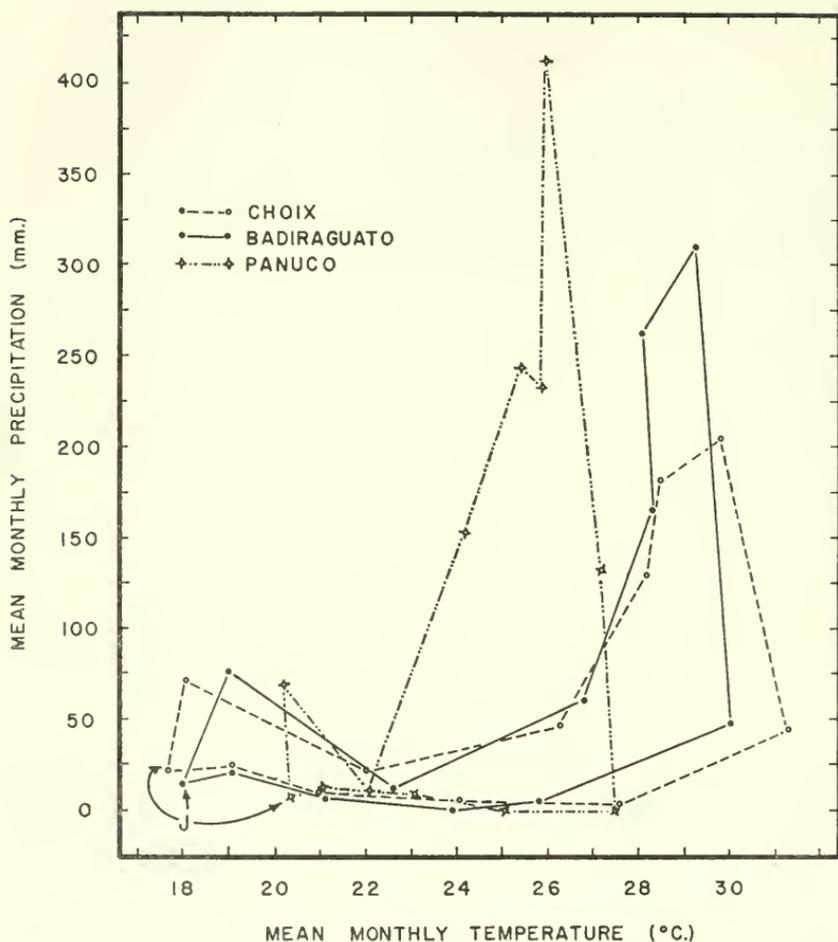


FIG. 6. Temperature-moisture climograph comparing the three highland localities in northern (Choix), central (Badiraguato), and southern (Pánuco) Sinaloa, México. Each point represents a month, proceeding counter-clockwise from January (J).

is noteworthy however that the first half of the year is nearly as dry in the southern highlands at Pánuco as it is in the northern lowlands at Ahome.

The distribution of rainfall is related to wind direction and ocean temperatures. The northern winds originate in the desert regions of Sonora and Baja California and carry little moisture. The southern winds carry moisture-laden clouds from the Pacific Ocean north into the Gulf. The mountainous terrain of Baja California prevents westerly winds off the Pacific Ocean from carrying rain into central Sinaloa and exerts a rain shadow effect on the northern portion of

the state. A comparison of wind-direction, seasonal rains, and migratory low pressure systems over western México indicates that northerly winds are associated with low pressure to the east and southerly winds are associated with low pressure to the northwest. The beginning of the rainy season coincides with the appearance of southerly winds that carry moist air into the Gulf of California and showers to the coastal lowlands. Although rain-laden clouds are carried overland by southerly onshore winds during July through September, the relief of the coastal plain is such that storm clouds do not release their rain until a slight increase in elevation is encountered. The coastal plain of Sinaloa is flat, and rain clouds often pass over without dropping moisture—for example, in central Sinaloa at Guamúchil and Badiraguato (Fig. 3). This contributes to the xeric conditions on the coastal plain as compared to the foothills, and is reflected in the composition of the flora and fauna.

Vegetation

The physiographic and climatic conditions in Sinaloa are reflected in the composition of the natural vegetation and together with it provide habitat for a rich and diverse amphibian and reptile fauna. The nature of the transition between the northern temperate and the southern tropical environments is gradual but clearly evident in a comparison of the xeric thorn woodland vegetation of the arid northern lowlands to the deciduous semiarid forest vegetation characteristic of the more mesic southern lowlands, or in a comparison of the pine forests of the northern highlands to the subtropical and tropical dry forests found at middle elevations in the southern portions of the state.

The vegetation of northwestern México, especially Sinaloa, has been studied by only a few workers. Brand (1936) summarized previous work and listed the more important references. Accordingly, a historic sketch prior to 1936 need not be repeated here. Brand recognized three different associations on the coastal plain as expressions of temperature and precipitation and a fourth association along the eastern border of the state. Shreve (1937) described the vegetation of the lowlands of Sinaloa and discussed the thorn forest with special reference to profile, density, foliation, stratification, and components.

The vegetation of the Río Mayo Valley, Sonora, was thoroughly studied by Gentry (1942). He recognized four major divisions: thorn forest from sea level to about 600 meters; short-tree forest in

areas from 300 to 1000 meters; oak forest from 900 to 1500 meters; and, pine forest at elevations from about 1500 to 2750 meters. Much of the information presented on the Río Mayo vegetation has been assimilated into the description of the vegetation of the northern and central sections of the state.

Two important papers by Gentry on the vegetation of two mountains in Sinaloa appeared in 1946. One dealt with the flora of Sierra Tacuichamona, an isolated peak in the central part of the state (Gentry, 1946a). The other pertained to the vegetation of Sierra Surotato in the northern highlands (Gentry, 1946b). General works (*e. g.*, Leopold, 1950) include Sinaloa in their coverage, but without specific details. Other than the papers by Shreve and Gentry, there are no detailed treatments of the flora of the state available at this time.

Because of the paucity of information pertaining to the vegetation of Sinaloa, we were faced with several problems in our attempt to present a vegetational classification that would be useful in interpreting the distributional patterns of the fauna and still meet the demands of most plant geographers by presenting a classification of the vegetation by type, rather than a classification of animal habitat based on vegetation, as proposed by Duellman (1965:640). Difficulty was encountered in those areas where the natural vegetation had been cleared and the land currently is being used for agricultural purposes. Agricultural development has been favored by the availability of hydroelectric power, and water resources made usable by the recent construction of dams on the Río Fuerte and on the Río Culiacán. As a result, large areas are under cultivation from Los Mochis south to Guasave, and extensive tracts are being cleared north and west of Culiacán. The floodplains of the northern rivers are mostly devoted to vast fields of sugar, cotton, garbanzos, tomatoes, and corn. In the agricultural areas the native vegetation has been almost completely destroyed, and it is nearly impossible to detect any changes in the physiognomy or composition of the natural vegetation, if such changes did exist.

A system of vegetation classification proposed by Holdridge (1947:367-368) is utilized in this study. Holdridge contended that a plant formation of a particular area is a reflection of the interaction between mean annual precipitation and mean annual biotemperature with respect to the amount of evaporation and transpiration. With the aid of the chart presented by Holdridge (1964:18), Sinaloa can be conveniently divided into five bioclimates.

Each bioclimate is characterized by a different plant formation. The five plant formations, all of which are in the tropical region, are: Tropical Thorn Woodland, Tropical Semi-arid Forest, Tropical Dry Forest, Subtropical Dry Forest, and Lower Montane Dry Forest (Fig. 7).

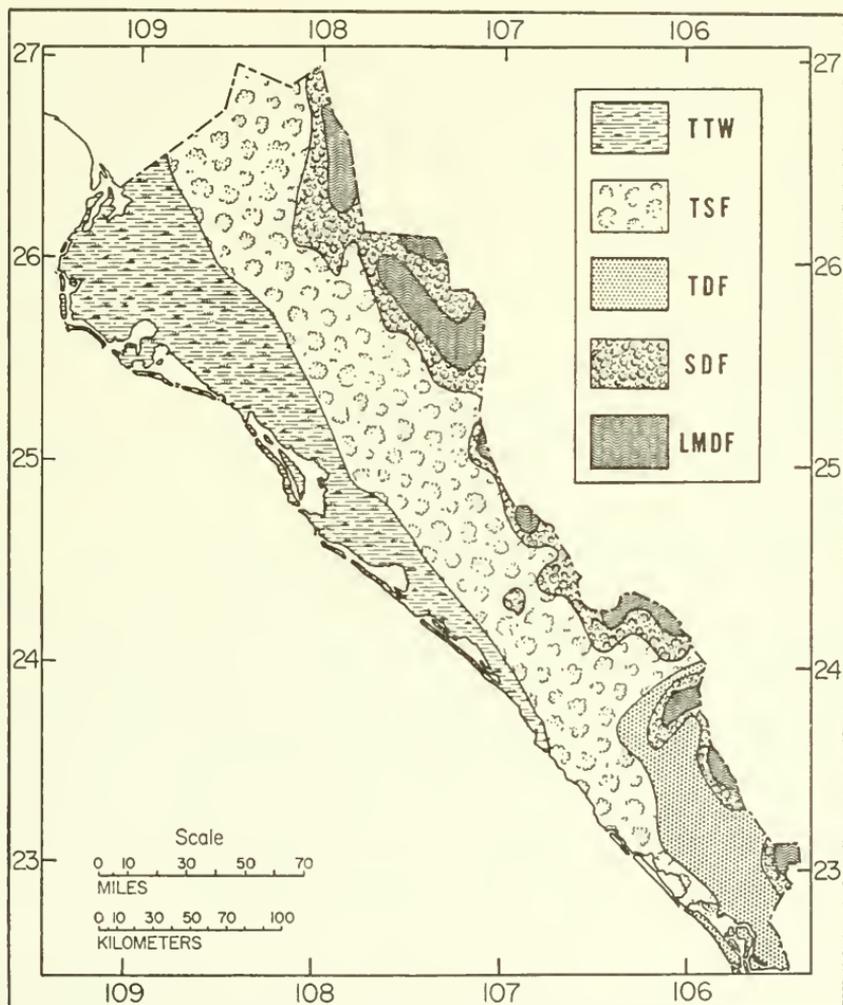


FIG. 7. Generalized vegetation map of Sinaloa, México. TTW = Tropical Thorn Woodland; TSF = Tropical Semi-arid Forest; TDF = Tropical Dry Forest; SDF = Subtropical Dry Forest; LMDF = Lower Montane Dry Forest.

Tropical Thorn Woodland

Tropical Thorn Woodland vegetation as used in this discussion includes: the subtropical mimosaeae-cacti vegetation, as understood

by Brand (1936:24-25); the northern portions of the thorn forest, as presented by Shreve (1937:608-611); the thorn forest as interpreted by Gentry (1942:27-30); and part of the thorn forest as discussed by Leopold (1959:35-36). Thorn woodland vegetation is found from sea level to about 500 meters elevation throughout the northern lowlands, southward along the coast to near the mouth of the Río Elota (Fig. 7).

Thorn woodland vegetation is not uniformly distributed in Sinaloa but is arranged in clumps, becoming nearly continuous in moist habitats. Thorn woodland is found on the lowland basaltic hills and mesas and to a lesser extent in the lowland valleys. The vegetation of the mesas and slopes is uniform in type of growth with close spacing of the individuals (Plate 1, Fig. 1). The vegetation found along the margins of arroyos and in valleys is varied and irregular in formation and individual spacing (Plate 1, Fig. 2). The arroyos support a riparian vegetation composed of evergreens and partially deciduous types. The valleys are often dominated by pure stands of *Prosopis chilensis* (Gentry, 1942:29).

The belt immediately along the coast is more arid than the interior. Likewise, the vegetation is reduced and more open (Plate 2, Fig. 1).

The average height of thorn woodland vegetation is about seven meters. There is a strong influx of succulent and thorny plants giving rise to a heterogeneous vegetation dominated by xeromorphic deciduous leaf types (Plate 2, Fig. 2). Creosote bush, saguaro, and ocotillo, common to the north in Sonora, are virtually unknown, being replaced by numerous species of *Caesalpinia*, *Cassia*, *Acacia*, *Cercidium*, *Jatropha*, and *Mimosa*. *Acacia cymbispina* forms about 60 per cent of the cover in thorn woodland (Shreve, 1937:609). Gentry (1942:30) mentioned *Acacia cymbispina* as the dominating successionist in *Milpa* clearings and along roads and trails in the valley of the Río Mayo, Sonora. Species of *Ficus*, *Enterolobium*, and *Taxodium*, and other tropical trees become increasingly numerous in the river valleys. Thickets of the characteristic desert plants including *Cercidium*, *Encelia*, and *Opuntia* have been reported in the valley of the Río Fuerte (Shreve, 1934:377). Other species of common plants found in the thorn woodland are: *Zizyphus sonorensis*, *Pithecollobium sonorae*, *Cercidium floridum*, *Pachycereus pecten-aboriginum*, *Franseria cordifolia*, *Karwinskia humboldtiana*, and *Croton alamosanus*.

Tropical Semiarid Forest

The Tropical Semiarid Forest vegetation as used here is essentially the same as: the semi-arid scrub, as described by Brand (1936:25-27); the southern part of the thorn forest (Shreve, 1937: 608-610; Leopold, 1959:35-36); the short-tree forest (Gentry, 1942: 30-34); the tropical deciduous forest (Leopold, 1959:34-35). Semiarid forest is found between 300 and 1000 meters elevation in northern Sinaloa and continues south along the foothills to the coast near La Cruz, and then into southern Sinaloa on the coastal plain. Semiarid forest is bordered on the south by dry forest and on the east by subtropical dry forest. In several places tropical vegetation advances far into the Sierra Madre along deep barrancas and river valleys that extend at low elevations for many miles inland from the coastal plain (Fig. 7).

The semiarid forest is characterized by taller and more closely spaced vegetation than thorn woodland. The change in physiognomy is primarily due to the general increase in mean annual precipitation. There is an overall increase in density, particularly of shrubs and other undergrowth, which continues southward through the formation. In the north the vegetation is more xeric than along the slopes or in the southern lowland (Plate 3, Fig. 1; Plate 3, Fig. 2). The prevalent height of the vegetation is about 10 meters, although in some areas it is often less.

The dominant plants of the semiarid forest belong to the family Leguminosae. The subfamilies Mimosoideae and Caesalpinioideae contain more than a quarter of the total tree and scrub species of the formation, and possibly contribute three-quarters of the individuals comprising the vegetation (Brand, 1936:26). Trees are the dominant plants and tend to a uniform height. Succulents are relatively unimportant except for the large columnar cactus, *Pachycereus pecten-arboriginum*, which is an abundant and conspicuous species in the semiarid forest (Plate 4). None of the desert shrubs, such as *Atriplex*, *Encelia*, *Franseria*, and *Viguiera* is found in southern Sinaloa. *Acacia cymbispina*, with its boat-shaped spines, dominates the vegetation and frequently forms 90 per cent of the stand in lowland areas (Plate 5). In certain regions the abundance of *Acacia cymbispina* determines the level of the forest canopy, as is the case in an extensive stand 40 kilometers south of Culiacán. Terrestrial bromeliads and epiphytic species of *Tillandsia* are more abundant in the semiarid forest than in the thorn woodland to the north. The floodplains and valleys support *Ficus*, *Enterolobium*,

Taxodium, *Chlorophora*, *Pithecollobium*, *Haematoxylon* and *Caesalpinia*. Some of these trees reach a height of 30 meters or more. Palms are locally abundant especially on the floodplains. Smaller cacti are far less important in the composition of the vegetation of the semiarid forest than in the plant formations to the north. The slender *Rathbunia alamosensis* and the erect, dark green *Opuntia fuliginosa* are frequently found, but never in large colonies (Shreve, 1937:612). Most of the common cacti all seem to be shade-enduring species.

A dense shrub vegetation occurs along the coast, especially bordering lagoons. This vegetation consists primarily of mangrove (*Rhizophora mangle*), which is found as far north as Tiburón Island, Sonora. Various palms, especially *Cocos nucifera*, are common near the beach. The dense and nearly continuous forest of this coastal association occurs from Mazatlán southward. To the north of Mazatlán the coastal association is more open and separated by long stretches of sandy beach.

Some of the common plants of the semiarid forest are: *Acacia cymbispina*, *Ipomoea arborescens*, *Pachycereus pecten-arboriginum*, *Caesalpinia platyloba*, *Pithecollobium sonorae*, *Cassia emarginata*, and *Bursera simaruba*.

Tropical Dry Forest

The Tropical Dry Forest, as used here, is homologous in part with Brand's Humid Scrub (1936:26-27); Shreve's Thorn Forest (1937:208-210); and Leopold's Tropical Deciduous Forest (1959:34-35). The Tropical Dry Forest in Sinaloa occurs from sea level to about 1000 meters elevation in the southern portion of the state (Fig. 7). The differences between dry forest and semiarid forest result from increase in mean annual precipitation. Greater rainfall causes the more mesic plants to be major constituents of the flora, whereas these same plants were restricted to water courses in the northern, more arid portions of the state.

The physiognomy of the dry forest indicates a general overall increase in height and density (Plate 6) of the component plants. Shreve (1937:608) pointed out the marked increase of trees with broad leaves in southern Sinaloa and northern Nayarit in contrast to the xeromorphic leaves characteristic of trees in the thorn woodland and semiarid forest. The vegetation is a relatively low forest, 15 to 25 meters high, of stocky, broad-leaved trees (Plate 7, Fig. 1). Along water courses the dry forest assumes the dense character of

tropical evergreen forest. Interspersed throughout the lower vegetation are trees, *Enterolobium*, *Ficus*, and *Taxodium mucronatum*, that often reach a height of 30 meters or more. Many trees and shrubs carry epiphytes and parasites. Orchids are abundant along many of the waterways in southern Sinaloa and northern Nayarit. Plants common in the semiarid forest (e. g., *Pachycereus pecten-arboriginum*) are much less abundant in the more moist dry forest.

The flat coastal plain of extreme southern Sinaloa supports a savanna type vegetation (Leopold, 1959:33). This formation is not a climatic climax but rather a result of the edaphic conditions of high water-table and poor drainage. In some regions, as near Teacapán, the plants utilize the subsurface water and remain leaved and green throughout the year; however, the high water-table prevents this forest from attaining the stature characteristic of the dry forest farther inland (Scott, 1962:8). Where forest is absent, the dominant plants of the savanna are coarse tropical grasses. Scattered trees may occur irregularly in the grassland. Palms and jícaros (*Crescentia alata*) are characteristic of the savanna in northern Nayarit.

Some of the common plants found in the dry forest of Sinaloa are: *Haematoxylum brasiletto*, *Erythrina occidentalis*, *Bursera grandifolia*, *Ceiba aesculifolia*, *Sapium lateriflorum*, *Castilla elastica*, *Cordia sonora*, *Jatropha cinerea*, *Sideroxylon capiri*, and *Ficus petiolaris*.

Subtropical Dry Forest

The subtropical Dry Forest occupies the central elevations along the western slope of the Sierra Madre Occidental between 1000 and 1500 meters (Fig. 7). This vegetation, equivalent to the Tropical Montane Forest of Gentry (1946a:359; 1946b:462), lies in about the same belt as the oak forest but has a different physiognomy and consists of different species. The presence of subtropical dry forest is attributed to conditions of exposure, soil, and local climate as affected by terrain.

This vegetation is generally limited to canyons and slopes where the greater amount of precipitation is retained by good soil and evaporation is reduced by cloud-cover. Gentry (1946b:453) credits the rain clouds and fog as a chief factor in supporting the abundant epiphytic growth and the varied forest of tropical nature. Shrubs are more dense than in the semiarid or dry forests at lower elevations (Plate 7, Fig. 2). Nearly all of the commonest species in the

canyons are shade-tolerant forms. The canyons are generally lined with trees as tall as 20 meters, including *Lysiloma*, *Brosimum*, *Platanus*, and *Oreopanax* (Plate 8, Fig. 1). There is a strong infusion of barranca and lowland trees in these canyons; *Ceiba acuminata*, *Ipomoea arborescens*, and *Inga eriocarpa* are often intermingled with highland species. Shrubbery is protected under the forest and is composed of numerous species. The moist slopes and canyon bottoms are thickly carpeted with shade-tolerant, broad-leaved herbs (Gentry, 1946b:460).

Plants characteristic of the subtropical dry forest are: *Lysiloma divaricata*, *Brosimum alicastrum*, *Ceiba acuminata*, *Bursera simaruba*, *Psidium sartorianum*, *Urera caracasana*, and *Phenax hirtus*.

Lower Montane Dry Forest

The Lower Montane Dry Forest vegetation includes the vegetation in Sinaloa referred to: the oak-agave-juniper association by Brand (1936:21); oak grassland and pine oak forest (Gentry, 1946a:361-362; 1946b:458-462); and pine-oak forest (Leopold, 1959:23-25). Oak forest is found in a relatively narrow strip along the western slope of the Sierra Madre, and is dominated by deciduous oaks and harsh bunch grasses. The oak forest occurs over the southern slopes at elevations of 1000 to 2000 meters and on the eastern side of Sierra Tacuichamona (Gentry, 1946a:361). At higher elevations, 1500 to 2400 meters, the dominant forest is a mixture of pine and oak (Plate 8, Fig. 2). There are only a few pure stands of pine in Sinaloa, and these are found only at the highest elevations. The oak and pine forests are all considered part of the Lower Montane Dry Forest (Fig. 7).

Gentry (1946a:361-362) listed four species of oak found on the eastern side of Sierra Tacuichamona: *Quercus albocincta*, *Q. tuberculata*, *Q. chihuahuensis*, and *Q. gentryi*. These same oaks are found on the southern exposures of the Sierra Surotato (Gentry, 1946b:460). On the more arid northern slope, a large part of the oak belt is occupied by harsh-leaved grasses, principally *Muhlenbergia*, *Tripsacum*, *Andropogon*, and *Heteropogon*.

At slightly higher elevations in the Sierra Surotato the forest is a mixture of pine and oak. *Pinus macrophylla*, *P. ayacahuite*, *P. oocarpa*, and *P. lumholtzii* are the common species of pine in northern Sinaloa. The species of oaks are different from those found on the Sierra Tacuichamona. *Quercus epileuca* is most abundant on moist, shady slopes and reaches a height of 20 meters.

Quercus pallescens, *Q. durifolia*, and *Q. candicans* are other common species in the oak-pine forest. *Arbutus xalapensis* is found with pines and oaks in some places in northern Sinaloa. No specific information is available concerning the pine and oak forests in the southern highlands of Sinaloa.

COMPOSITION OF THE HERPETOFAUNA

As presently understood, the herpetofauna of Sinaloa includes 131 species: 32 frogs (24.4% of the total number of species, 10 turtles (7.6%), 33 lizards (25.2%), 55 snakes (42.0%), and one crocodylian (0.8%). Although no salamanders have been reported from Sinaloa, additional collecting in the Lower Montane Dry Forest in the eastern part of the state will probably reveal their presence.

A comparison of the herpetofaunal diversity of Sinaloa with that of Michoacán and of Arizona is presented in Table 1. The data

TABLE 1.—Comparison of the Herpetofaunas of Arizona, Sinaloa, and Michoacán by Major Components.

	Arizona (295,024 sq. km.)		Sinaloa (58,092 sq. km.)		Michoacán (60,093 sq. km.)	
	Number	Percent	Number	Percent	Number	Percent
Salamanders.....	1	0.9	0	0.0	6	3.7
Anurans.....	20	17.5	31	25.6	38	23.4
Turtles.....	4	3.5	5	4.1	3	1.8
Crocodylians.....	0	0.0	1	0.8	1	0.6
Lizards.....	41	36.0	31	25.6	46	28.2
Snakes.....	48	42.1	53	43.9	69	42.3
Totals.....	114	100.0	121	100.0	163	100.0

for Michoacán are from Duellman (1965); those for Arizona are from Lowe (1964). Only the native terrestrial species are pertinent to the discussion. The marine turtles, the sea snake, and those forms which are known to be introduced are excluded.

There is an increase in the number of species of amphibians and reptiles from Arizona (114 species) through Sinaloa (121 species) to Michoacán (154 species) independent of total area. This cline in herpetofaunal diversity along a latitudinal gradient generally conforms to the results expected in moving from temperate to tropical environments. However, it should be noted that not all components conform to the north-south increase in diversity. The

lizards, for example, exhibit the least diversity in Sinaloa; they are more numerous in Michoacán than in Arizona but constitute a larger percentage of the herpetofauna in the latter region. In contrast, the number and percentage of turtles are lowest in Michoacán and highest in Sinaloa. Both frogs and snakes follow the expected pattern, increasing in number from Arizona to Michoacán. It is interesting to note that while snakes increase in number from north to south, their percentage of the total fauna is nearly the same in all three areas.

Distribution Within Habitats

The distribution of amphibians and reptiles in the five vegetation zones in Sinaloa is summarized in Table 2. Each species and subspecies has been designated as being abundant (A), moderately abundant (M), apparently rare (R), or absent (—) in each habitat. Locality records that we consider questionable are designated (?). The altitudinal distribution is based primarily on locality data associated with specimens examined, rounded off to the nearest 100-meter interval. If specimens lacked data as to elevation of capture, the locality is designated by the nearest of the following altitudes: 300, 900, 1500, 2100 meters (see Fig. 1).

Records on or very near the boundary between the two vegetation zones generally were assigned to a zone on the basis of total distributions. For example, a species which is moderately abundant in the Tropical Semiarid Forest and recorded from the Tropical Thorn Woodland only at a border locality is not included in the Tropical Thorn Woodland herpetofauna. This procedure compensates for the transition and interdigitation of borders between two vegetation zones and emphasizes the ecotonal nature of each boundary line.

Tropical Thorn Woodland.—Thorn woodland forest occurs in the most arid parts of Sinaloa along the northern Pacific coast. Sixty-one species and subspecies of amphibians and reptiles are known from this zone; of these 16 are considered abundant. They include: *Scaphiopus couchii*, *Leptodactylus occidentalis*, *Bufo kelloggi*, *B. marinus*, *B. mazatlanensis*, *Rana pipiens*, *Holbrookia maculata*, *Sceloporus clarkii boulengeri*, *Urosaurus ornatus lateralis*, *Cnemidophorus costatus griseocephalus*, *Leptodeira punctata*, *Masticophis flagellum piceus*, *M. striolatus*, *Natrix v. valida*, *Thamnophis cyrtopsis collaris*, and *Crotalus b. basiliscus*.

Many species characteristic of this area have exploited the new

TABLE 2.—Distribution of Amphibians and Reptiles in Sinaloa by Vegetation Types and Altitude. A, abundant; M, moderately abundant; R, apparently rare; —, absent; ?, questionable record; *, introduced.

SPECIES	Tropical Thorn Woodland	Tropical Semiarid Forest	Tropical Dry Forest	Subtropical Dry Forest	Lower Montane Dry Forest	Altitudinal Range, Meters
ORDER SALIENTIA						
Family Pelobatidae						
<i>Scaphiopus couchii</i>	A	A	M	—	—	0-400
Family Leptodactylidae						
<i>Eleutherodactylus augusti cactorum</i>	—	R	R	M	—	100-1500
<i>Eleutherodactylus hobartsmithi</i>	—	R	R	R	—	500-1100
<i>Eleutherodactylus occidentalis</i>	—	R	R	R	—	200-1500
<i>Eleutherodactylus vocalis</i>	—	R	M	M	R	400-1200
<i>Leptodactylus occidentalis</i>	A	A	A	—	—	0-700
<i>Syrrophus interorbitalis</i>	—	R	—	—	—	0-400
<i>Syrrophus modestus</i>	—	—	M	R	R	300-1500
<i>Tomodactylus niditus petersi</i>	—	—	—	M	R	900-1900
<i>Tomodactylus sazaatilis</i>	—	—	—	R	—	1900
Family Bufonidae						
<i>Bufo alvarius</i>	M	?	—	—	—	0-300
<i>Bufo kelloggi</i>	A	A	M	—	—	0-200
<i>Bufo marinus</i>	A	A	A	—	—	0-500
<i>Bufo marmoratus</i>	R	A	M	—	—	0-400
<i>Bufo mazatlanensis</i>	A	A	A	R	—	0-1000
<i>Bufo occidentalis</i>	R	—	—	M	M	1100-2000
<i>Bufo punctatus</i>	R	R	—	—	R	0-2100
Family Hylidae						
<i>Diadlena spatulata</i>	—	M	M	—	—	0-300
<i>Hyla arenicolor</i>	—	—	—	R	R	1500-2100
<i>Hyla smaragdina</i>	—	—	R	M	R	500-1500
<i>Hyla smithi</i>	R	A	A	R	—	0-800
<i>Phrynohyas venulosa</i>	—	—	R	—	—	0-300
<i>Phyllomedusa dacnicolor</i>	M	A	A	—	—	0-500
<i>Pterohyla fodiens</i>	M	A	A	—	—	0-300
<i>Smitisca baudinii</i>	M	A	A	R	—	0-800
Family Microhylidae						
<i>Gastrophryne olivacea mazatlanensis</i>	M	A	—	—	—	0-300
<i>Gastrophryne usta usta</i>	—	R	M	—	—	0-300
<i>Hypopachus oxyrrhinus oxyrrhinus</i>	—	M	M	—	—	0-300
Family Ranidae						
<i>Rana catesbeiana*</i>	M	—	—	—	—	0-200
<i>Rana pipiens</i>	A	A	A	M	R	0-1700
<i>Rana pustulosa</i>	—	?	—	R	R	1000-1500
<i>Rana sinaloae</i>	—	—	M	M	M	700-2000
ORDER TESTUDINES						
Family Kinosternidae						
<i>Kinosternon integrum</i>	M	A	A	R	—	0-1100
Family Emydidae						
<i>Chrysemys scripta hiltoni</i>	M	—	—	—	—	0-100
<i>Chrysemys scripta ornata</i>	—	M	M	—	—	0-200
<i>Rhinoclemys pulcherrima pulcherrima</i>	?	R	R	R	—	0-1100
<i>Terrapene nelsoni klauberi</i>	—	R	—	—	—	0-300
Family Testudinidae						
<i>Gopherus agassizii</i>	R	—	—	—	—	0-300
Family Chelonidae						
<i>Caretta caretta gigas</i>	—	—	—	—	—	Marine
<i>Chelonia mydas</i>	—	—	—	—	—	Marine
<i>Eretmochelys imbricata</i>	—	—	—	—	—	Marine
<i>Lepidochelys olivacea</i>	—	—	—	—	—	Marine
Family Dermochelyidae						
<i>Dermochelys coriacea</i>	—	—	—	—	—	Marine

TABLE 2.—Distribution of Amphibians and Reptiles in Sinaloa by Vegetation Types and Altitude.—Continued

SPECIES	Tropical Thorn Woodland	Tropical Semi-arid Forest	Tropical Dry Forest	Subtropical Dry Forest	Lower Montane Dry Forest	Altitudinal Range, Meters
ORDER SQUAMATA						
Suborder Sauria						
Family Gekkonidae						
<i>Coleonyx variegatus fasciatus</i>	R	R	R	—	—	0-300
<i>Gehyra mutilata</i> *.....	R	R	—	—	—	0-100
<i>Hemidactylus frenatus</i> *.....	R	—	—	—	—	0-100
<i>Phyllodactylus homolepidurus homolepidurus</i>	R	—	—	—	—	0-100
<i>Phyllodactylus tuberculosus sazatis</i>	M	A	A	R	—	0-1700
Family Iguanidae						
<i>Anolis nebulosus</i>	M	A	A	M	R	0-2000
<i>Anolis utovanae</i>	—	R	—	—	—	50
<i>Callisaurus draconoides bogerti</i>	M	M	R	—	—	0-100
<i>Callisaurus draconoides brevipes</i>	—	M	—	—	—	150-400
<i>Ctenosaura hemilopha</i>	M	A	—	—	—	0-900
<i>Ctenosaura pectinata</i>	R	A	A	—	—	0-900
<i>Dipsosaurus dorsalis sonoriensis</i>	M	—	—	—	—	0-300
<i>Holbrookia maculata elegans</i>	A	A	—	—	—	0-600
<i>Iguana iguana rhinolopha</i>	—	M	A	—	—	0-300
<i>Phrynosoma solare</i>	M	M	—	—	—	0-900
<i>Sceloporus bulleri</i>	—	—	—	—	—	1000-2000
<i>Sceloporus clarkii boulenperi</i>	A	A	A	M	R	0-1700
<i>Sceloporus horridus albiventris</i>	—	M	M	R	—	0-600
<i>Sceloporus jarrovi jarrovi</i>	—	—	—	R	R	1100-2000
<i>Sceloporus magister magister</i>	M	—	—	—	—	0-300
<i>Sceloporus nelsoni</i>	—	A	A	M	R	0-1900
<i>Sceloporus shannonorum</i>	—	—	—	—	R	1800-2000
<i>Sceloporus utiformis</i>	—	M	M	R	—	0-1800
<i>Urosaurus bicarinatus tuberculatus</i>	R	A	M	R	—	0-1100
<i>Urosaurus ornatus lateralis</i>	A	M	—	—	—	0-500
Family Scincidae						
<i>Eumeces callicephalus</i>	—	M	R	—	—	0-600
<i>Eumeces colimensis</i>	—	—	—	R	—	1700
<i>Eumeces parvulus</i>	—	—	—	R	R	800-1500
Family Teiidae						
<i>Cnemidophorus costatus griseocephalus</i>	A	M	—	R	—	0-900
<i>Cnemidophorus costatus huico</i>	—	R	A	R	—	0-1200
<i>Cnemidophorus costatus mazatlanensis</i>	—	A	R	R	R	0-2000
<i>Cnemidophorus costatus nigrigularis</i>	R	A	—	R	—	0-900
<i>Cnemidophorus tigris</i>	M	M	—	—	—	0-200
Family Anguidae						
<i>Gerrhonotus kingii ferrugineus</i>	—	—	—	R	—	1150
<i>Gerrhonotus liocephalus liocephalus</i>	—	—	—	—	R	1900-2200
Family Helodermatidae						
<i>Heloderma horridum exasperatum</i>	R	R	—	—	—	100-400
<i>Heloderma horridum horridum</i>	—	A	M	R	—	0-500
<i>Heloderma suspectum suspectum</i>	R	—	—	—	—	0-100
SUBORDER SERPENTES						
Family Typhlopidae						
<i>Typhlops braminus</i> *.....	—	R	—	—	—	0-100
Family Leptotyphlopidae						
<i>Leptotyphlops humilis dugesii</i>	—	M	R	—	—	0-300
Family Boidae						
<i>Boa constrictor imperator</i>	M	A	A	—	—	0-400

TABLE 2.—Distribution of Amphibians and Reptiles in Sinaloa by Vegetation Types and Altitude.—*Concluded*

SPECIES	Tropical Thorn Woodland	Tropical Semiarid Forest	Tropical Dry Forest	Subtropical Dry Forest	Lower Montane Dry Forest	Altitudinal Range, Meters
Family Colubridae						
<i>Arizona elegans noctivaga</i>	—	R	R	—	—	0-100
<i>Coniophanes lateritus lateritus</i>	—	R	R	—	—	0-500
<i>Conopsis nasus nasus</i>	—	—	—	R	R	1500-2000
<i>Dryadophis cliftoni</i>	—	—	—	M	M	700-2000
<i>Dryadophis melanolomus stuarti</i>	—	R	R	—	—	0-300
<i>Drymarchon corais rubidus</i>	R	A	M	R	—	0-1200
<i>Drymobius margaritiferus statulosus</i>	—	M	A	R	—	0-500
<i>Elaphe triaspis intermedia</i>	—	A	M	R	—	0-1000
<i>Geagras redimitus</i>	—	R	—	—	—	0-100
<i>Geophis dugesii</i>	—	—	—	—	R	1800-2000
<i>Gyalopion quadrangularis</i>	M	A	M	R	—	0-1200
<i>Hypsiglena torquata</i>	M	A	M	—	—	0-500
<i>Imantodes gemmistratus latistratus</i>	R	A	A	R	—	0-1200
<i>Lampropeltis getulus nigrilus</i>	R	—	—	—	—	0-300
<i>Lampropeltis triangulum nelsoni</i>	M	A	A	R	—	0-1000
<i>Leptodeira maculata</i>	—	R	A	R	—	0-1000
<i>Leptodeira punctata</i>	A	A	A	—	—	0-300
<i>Leptodeira septentrionalis polysticta</i>	—	R	—	—	—	0-300
<i>Leptodeira splendida ehippiata</i>	—	M	M	M	—	100-1500
<i>Leptophis diplotropis</i>	R	A	A	M	R	0-2000
<i>Masticophis bilineatus</i>	M	A	A	—	—	0-600
<i>Masticophis flagellum piceus</i>	A	M	A	—	—	0-500
<i>Masticophis striolatus</i>	A	A	A	M	R	0-2000
<i>Natrix valida valida</i>	A	A	A	—	—	0-300
<i>Oxybelis aeneus auratus</i>	—	A	A	—	—	0-600
<i>Phyllorhynchus browni</i>	M	A	—	—	—	0-300
<i>Phyllorhynchus decurtatus</i>	—	R	—	—	—	0-300
<i>Pituophis melanoleucus affinis</i>	M	M	M	—	—	0-500
<i>Pseudoficimia frontalis</i>	—	A	R	—	—	0-500
<i>Rhadinaea hesperia hesperioides</i>	—	—	—	R	R	700-1900
<i>Rhinocheilus lecontei antonii</i>	M	A	A	—	—	0-200
<i>Salvadora bairdii</i>	—	R	R	R	R	500-2000
<i>Salvadora hexalepis deserticola</i>	M	M	R	—	—	0-500
<i>Sonora aemula</i>	R	R	—	—	—	0-300
<i>Storeria storerioides</i>	—	—	—	—	R	1900-2000
<i>Sympholis lippiens</i>	—	M	R	—	—	0-300
<i>Tantilla calamarina</i>	—	R	—	—	—	0-300
<i>Tantilla yaquia</i>	—	M	R	—	—	0-1000
<i>Thamnophis cyrtopsis collaris</i>	A	A	M	M	M	0-2000
<i>Trimorphodon lambda paucimaculatus</i>	M	A	A	R	R	0-1300
<i>Trimorphodon tau</i>	—	A	—	—	—	0-900
<i>Tropidodipsas annulifera</i>	—	M	R	R	—	0-1200
<i>Tropidodipsas philippii</i>	—	M	R	—	—	0-300
Family Elapidae						
<i>Micruroides euryzanthus neglectus</i>	—	R	—	—	—	0-300
<i>Micrurus distans distans</i>	R	M	M	—	—	0-300
Family Hydrophiidae						
<i>Pelamis platurus</i>	—	—	—	—	—	Marine
Family Viperidae						
<i>Agkistrodon bilineatus bilineatus</i>	—	M	M	—	—	0-300
<i>Crotalus atrox</i>	M	—	—	—	—	0-300
<i>Crotalus basiliscus basiliscus</i>	A	A	A	M	R	0-2000
<i>Crotalus lepidus</i>	—	—	—	—	R	1800-2000
<i>Crotalus molossus molossus</i>	—	R	—	—	—	0-300
<i>Crotalus stejnegeri</i>	—	—	—	R	—	800-1200
ORDER CROCODYLIA						
Family Crocodylidae						
<i>Crocodylus acutus</i>	—	M	M	—	—	0-100

habitats created by irrigation projects associated with the tremendous agricultural development in the Los Mochis and Guasave areas. This is especially true of the frogs *Leptodactylus occidentalis*, *Rana catesbeiana*, and *R. pipiens*, and the snakes *Leptodeira punctata*, *Natrix v. valida*, and *Thamnophis cyrtopsis collaris*.

Most of the amphibians are nocturnal and generally are found close to permanent water. Many of the lizards, however, including several species whose ranges lie primarily in northern desert regions, are diurnal and terrestrial. Characteristic species exhibiting this distributional pattern are *Dipsosaurus dorsalis*, *Urosaurus ornatus*, *Phrynosoma solare*, *Sceloporus magister* and *Cnemidophorus tigris*. Nocturnal lizards with similar distributions to the north are *Phyllodactylus homolepidurus* and *Heloderma suspectum*.

With the exception of the three species associated with irrigation ditches and the two large diurnal racers, *Masticophis flagellum* and *M. striolatus*, snakes are not particularly abundant in the thorn woodland zone.

Tropical Semiarid Forest.—Semiarid forest is the most extensive plant formation in Sinaloa, covering nearly one-half of the state. The number of amphibian and reptilian species is correspondingly large. Of the 96 species and subspecies recorded from this zone, 43 are considered abundant.

The amphibians that were listed as abundant in the thorn woodland, as well as the following species, are abundant in the semiarid forest: *Bufo marmoratus*, *Hyla smithi*, *Phyllomedusa dacnicolor*, *Pterohyla fodiens*, *Smilisca baudinii*, and *Gastrophryne olivacea*. Hyliid frogs constitute the major additions.

Among the lizards, the increase in relative density of *Anolis nebulosus*, *Ctenosaura pectinata*, *Iguana iguana*, *Sceloporus nelsoni*, *Urosaurus bicarinatus*, and probably *Eumeces callicephalus* is correlated with the increase in vegetation density and number of suitable habitats therein.

Several species of snakes are more abundant in the semiarid forest than in the thorn woodland. Included are *Boa constrictor*, *Drymarchon corais*, *Elaphe triaspis*, *Imantodes gemmistratus*, *Lampropeltis triangulum*, *Leptophis diplotropis*, and *Oxybelis aeneus*. The appearance or increase of these species probably reflects change from a dry to a more moist environment. Several of these species are primarily arboreal and appear in response to the greater complexity and density of the semiarid forest vegetation.

Tropical Dry Forest.—The dry forest is found in the southern parts of the state. This environment is characteristically more moist than the other lowland zones and is inhabited by 73 species and subspecies of amphibians and reptiles. Most species that are abundant in the semiarid forest are also abundant in the dry forest; additionally, *Iguana iguana* and *Drymobius margaritiferus* are considered abundant in dry forest. In the lowlands certain species are almost restricted to the dry forest. Among these are *Phrynohyas venulosa*, *Syrrophus modestus*, *Gastrophryne usta*, and *Leptodeira maculata*. Other species that occur to the north are conspicuously rare or absent in the dry forest. Included are *Gastrophryne olivacea*, *Coleonyx variegatus*, *Callisaurus draconoides*, *Holbrookia maculata*, *Phyllorhynchus browni*, and *Salvadora hexalepis*.

Subtropical Dry Forest.—Relatively little is known about the herpetofauna of this vegetation type in Sinaloa, due to the inaccessibility of areas having subtropical dry forest. As presently understood 54 species and subspecies have been recorded in this zone. Many records are from localities at the periphery of the range of primarily lowland species. There is, however, a distinctive group of species characteristic of this vegetation type. Included are *Eleutherodactylus hobartsmithi*, *E. occidentalis*, *E. vocalis*, *Tomodactylus niditus*, *T. saxatilis*, *Hyla smaragdina*, *Rana pustulosa*, *R. sinaloae*, *Eumeces colimensis*, *E. parvulus*, *Gerrhonotus kingii*, *Dryadophis clifftoni*, *Leptodeira splendida*, *Rhadinaea hesperia*, and *Crotalus stejnegeri*. Some of these species range into the lowlands, usually along riparian habitats. Others are recorded from higher elevations. An increase in moisture and a well developed litter on the forest floor probably are important factors determining the distributions of these forms in the subtropical dry forest as opposed to zones previously discussed.

Lower Montane Dry Forest.—This vegetation type is restricted to high elevation in scattered localities along the Sierra Madre Occidental in eastern Sinaloa. The only site visited in the montane forest was on Highway 40 near the Durango border. Ten species of amphibians and 21 species of reptiles have been collected in this habitat. Characteristic species include *Bufo occidentalis*, *Hyla arenicolor*, *Sceloporus bulleri*, *S. jarrovii*, *S. shannonum*, *Gerrhonotus liocephalus*, *Conopsis nasus*, *Geophis dugesii*, *Storeria storerioides*, and *Crotalus lepidus*. Most of these are widely distributed on the Mexican plateau, or are restricted to high elevations in the mountains of western México.

Lizards of the genus *Sceloporus* are the most conspicuous reptiles in this formation. *Sceloporus jarrovi* and *S. bulleri* are found on logs and on tree trunks; *S. shannorum* apparently is entirely arboreal. The small snakes of the genera *Conopsis*, *Geophis*, and *Storeria* are semifossorial, usually being found under logs or in the litter of the forest.

Faunal Assemblages

There are two major faunal assemblages in Sinaloa, one in the lowlands and one in the highlands. The lowland assemblage, comprising 105 species, will be discussed in detail elsewhere (McDiarmid, MS). The highland assemblage consists of 58 species that can be divided into two groups: foothill and canyon species generally associated with the subtropical dry forest vegetation; and highland species generally associated with the pine and oak forests characteristic of the lower montane dry forest. Species indicative of each assemblage were mentioned in the preceding discussion of distributions by vegetation types.

ACCOUNTS OF SPECIES AND SUBSPECIES

Each kind of amphibian and reptile known to occur in Sinaloa is discussed with reference to its systematic status, variation, and distribution. Observations pertaining to life history and ecology also are presented. Some taxonomic usages herein are not in accord with the current systematic arrangement; we have included in the species accounts sufficient data to justify the changes or synonymies presented. Some systematic problems remain, either because of insufficient data to support changes that we think warranted or because the problems were inherently impractical to undertake within the scope of our study. These problems are mentioned in the hope that our ideas might stimulate investigations by other workers.

This study is based primarily on specimens deposited in the Museum of Natural History at the University of Kansas and in the Los Angeles County Museum of Natural History. Additional information taken from the literature is included when appropriate. We have made a special effort to examine or list all available specimens of amphibians and reptiles collected in the state.

A synonymy is provided at the beginning of each species account. It includes reference to the original proposal of the specific epithet, the first usage of the name-combination used by us, and in a few

cases, other names or combinations that have been used in the past when their inclusion is considered important in clarifying the presentation (these references are not included in the literature cited). A statement of the type locality as originally designated follows the reference to the original description.

Remarks.—The majority of the specimens discussed in this section are in the Museum of Natural History, University of Kansas. Other specimens that were examined and that contributed information to the discussion are listed by museum numbers. Most of the notes on ecology and natural history are based on observations by the second author and on specimens in the Los Angeles County Museum. All measurements are in millimeters. Measurements and counts are presented as the range of variation followed by the mean (in parentheses); where no mean is given the measurements are listed individually. In some cases damaged or poorly preserved specimens were examined for some characteristics but not for others; these specimens are designated by museum numbers. Paired characteristics are presented as left-right.

Distribution in Sinaloa.—The distribution of each species or subspecies in Sinaloa is briefly stated. The distribution of highland taxa is not so well known as is the distribution of those in the lowlands.

Specimens examined.—This section includes all specimens that were seen by either or both of us. If data from a specimen or series of specimens are presented in the remarks section of the species account, then the appropriate museum numbers are designated by an asterisk in the list of specimens examined. Numbers not preceded by an asterisk refer to specimens that were examined but only contributed information pertaining to life history, ecology, or distribution.

Literature records.—In most cases when a species was reported from a single locality in different papers, some of the older literature citations are omitted. If pertinent information was presented, then the citation is listed.

Additional records.—This list includes locality records based on specimens in museums, institutions, or private collections that were not examined by us and that have not been previously reported in the literature. Most of these records were supplied by curators or were taken from the catalogs of the different collections.

All place names are in alphabetical order. The localities based

on a certain place name are listed in a clockwise direction starting from north and at increasing distances (*i. e.*, Mazatlán; N Mazatlán; 5 mi. N Mazatlán; 7 mi. N Mazatlán; 3 mi. NE Mazatlán). Some distances and elevations cited for *specimens examined* have been converted to the metric system, but all distances and elevations listed in *literature records* and *additional records* are retained in their original form. A map of the distribution of each species or subspecies is included. Open symbols indicate either *literature records* or *additional records*; solid symbols indicate *specimens examined*. In some instances, a single symbol represents several records or specimens depending on the distances between localities.

Abbreviations used for various museums, institutions, and private collections are as follows:

AMNH	American Museum of Natural History, New York
ASDM	Arizona-Sonora Desert Museum, Tucson
CAS	California Academy of Sciences, San Francisco
CSCLB	California State College at Long Beach
EHT-HMS	Edward H. Taylor-Hobart M. Smith, private collections (now in Field Museum of Natural History and University of Illinois Museum of Natural History)
FAS	Frederick A. Shannon, private collection (now in University of Illinois Museum of Natural History)
FMNH	Field Museum of Natural History, Chicago
JFC	Joseph F. Copp, private collection, La Jolla, California
JLC	James L. Christiansen, private collection (now in the collection of the University of Utah)
JMS	Jay M. Savage, osteology collection, University of Southern California
JRM	John R. Meyer, private collection (now in the Texas Cooperative Wildlife Collection)
KU	University of Kansas, Museum of Natural History
LACM	Los Angeles County Museum of Natural History
LMK	Laurence M. Klauber, private collection, San Diego
LSU	Louisiana State University
MCZ	Museum of Comparative Zoology, Harvard University
MVZ	Museum of Vertebrate Zoology, University of California
PR	Philip J. Regal, private collection, Los Angeles, California
RGW	Robert G. Webb, private collection, El Paso, Texas
RSF	Richard S. Funk, private collection, Yuma, Arizona
SDSC	San Diego State College
SDSNH	San Diego Society of Natural History
SM	Strecker Museum, Baylor University, Waco, Texas
SU	Stanford University
TCWC	Texas Cooperative Wildlife Collection, Texas A. and M.
TMM	Texas Memorial Museum, Austin, Texas
TNHC	Texas Natural History Collection, University of Texas, Austin
UAZ	University of Arizona
UCLA	University of California at Los Angeles
UF	Florida State Museum, Gainesville
UIMNH	University of Illinois, Museum of Natural History
UMMZ	University of Michigan, Museum of Zoology
UNM	University of New Mexico
USNM	United States National Museum
UU	University of Utah

No new taxa are described in this paper. The following 21 species or subspecies are reported from Sinaloa for the first time: *Eleutherodactylus hobartsmithi*, *Syrrophus modestus*, *Rana pustulosa*, *Hyla smaragdina*, *Chrysemys scripta hiltoni*, *Hemidactylus frenatus*, *Phyllodactylus homolepidurus homolepidurus*, *Sceloporus magister magister*, *Cnemidophorus tigris*, *Gerrhonotus kingii ferrugineus*, *Gerrhonotus liocephalus liocephalus*, *Heloderma suspectum suspectum*, *Coniophanes lateritius lateritius*, *Dryadophis melanolomus stuarti*, *Geophis dugesii*, *Leptodeira septentrionalis polysticta*, *Phyllorhynchus decurtatus*, *Salvadora bairdii*, *Sonora aemula*, *Storeria storerioides*, *Crotalus molossus molossus*.

The type localities of the following 35 nominal species or subspecies are in Sinaloa:

Syrrophus interorbitalis Langebartel and Shannon, 1956:161.—Thirty-six miles north of Mazatlán.

Tomodactylus saxatilis Webb, 1962a:177.—Eight miles west of El Palmito [Durango].

Bufo kelloggi Taylor, 1938:510.—Two miles east of Mazatlán.

Bufo mazatlanensis Taylor, 1940c:492.—Two miles east of Mazatlán.

Diaglena spatulata (Günther), 1882:279.—Presidio, México.

Prynohyas latifasciata Duellman [= *P. venulosa* (Laurenti) according to McDiarmid, 1968], 1956:24—Presidio.

Pternohyla fodiens Boulenger, 1882:326.—Presidio, W. México.

Gastrophryne olivacea mazatlanensis Taylor, 1943:355.—Two miles east of Mazatlán.

Hypopachus oxyrrhinus oxyrrhinus Boulenger, 1883:344.—Presidio de Mazatlán.

Rana forreri Boulenger [= *R. pipiens* Schreber], 1883:343.—Presidio.

Rana sinaloae Zweifel, 1954a:131.—Fourteen miles by (road) southwest of El Batel, 4200 feet.

Chrysemys scripta ornata (Gray), 1831:30.—Mazatlán.

Phyllodactylus tuberculosus saxatilis Dixon, 1964:31.—Eight miles northeast of Villa Unión, 200 feet.

Anolis utowanae Barbour, 1932:12.—About ten miles north of Mazatlán.

Callisaurus draconoides bogerti Martín del Campo, 1943:619.—Isla de los Chivos, en el Puerto de Mazatlán.

Ctenosaura teres brachylopha Cope [= *C. pectinata* (Wiegmann)], 1886:269.—Mazatlán.

Holbrookia maculata elegans Bocourt, 1874:164.—Mazatlán.

Sceloporus clarkii boulengeri Stejneger, 1893:180.—Presidio.

Sceloporus nelsoni Cochran, 1923:185.—Plomosas.

Sceloporus shannonorum Langebartel, 1959:25.—Thirty-seven miles by road from Concordia, near the Durango-Sinaloa border, state not determined.

Eumeces humilis Boulenger [= *E. callicephalus* Bocourt, according to Loomis and Stephens, M.S.] 1887:377.—Presidio.

Cnemidophorus costatus mazatlanensis Zweifel, 1959a:89.—Two miles north Coyotitán.

Cnemidophorus costatus nigrigularis Zweifel, 1959a:93.—Ten and one-half miles northwest of Culiacán.

Dryadophis cliftoni Hardy, 1964:714.—Plomosas, 22 kilometers east of Matatán, 762.5 meters.

- Drymarchon corais rubidus* Smith, 1941d:474.—Rosario.
Gyalopion quadrangularis (Günther), 1893:99.—Presidio.
Leptodeira pacifica Cope [= *L. punctata* (Peters)], 1868:310.—Mazatlán.
Leptodeira personata Cope [= *L. maculata* (Hallowell)], 1868:310.—Mazatlán.
Salvadora hexalepis celeris Smith [= *S. h. deserticola* Schmidt], 1941a:9.—San Blas.
Sphenocalamus lineolatus Fischer [= *Geagrass redimitus* Cope], 1883:5.—Mazatlán.
Tantilla bimaculata Cope [= *T. calamarina* Cope], 1876:143.—Mazatlán.
Trimorphodon lambda paucimaculata Taylor, 1938:527.—Mazatlán.
Tropidodipsas philippii (Jan), 1863:101.—Mazatlán.
Tropidonotus quadriserialis Fischer [= *Natrix valida* (Kennicott)], 1879:82.—Mazatlán.
Micruroides euryxanthus neglectus Roze, 1967:4.—Sixteen and three-tenths miles north-northwest of Mazatlán.
Crotalus stejnegeri Dunn, 1919:214.—Plomosas.

The type localities of the following six forms have been restricted to Sinaloa:

- Kinosternon hirtipes hirtipes* Wagler, 1830:37.—Mazatlán (by Smith and Taylor, 1950a:343).
Rhinoclemmys pulcherrima (Gray), 1855:25.—Presidio de Mazatlán (by Smith and Taylor, 1950a:343).
Anolis nebulosus (Wiegmann), 1834:47.—Mazatlán (by Smith and Taylor, 1950a:343).
Urosaurus ornatus lateralis (Boulenger), 1885b:214.—Presidio (by Oliver, 1943:97).
Leptodeira punctata (Peters), 1867:93.—Mazatlán (by Smith and Taylor, 1950a:343).
Masticophis striolatus (Mertens), 1934:190.—Presidio de Mazatlán (by Smith and Taylor, 1950a:343).

In this work we do not accept type locality restrictions that are not substantiated by evidence (*i. e.*, Smith and Taylor, 1950a); such restrictions are not included in the synonymies.

Class AMPHIBIA

Order SALIENTIA

Family Pelobatidae

Scaphiopus couchii Baird

Scaphiopus couchii Baird, Proc. Acad. Nat. Sci. Philadelphia, 7:62, 1856 (based on specimens from Río Nazas in Coahuila, and Matamoros in Tamaulipas).

Remarks.—Several authors have suggested that *Scaphiopus couchii* in western México differs from *S. couchii* in eastern México by having the skin of the occipital and interorbital region almost

completely co-ossified with the skull, a wider metatarsal tubercle, larger eye, wider skull (Taylor, 1938:508), fewer large cream-colored blotches (Davis and Dixon, 1957b:145), and the absence of vaguely outlined paravertebral light lines (Smith and Sanders, 1952:209). Based on an examination of 101 specimens from Sinaloa, Tamaulipas, and Texas, no consistent differences warranting subspecific designation of the population in western México were observed.

Spadefoot toads were collected at night on the road or at temporary ponds throughout the lowlands. Breeding commences with the first heavy rains and continues through September. Calling males were collected in the first week of July and amplexing pairs were secured at La Cruz on August 18 and 20. All calling males were floating in the water.

Distribution in Sinaloa.—Known from throughout the lowlands of the state. See Fig. 13.

Specimens examined.—Aguapepe (CAS 89756); 2.1 mi. NE Concordia (CSCLB 1850-53); 4.7 mi. NE Concordia (CSCLB 1859); 14 mi. N Culiacán (CSCLB 1869); 21.4 mi. S Culiacán (LACM 6043); 2.9 mi. N Elota (CSCLB 1862, 1866); 3 mi. S Espinal (CSCLB 1855); Guamúchil (UCLA 14806); La Cruz, 9 m. (° KU 73772-74; LACM 6000-03); 5 mi. NE La Cruz (LACM 6039-40); 10 mi. NE La Cruz (LACM 6025-33); 61 km. N Los Mochis (° KU 62201); 18.4 mi. NW Los Mochis turnoff (on hwy. 15) (UAZ 7657, 7660-67); 20.7 mi. NW Los Mochis turnoff (on hwy. 15) (UAZ 7669-70); 30 km. NNW Los Mochis (° KU 37826); Matatán, 170 m. (° KU 73771); 7.3 km. SW Matatán, 155 m. (° KU 78251-52); Mazatlán (CAS 89709-10; CSCLB 1861); N Mazatlán (LACM 6011); 5 mi. N Mazatlán (CSCLB 1846-48); 8 mi. N Mazatlán (CSCLB 1854); 10.3 mi. N Mazatlán (LACM 6006-07); 10.6 mi. N Mazatlán (CSCLB 1864); 11.3 mi. N Mazatlán (LACM 6044); 13.5 mi. N Mazatlán (UAZ 7668); 16.7 mi. N Mazatlán (CSCLB 1867); 20.7 mi. N Mazatlán (JMS osteo. coll.); 22.5 mi. N Mazatlán (LACM 6010); 41 mi. N Mazatlán (LACM 6041); 1.2 mi. W hwy. 15 [ca. 55 mi. N Mazatlán] nr. Río Piaxtla (CSCLB 1863, 1865); 8 km. SSE Rosario (° KU 29888-89); San Ignacio (LACM 6034-37); 1.5 km. ENE San Lorenzo (° KU 48045-71); Teacapán (LACM 6508-14); 9.5 mi. S Tropic of Cancer [on hwy. 15] (CSCLB 1856-58); 9 km. NE Villa Unión (° KU 75199); 12.8 mi. SE Villa Unión (LACM 6038).

Literature records.—Concordia, 400 ft.; 20 mi. N Mazatlán, 150 ft. (Davis and Dixon, 1957b:145); 2 mi. E Mazatlán (Taylor, 1938:508).

Additional records.—23.3 mi. S Caitime (FAS 8588-89); 1.1 mi. E Concordia (CAS 99617-8); 2 mi. N Culiacán (AMNH 59285); 7-8 mi. N Culiacán (FAS 12620); 1 mi. NE El Fuerte (UIMNH 40681-82); 1.3 mi. S Río Elota (CAS 99644-5); West half La Cruz Rd. (CAS 99655); 13 mi. NNE Los Mochis (UIMNH 40654-55); Mazatlán (CAS 95735-39; FMNH 110607, 110610, 110616-17, 110620, 110622-23, 110627, 110629, 110632; UIMNH 31815-21; UMMZ 115392 [6 spec.]); 8.5 mi. N Mazatlán (CAS 99385); 9.6 mi. N Mazatlán (CAS 99393); 9.8 mi. N Mazatlán (CAS 99395-96); 10.7 mi. N Mazatlán (CAS 99400-01); 10.9 mi. N Mazatlán (CAS 99402); 11.0 mi. N Mazatlán (CAS 99403); 12.3 mi. N Mazatlán (CAS 99404); 14.1 mi. N Mazatlán (CAS 99406); 22.1 mi. N Mazatlán (CAS 99413-15); 22.3 mi. N Mazatlán (CAS 99416-17); 22.4 mi. N Mazatlán (CAS 99421-22); 22.7 mi. N Mazatlán (CAS 99424); 22.7-37.4 mi. N Mazatlán (CAS 99425); 43.9 mi.

N Mazatlán (CAS 99426-27); 44.0 mi. N Mazatlán (CAS 99428); 44.6 mi. N Mazatlán (CAS 99429); 61.0 mi. N Mazatlán (CAS 99431); 61.4 mi. N Mazatlán (CAS 99432); 62.9 mi. N Mazatlán (CAS 99433); 63.3 mi. N Mazatlán (CAS 99434); 63.7 mi. N Mazatlán (CAS 99435); 2.5 mi. SE Mazatlán (FAS 7906-09); 10-15 mi. S Mazatlán (FAS 12621); 3.5 mi. NNW Mazatlán, 25 ft. (UMMZ 115393); 11.8 mi. NNW Mazatlán, 150 ft. (UMMZ 115394 [10 spec.]); 15.6 mi. NNW Mazatlán, 200 ft. (UMMZ 115395 [8 spec.]); 18.6 mi. NNW Mazatlán, 200 ft. (UMMZ 115396); 18.6 mi. S Río Presidio (CAS 99690); Rosario (UIMNH 8020).

Family Leptodactylidae

Eleutherodactylus augusti cactorum Taylor

Eleutherodactylus cactorum Taylor, Univ. Kansas Sci. Bull., 25:391, July 10, 1939 (type locality, kilometer 226, 20 miles northwest Tehuacán, Puebla).

Eleutherodactylus augusti cactorum: Zweifel, Amer. Mus. Novitates, 1813:20, December 23, 1956.

Remarks.—In eight specimens the diameter of tympanum is 2.7-4.3 (3.4) and greatest width of head 19.4-32.9 (24.8). The diameter of the tympanum averages 13.6 per cent of the width of the head.

Dark purplish gray color dorsally (in preservative) is one of the diagnostic characters of this subspecies (Zweifel, 1956:20). Of the specimens examined, three collected in the summer of 1963 are purplish gray dorsally; those collected in 1955 and earlier are brown dorsally. All specimens examined by us agree with the description by Zweifel (1956:2-24).

One individual was found in a mine shaft in a corn field, and two were in tropical deciduous forest less than 200 meters from a boulder-strewn stream inhabited by *Hyla smaragdina* and *Syrrophus modestus*. A specimen (LACM 6201) was found on the road following a heavy rain on July 12. The road passes through a hilly area, suggesting that the frogs are inhabitants of rocky canyons and arroyos in the region north of Mazatlán.

Distribution in Sinaloa.—Along the foothills of the Sierra Madre Occidental and in the canyons and arroyos in the southern part of the state. See Fig. 14.

Specimens examined.—8.8 mi. N Coyotitán (LACM 6201); 41 mi. N Mazatlán (LACM 6202); San Ignacio, 210 m. (KU 73813); Santa Lucía, 1100 m. (° KU 75238); 1 km. NE Santa Lucía, 1155 m. (° KU 78253); 2.2 km. NE Santa Lucía, 1155 m. (° KU 78254); 2.4 km. E Santa Lucía (° KU 41552-56).

Literature record.—36 mi. N Mazatlán (Zweifel, 1956:21).

Additional records.—6-7 mi. NE Concordia (UMMZ 123026); 1.5 km. S El Cajón, 750 m. (KU 93465-66).

Eleutherodactylus hobartsmithi Taylor

Eleutherodactylus hobartsmithi Taylor, Trans. Kansas Acad. Sci., 39:355, April 3, 1936 (type locality, "Near Uruapan, Michoacán").

Remarks.—Ten males differ from the original description in having the limbs distinctly barred with dark gray to black; the bars are more conspicuous on the forelimbs. There is no dark line from tip of snout to the eye, the tips of the digits are definitely widened, and the tympanum is distinctly larger (1.7-2.2; mean 1.9) than the eye (1.6-1.8; mean 1.7). In two specimens the testes are white (captured 13 July 1960 and 12 July 1963); in the others the testes are heavily pigmented with black.

In life, the back and legs are orange to orangish brown with an inverted brown "V"-shaped mark between the shoulders, and with brown bands on the legs. The iris is a rose-gold, the belly yellow. The dorsal coloration in life is pinkish gray according to Taylor (1940c:501). Smith (1947:408) reported a frog of this species from "near Aquiapan, México" that possessed vestiges of vomerine teeth. All the specimens examined by us lack any trace of vomerine teeth. The tarsal tubercles are distinct. Reference of this species to *Eleutherodactylus* follows Lynch (1965:3).

Distribution in Sinaloa.—Known only from the southern highlands near Santa Lucía. See Fig. 19.

Specimens examined.—2.4 mi. E Chupaderos (JFC 62:71); Santa Lucía, 1100 m. (° KU 75253-62); 4 mi. W Santa Lucía (JFC 62:4-13).

Additional records.—Santa Lucía, 1100 m. (KU 80324); Highway 40, 24.8 mi. E Junc. Hwy. 15 and 40 (Villa Unión) (CAS 99313, 99315).

Eleutherodactylus occidentalis Taylor

Eleutherodactylus occidentalis Taylor, Proc. Biol. Soc. Washington, 54:91, July 31, 1941 (type locality, Hacienda El Florencio, Zacatecas).

Remarks.—A male (KU 78255) has a snout-vent length of 28 mm., white testicular membranes, first finger longer than second, vomerine teeth, and an inner metatarsal tubercle strongly compressed and cream-colored. This frog, and several others, probably of the same species, called from a deep, dry, thickly wooded ravine during a light rain on July 19. The frogs were clinging horizontally to small twigs of bushes 0.3 to one meter above the ground. The call was a single-note peep emitted at intervals of one to ten minutes. Peters (1954:6) described the call for this species in Michoacán as a piercing whistle of five or six single notes.

Another specimen, a juvenile, was active in wet grass at the edge

of the forest about 10 a. m. This was one of the few Sinaloan frogs exhibiting a diurnal activity period.

Distribution in Sinaloa.—Known only from intermediate elevations in the southern part of the state. See Fig. 15.

Specimens examined.—San Ignacio (LACM 6203); 5 km. SW San Ignacio, 200 m. (* KU 78255).

Literature records.—Plomosas (Kellogg, 1932:111; Smith and Taylor, 1948:62).

Additional records.—7.1 mi. E Concordia (CAS 99622); 9.8 mi. E Concordia (CAS 99613); 15.7 mi. E Concordia (CAS 99610).

Eleutherodactylus vocalis Taylor

Eleutherodactylus vocalis Taylor, Univ. Kansas Sci. Bull., 26:401, pl. 44, Fig. 8, November 27, 1940 (type locality, Hacienda El Sabino, Michoacán); Lynch, Herpetologica, 21:105, June 25, 1965.

Remarks.—According to Taylor (1940a:401) the tibiotarsal articulation reaches to between the eye and the nostril, and the heels do not touch when the limbs are folded. The heels do not touch in 13 of 25 specimens examined from Sinaloa, but of the remaining 12, 11 overlap (KU 41531 excluded). The tibiotarsal articulation reaches to the eye in two, beyond the eye in four, to the snout in 17, and beyond the snout in two. Duellman (1958b:7) obtained similar results for specimens from Colima. Zweifel (1959c:2) reported sexual dimorphism in specimens from Nayarit; the length of tympanum (including ring) divided by width of head was 0.24-0.26 (0.254) in three males and 0.15-0.18 (0.170) in eight females; in these specimens the snout-vent length ranged from 31 to 58 mm. The same ratio for 19 adults (snout-vent lengths of more than 32 mm.) from Sinaloa is 0.16-0.18 (0.169) in four males and 0.16-0.21 (0.177) in 15 females. The tarsal fold is pale in specimens from Colima, but dark in those from Veracruz and Chiapas (Duellman, 1958b:7). Of the 63 specimens examined by us from Nayarit, Jalisco, Oaxaca, Veracruz, and Chiapas, only seven (four from Veracruz and three from Chiapas) have dark tarsal folds. Duellman (1960:56) recorded 15 specimens from a total of 200 that had a pale middorsal stripe. Two of the 25 specimens from Sinaloa have a pale middorsal stripe.

Eleutherodactylus vocalis frequently is found near streams or in rocky canyons. One individual (KU 73812) was found in a small crevice of a mine shaft in the pine-oak forest zone of northern Sinaloa; two other specimens were taken in mines.

Distribution in Sinaloa.—Known from the foothills below 1200 meters in southern Sinaloa and from near Choix in the north. See Fig. 15.

Specimens examined.—16 km. NNE Choix, 520 m. (* KU 73812); 2.4 mi. E Chupaderos (JFC 62:72-73); 1 mi. W Copala (CSCLB 1668-69); 1 mi. E Pánuco (CSCLB 1667); Plomosas, 760 mm. (* KU 73814-16); 0.4 mi. E Potrerillos (JFC 62:14-15); Santa Lucía, 1100 m. (* KU 75251; CSCLB 1671-72); 2.2 km. NE Santa Lucía, 1150 m. (* KU 78256); 2.4 km. E Santa Lucía (KU 44555); 2-3 km. E Santa Lucía (* KU 41530-41, 41558-60, 44556-59); 3 mi. E. Santa Lucía (CSCLB 1670); 5 km. SW Santa Lucía, 660 m. (* KU 80686); 4.0 mi. W Santa Lucía (JFC 62:1-3).

Literature record.—18 mi. NE Concordia (Webb, 1960:289).

Additional records.—10.7 mi. N Concordia (MCZ 32577-79); 1.3 mi. N Santa Lucía (MCZ 32580-81); 24.8 mi. E (by highway 40) Junction highway 15 and 40 (Villa Unión) (CAS 99302-09).

Leptodactylus occidentalis Taylor

Leptodactylus occidentalis Taylor, Trans. Kansas Acad. Sci., 39:349, 1937 (type locality, Tepic, Nayarit).

Remarks.—From *Leptodactylus melanonotus*, *L. occidentalis* usually differs as follows: head narrower at eye level; tympanum smaller; throat and chest lightly pigmented with black and dark brown (instead of heavily pigmented with dark gray); ventral glands dark brown or black, sharply defined, absent from the throat, and absent or reduced on the mid-ventral surface. A re-evaluation of the importance of these characters is considered necessary, especially with reference to the ventral glands.

Duellman (1961:32) suggested that size might be another valid character for separating these two species. The average snout-vent length in samples of adult males from Sinaloa (16), Veracruz (5), Campeche (9), Guatemala (8), Nicaragua (10), Costa Rica (21), and Panama (9) varied from 32 to 36 mm. No geographic trend in size was noticed.

Three specimens (LACM 6207, 6221, 6222) from the southern lowlands are intermediate between the two nominal species in the position and color of the ventral glands. Duellman (1961:33) mentioned *L. melanonotus* from Acajoneta, Nayarit. If he is correct in the allocation of the Acajoneta frogs, then it is possible that populations of *Leptodactylus* from southern Sinaloa are intermediate between the two recognized species. Because of the lack of material from the critical region, we refer all *Leptodactylus* from Sinaloa to *L. occidentalis*.

During the dry season individuals were found beneath rocks along streams, near wells, and in moist canyons. In the rainy

season specimens were collected wherever there was sufficient water. During the breeding season males were heard calling from flooded fields, roadside ponds, rocky streams in arroyos, and temporary rain ponds. Males usually call from deep grass around the pond, sometimes concealed beneath debris. Foam nests were found in mid-July near San Ignacio. The nests were concealed in deep grass in a field flooded by one to two inches of water.

Distribution in Sinaloa.—*Leptodactylus occidentalis* occurs throughout Sinaloa below about 700 meters. See Fig. 16.

Specimens examined.—1 mi. N Ahome, Río Fuerte (UAZ 10896); 8 km. N Carrizalejo, 460 m. (* KU 78033-34); 16 km. NNE Choix, 520 m. (* KU 73819); 1 km. S Concepción, 75 m. (* KU 63664-74); Coyotitán (JFC 62: 18-26); Culiacán (CSCLB 1572-77); 51 km. SSE Culiacán (* KU 37810-11); 6 km. NE El Fuerte, 150 m. (* KU 78029-31); 6 mi. N (by hwy. 15) Río Elota (CSCLB 6220); 10 mi. S Espinal (CSCLB 6771); 12.5 mi. N Guamúchil (CSCLB 1738-47); 19.2 mi. N Guasave (CSCLB 1748-50); 7 mi. SE Guasave (CSCLB 1584); Isla Palmito de la Virgen, 5 m. (* KU 73820); 10 mi. E La Cruz (CSCLB 6219); 1.3 mi. S (on hwy. 15) La Cruz turnoff (JFC 62:30-38); 3.1 mi. N Los Mochis (JFC 62:59-69); 5 km. N Los Mochis (* KU 73830-34); 0.5 mi. NE Los Mochis turnoff [on hwy. 15] (UAZ 8161-66); E Los Mochis (CSCLB 1579-83); 6 km. W Los Mochis, 2 m. (* KU 78032); 7.3 km. SW Matatán, 155m. (* KU 78259-61); Mazatlán (CSCLB 1590-93; SDSC 1773; UAZ 8153-60); 3.3 mi. N Mazatlán (UAZ 8169); 2.3 mi. E, 1 mi. N Mazatlán (UAZ 8170); 2.6 mi. NW Mazatlán (UAZ 8167-68); 14.2 mi. WNW (by rd.) Pericos turnoff (on hwy. 15), Rancho de los Pocitos (UAZ 8125-52); Rosario, 150 m. (* KU 73822); 4 mi. N San Blas, 400 ft. (JRM 1112-18); 3.6 mi. SW San Blas (CSCLB 1585); San Ignacio, 215 m. (* KU 73823-29; LACM 6208-14, 6216-18); 10.2 mi. W (by rd.) San Miguel (on rd. to Higueras) (UAZ 10902); Teacapán (LACM 6221, 6223-26); Highway 15 at Tecuala turnoff [Nayarit] (LACM 6222); Villa Unión, 15 m. (* KU 67957, 73821, 78263-66); 8 km. N Villa Unión, 135 m. (* KU 80687); 10 km. N Villa Unión (* KU 78262); 8.4 mi. NE Villa Unión (LACM 6205-07); 13 km. ENE Villa Unión, 60 m. (* KU 67956); 3 km. W Villa Unión (* KU 29901-07).

Literature records.—Chele (Duellman, 1961:33); Costa Rica (Smith and Van Gelder, 1955:145); Culiacán (Duellman, 1961:33); El Dorado (Fugler and Dixon, 1961:8); Mazatlán (Smith and Taylor, 1948:56); nr. Mazatlán (Kellogg, 1932:89; Taylor, 1938:514); 1-2 mi. E Mazatlán (Taylor, 1937:349); Presidio (Kellogg, 1932:89); 10 mi. S Presidio (Taylor, 1937:349); Rosario (Duellman, 1961:33).

Additional records.—N. Bank Río Baluarte, 3 mi. N bridge (CAS 99265-85); 11 mi. NE Concordia (SM 10095, 10287-88, 12113); 12 mi. NE Concordia (SM 10071, 10073-79, 10081-84); Culiacán (AMNH 58382-402, 64176-77 + 27 spec. untagged); 10 mi. N Culiacán (FAS 10073); 19 mi. NW Culiacán (AMNH 68050-51); 1 mi. NE El Fuerte (FMNH 71374-441); N Los Mochis, Río Fuerte and hwy. 15 (AMNH 64174-75); 3.3 mi. N. Los Mochis (UF 12863); 15 mi. N Los Mochis (SM 10667-72); 6 mi. S Los Mochis (SDSNH 19891); Mazatlán (MCZ 44301; USNM 147966-79); N Mazatlán (AMNH 12591-600, 13235-46); E Mazatlán (UIMNH 7801); 22 mi. N Mazatlán (AMNH 68052; CAS 99412; FAS 7808-11; SM 10094); 36 mi. N Mazatlán (FAS 9594; UIMNH 38159); 1-2 mi. E Mazatlán (UIMNH 29700); 1.3 mi. W, 2.5 mi. N. Mazatlán (FAS 9049); 10.2-10.8 mi. SE Navolato (CAS 99660-79); Piaxtla (AMNH 71417); 9 mi. NW Piaxtla (SM 10673-77); Rosario (UIMNH 7791-96, 7802-04, 62645-47); 11 mi. NE Rosario, Río Baluarte (UMMZ 113062 [2 spec.]); 3 mi. E San Pedro, 550 ft. (KU 93467); 3 mi. SE Villa Unión (SM 10678).

Syrrophus interorbitalis Langebartel and Shannon

Syrrophus interorbitalis Langebartel and Shannon, *Herpetologica*, 12:161, September 1, 1956 [type locality, 36 miles north of Mazatlán (center of city), Sinaloa].

Remarks.—This species has been collected along a rocky creek bed in tropical deciduous forest (Langebartel and Shannon, 1956:161), and in a crack of a granite boulder “on a densely vegetated rocky road shoulder” (Campbell and Simmons, 1962:194). Campbell and Simmons reported hearing calls that could have been from this species from an area north of Culiacán (probably tropical semiarid forest) to south of Mazatlán. Duellman (1958c:10) suggested that this species occurs along the lowlands of Sinaloa, possibly into southern Sonora.

Distribution in Sinaloa.—Known only from the central lowlands. See Fig. 17.

Specimen examined.—7.1 mi. S (by rd.) Guamúchil (UAZ 8232).

Literature record.—65 mi. N Mazatlán (Campbell and Simmons, 1962:194).

Syrrophus modestus Taylor

Syrrophus modestus Taylor, *Univ. Kansas Sci. Bull.*, 28:304, November 12, 1942 (type locality, Hacienda Paso del Río, Colima).

Remarks.—Duellman (1958c:6-7) described *Syrrophus modestus pallidus* in Nayarit as having, in life, a pale tan ground color (“light-gray ground color,” p. 5) and interconnecting dark brown spots dorsally, grayish white belly, white vocal sac, and a dark golden iris. In contrast, *S. m. modestus* in Colima has a red-rust ground color with scattered irregular black spots above, a pale gray belly, and a golden iris. Zweifel (1960:93-94) recorded *S. m. pallidus* from the Tres Mariás Islands as being golden brown above with spots darker and browner than ground color and some grayish patches, pale belly and brownish throat.

Specimens from Sinaloa (KU 75263-72, 78527-28) differ from the above descriptions in having an orange to pale grayish golden ground color above, and dark brown spots or reticulations that become darker anteriorly. In life, the thighs were orange with brown blotches dorsally and white ventrally; the belly was grayish white in the groin, fading to brownish black on chest and throat; the iris was silver-gold to gold color with a pinkish and a pale greenish tint. Three of 12 frogs from Sinaloa have dark throats, which, as seen under high magnification, result from expanded melanophores. These are present also, but contracted, in the white-throated frogs.

Examination of 42 specimens (in alcohol) of *Syrrophus* from

Sinaloa and Nayarit indicate a wide range of variation in color and pattern. The dorsal ground color varies from pale brown or tan to dark brown or gray-brown. Dorsal mottling is variable; some specimens lack distinct dorsal pattern but have a few dark brown flecks laterally; others show all degrees of pattern from fine brown or dark brown mottling to individuals with large distinct reticulations. No specimens have an interorbital bar. All show some brown mottling on arms and legs, tending to form distinct bands in many individuals. None of the differences in pattern and color in the preserved material could be attributed to geographic variation. It is suspected that much of this color variation can be attributed to the various methods of preservation. There is also considerable variation in the size of the metatarsal tubercles. Because of the lack of detailed color notes from living individuals over a wide geographic range of the species and the variation present in the preserved material, we refrain from assigning the Sinaloan population to a subspecific status.

Distribution in Sinaloa.—Known from several localities along the Concordia-Santa Lucía road. See Fig. 17.

Specimens examined.—3 mi. NE Copala (RGW 3056-57); 1 mi. NE Copala (RGW 3670); 3.4 mi. NE Concordia (CSCLB 620-23); Santa Lucía, 1100 m. (* KU 75263-72); 1 km. NE Santa Lucía, 1150 m. (* KU 78257); 1 km. NE Santa Lucía (CSCLB 1712-14); 2.2 km. NE Santa Lucía, 1150 m. (* KU 78258); 16.9 mi. W Santa Rita (LACM 6234-35); 19.6 mi. NE (by road) Villa Unión (LACM 6233); 47.2 mi. NE Villa Unión (CSCLB 624).

Additional records.—5 mi. E Copala (CAS 91939-55); Santa Lucía, 1100 m. (KU 80320).

Tomodactylus nitidus petersi Duellman

Tomodactylus petersi Duellman, Occas. Papers Mus. Zool., Univ. Michigan, 560:5, October 22, 1954 (type locality, one fourth mile east of Coalcomán, Michoacán).

Tomodactylus nitidus petersi: Dixon, Texas Jour. Sci., 9:390, December 4, 1957.

Remarks.—Specimens of *Tomodactylus nitidus petersi* from the eastern Sinaloan highlands are melanistic and agree in all characteristics with those examined by Dixon (1957b:385). Webb and Baker (1962:330) recorded this subspecies from mixed boreal—tropical forest in Durango.

Distribution in Sinaloa.—Known only from the southern highlands. See Fig. 18.

Specimens examined.—0.5 km. S Santa Lucía (CSCLB 1719); 0.9 mi. W Santa Rita (LACM 6236); 1.2 mi. W Santa Rita (LACM 6238); 3.5 mi. W Santa Rita (LACM 6237); 47.2 mi. NE Villa Unión (CSCLB 1718).

Literature records.—49 mi. NE Concordia, 4800 ft. (Dixon, 1957a:64); "mountains of eastern Sinaloa," 5600 ft. (Dixon, 1957b:385).

Tomodactylus saxatilis Webb

Tomodactylus saxatilis Webb, Univ. Kansas Publ., Mus. Nat. Hist., 15:177, 1 fig., March 7, 1962 (type locality, eight miles west of El Palmito, Sinaloa, approx. 6100 feet).

Remarks.—This frog occurs in the lower montane dry forest of southeastern Sinaloa. It has been recorded also in mixed boreal—tropical forest near Pueblo Nuevo in Durango (Webb and Baker, 1962:330).

Distribution in Sinaloa.—Known only from the type locality. See Fig. 19.

Specimens examined.—8 mi. W El Palmito [Durango] (KU 63326 holotype, KU 63327-33 paratypes).

Family Bufonidae

Bufo alvarius Girard

Bufo alvarius Girard, in Baird, Report on the United States and Mexican Boundary Survey, 2:26, pl. 41, Figs. 1-6, 1859 (type locality, valley of the Gila and Colorado rivers).

Remarks.—Two adult specimens of *Bufo alvarius* are olive drab dorsally with yellowish cream venters. Glands are present on fore and hind limbs. A female with egg-filled ovaries has a snout-vent length of 150 and a male has snout-vent length of 144. The increase of favorable habitats created by cultivation probably has aided the dispersal of this species in Sinaloa.

Distribution in Sinaloa.—*Bufo alvarius* occurs in the lowland tropical thorn forest of northern Sinaloa. See Fig. 17.

Specimens examined.—10 km. ESE Guasave (° KU 43571-72); 5.4 mi. SW San Blas (CSCLB 1771).

Literature records.—7 mi. W Guamúchil (Riemer, 1955:17); 24 mi. N Los Mochis, 50 ft.; 35-45 mi. N Los Mochis, 100 ft. (Davis and Dixon, 1957b:145).

Additional record.—20 mi. N Culiacán (FAS 12611) [needs verification].

Bufo kelloggi Taylor

Bufo kelloggi Taylor, Univ. Kansas Sci. Bull., 24:510, February 16, 1938 (type locality, two miles east of Mazatlán, Sinaloa).

Remarks.—The snout-vent lengths for 12 females of *Bufo kelloggi* are 33.6-48.8 (38.8), and for 29 males are 28.4-40.1 (35.1).

Specimens were first encountered on July 12 near La Cruz during a light rain. Several large choruses were found in late August between Espinal and the Río Elota. Calling males were first heard in mid-August, suggesting that the species breeds later in the rainy season than most of the other species in the state. Males usually call out of water, often perched on small islands in a pond.

Distribution in Sinaloa.—*Bufo kelloggi* occurs throughout the coastal lowlands below 200 meters. See Fig. 19.

Specimens examined.—16 km. NW Acaponeta (Nayarit) (° KU 60472); 4.7 mi. NE Concordia (CSCLB 1734-35); 20 mi. N. Culiacán (LACM 6077-82); 32 km. N Culiacán (° KU 73777-87); 12 mi. N (on hwy. 15) Río Elota (LACM 6071-76); 15.4 mi. N (on hwy. 15) Río Elota (LACM 6052); 32.5 mi. SE Guamúchil (CSCLB 1737); Isla Palmito de la Virgen, 5 m. (° KU 73776); 1-3 mi. E La Cruz (LACM 6065-70); 5 mi. E La Cruz (LACM 6053-64); 39 km. N Los Mochis (° KU 60473-79); 18.4 mi. NW Los Mochis turnoff (on hwy. 15) (UAZ 11487); 20.7 mi. NW Los Mochis turnoff (on hwy. 15) (UAZ 11493-94); Mazatlán (CSCLB 1736); 3 mi. N Mazatlán (UAZ 11490); 5 mi. N Mazatlán (CSCLB 1733); 5.4 mi. SE Mazatlán (UAZ 11489); 2.5 mi. NW Mazatlán (UAZ 11488, 11491-92, 13796-80); Villa Unión (° KU 75205-24); 3.7 km. E Villa Unión, 30 m. (° KU 78267).

Literature records.—13-35 m. N Culiacán; 33 mi. SE Escuinapa (Bogert, 1962:34); 4-33 mi. SE Escuinapa, 50 ft. (Davis and Dixon, 1957b:145); 13 mi. N Los Mochis (Bogert, 1962:34); 24 mi. N Los Mochis (Davis and Dixon, 1957b:145); 13 mi. NE Los Mochis (Smith and Chrapliwy, 1958:267); Mazatlán (Kellogg, 1932:53; Taylor, 1938:510); 2 mi. N Mazatlán; 6 mi. S Mazatlán; 6 mi. SW San Blas (Bogert, 1962:34).

Additional records.—Copala (CAS 89758-59); 2.4 mi. N. Escuinapa (CAS 99600); 0.9 mi. E La Cruz (CAS 99646); Mazatlán (FMNH 100717-18; UIMNH 39729); 27.9 mi. N Mazatlán (UF 12859); 36 mi. N Mazatlán (UIMNH 39475); 2 mi. E Mazatlán (UIMNH 23450-59; USNM 134258); 15.6 mi. NNW Mazatlán, 200 ft. (UMMZ 115347 [2 spec.]).

Bufo marinus (Linnaeus)

Rana marina Linnaeus, *Sistema naturae*, ed. 10, 1:211, 1758 (based on a specimen from America).

Bufo marinus: Schneider, *Historias amphibiarum naturalis et literariae*, 1:219, 1799.

Remarks.—*Bufo marinus* is common throughout the lowlands of Sinaloa. Taylor (1938:508) found one specimen under a board on the sandy beach of the Río Mazatlán near Presidio. In the dry season individuals congregate along streams and irrigation ditches. Bogert and Oliver (1945:340) found hibernating toads under boulders along the river [Río Culiacán?] at Culiacán. Large numbers of juvenile toads (snout-vent length approximately 20) were observed on the rocky shore of the Río Fuerte in June, up to 150 meters from the water.

Small young are easily identified by the presence of a white spot on the upper jaw just below the eye, an enlarged triangular parotoid gland, the presence of a row of warts (sometimes connected) extending from the posterior tip of the parotoid gland along the side of the body, and the presence of a prominent tarsal fold. The white spot is absent in some toads measuring more than 100 mm. in snout-vent length, but the parotoid gland and lateral row of warts usually are more distinct in larger toads. These large ubiquitous toads were observed several times in towns and villages

sitting beneath street lights or in patios of cafes and houses, eating the myriad of insects attracted to the lights. Males were heard calling along the Río Piaxtla at La Cruz on July 1 after a heavy rain had flooded the river. On August 16, several hundred individuals were found dead on the road about 28 miles north Mazatlán. Evidently a large flooded field to the east of the road had served as a breeding pond.

Distribution in Sinaloa.—*Bufo marinus* occurs throughout the lowlands of Sinaloa up to elevations of about 500 meters. See Fig. 20.

Specimens examined.—Aguaje (UCLA 14833); nr. Concepción (LACM 6097); Concordia (° KU 78278; UNM 9981-97); 4.5 mi. NE Concordia (UAZ 11564, 14380); 8 km. E. Concordia (° KU 78279); 6 km. E. Cosalá, 460 m. (° KU 73789); N Culiacán (CSCLB 1767-68); 51 km. SSE Culiacán (° KU 37742); 79.6 mi. S Culiacán (UAZ 12331-32); 6 km. NE El Fuerte, 150 m. (° KU 78040-69); 8 km. NE El Fuerte, Río Fuerte, 160 m. (° KU 78070-78); Elota (° KU 78270); 18 km. NE Elota (° KU 62250); Escuinapa (LACM 8622-23); 2 mi. N Higuera (UAZ 11079, 11579); 5 mi. NE La Cruz (LACM 6085); 1-3 mi. E La Cruz (LACM 6092-96); 5 km. N Los Mochis (° KU 73795); 8 km. N Los Mochis (PR 530); 4 mi. NE Los Mochis (UAZ 9450); 7.3 km. SW Matatán, 155 m. (° KU 78269, 78280); Mazatlán (UAZ 11562); 7.2 mi. N Mazatlán (UAZ 11531-32); 12.5 mi. N Mazatlán (UAZ 11533); 55 mi. N Mazatlán, Río Piaxtla (CSCLB 1769-70); 5.3-11.7 mi. SE Mazatlán (UAZ 11556); 1 mi. W Pánuco (CSCLB 2459-60), 1 mi. W highway 15 along Río Piaxtla (CSCLB 2464); Rancho Huanacastle (LACM 6100-16); 7 km. N Rosario (° KU 29863); 10.3 mi. SW San Blas (CSCLB 1766); San Ignacio (LACM 6089-91); 1 mi. S. San Ignacio (LACM 6086-88); San Miguel, Río Fuerte, 115 m. (° KU 44532-35); Río Sinaloa (LACM 6117-28); 5 km. NE Trancas (° KU 78271-75); Villa Unión (° KU 62249, 78281); 1 km. NE Villa Unión (° KU 75225-30); 24.7 mi. NE Villa Unión (CSCLB 1764-65); 3.7 km. E Villa Unión, 30 m. (° KU 78276-77); 7.8 mi. E (by hwy 40) Villa Unión (LACM 6099); 12.4 mi. E (by hwy. 40) Villa Unión (LACM 6098).

Literature records.—Culiacán, Río Culiacán (Bogert and Oliver, 1945:340); Mazatlán (Smith and Taylor, 1948:42); Presidio (Taylor, 1938:508).

Additional records.—11 mi. NE Concordia (SM 10282-86); 18.0 mi. E Concordia (CAS 99626); 2 mi. ENE Copala, 1400 ft. (TCWC 12291); nr. Coyotitán (AMNH 67930-31); Culiacán (AMNH 43900-03); 18.5 mi. E Culiacán, arroyo de Soualoua (UMMZ 113091-94 [4 spec.]); El Dorado (LUS 7840); 1 mi. NE El Fuerte (UIMNH 40689-90); Elota (AMNH 43879, 43890-94); N Los Mochis, Río Fuerte at hwy. 15 (AMNH 64219); 15 mi. N Los Mochis (SM 10828-30); 49 mi. NNW Mazatlán, nr. Río Piaxtla (AMNH 67932); Palmar de Sepúlveda (UMMZ 123851); 9 mi. W Piaxtla (SM 10742); 9 mi. NW Piaxtla (SM 10825-27); Rosario (UIMNH 7516, 7519-36, 62526-31); 3 mi. SE Rosario (UIMNH 7544-45); 24.8 mi. E hwy. 15 [Villa Unión] on hwy 40 (CAS 99316-17).

Bufo marmoratus Wiegmann

Bufo marmoratus Wiegmann, Isis von Oken, 26:66, 1833 (based on a specimen from Veracruz, Veracruz).

Remarks.—Examples of *Bufo marmoratus* from Sinaloa have curved to slightly angled supraorbital and postorbital crests. The pale-colored, diagonal lateral stripe of females and the concentra-

tion of tubercles in a broad band on the back of males are present in the Sinaloan toads examined. The males may have a narrow middorsal line or none at all.

Nearly all specimens were found on the road at night during or just after a rain. Most females were taken in the first two weeks of July and contained eggs. No males were heard vocalizing nor were any amplexing pairs seen.

Distribution in Sinaloa.—Although much more common in the southern part of the state, *Bufo marmoratus* occurs throughout the lowlands up to 400 meters. See Fig. 21.

Specimens examined.—Chupaderos (CSCLB 1840); 2 mi. W Chupaderos (CSCLB 1841); 3 mi. W Chupaderos (CSCLB 1842); 4 mi. W Chupaderos (CSCLB 1843); 4.5 mi. NE Concordia (LACM 6129); 4.7 mi. NE Concordia (CSCLB 1783-84); 29.2 mi. NW Culiacán (LACM 6136); 54 mi. SE Culiacán (UAZ 11630-31, 11782); 51 km. SSE Culiacán (° KU 37644); 13.4 mi. N (hwy. 15) Río Elota (LACM 6137); 0.5 mi. S Espinal (CSCLB 1778-79); 3 mi. S Espinal (CSCLB 1780); Matatán, 170 m. (° KU 73796); 55 mi. N Mazatlán, Río Piaxtla (CSCLB 1785, 1844-45); 4 mi. N San Blas, 400 ft. (JRM 1125); San Ignacio, 210 m. (° KU 73797-98; LACM 6130, 6132-33); 6.8 mi. N (on hwy. 15) turnoff to San Ignacio (LACM 6131); 16 mi. N (on hwy. 15) turnoff to San Ignacio (LACM 6134-35); 2 km. ENE San Lorenzo (° KU 47925-44); 24.7 mi. NE Villa Unión (CSCLB 1772-77); 26 mi. NE Villa Unión (CSCLB 1781-82).

Literature records.—Mazatlán (Kellogg 1932:60; Martín del Campo, 1941:760; Smith and Taylor, 1948:45); Rosario (Kellogg, 1932:60; Smith and Taylor, 1948:45).

Additional records.—7.8 mi. S Río Bahuarte (CAS 99627-28); 7-8 mi. N Culiacán (FAS 12531); 63-68 mi. S Culiacán (FAS 12793); 16-18 mi. NW Culiacán (AMNH 67944-45); 78 mi. N Mazatlán (CAS 99436); 49 mi. NNW Mazatlán, nr. Río Piaxtla (AMNH 67946-47); Rosario (UIMNH 62582-85); 3 mi. SE Rosario (UIMNH 7546-50); Villa Unión, Río Presidio (UMMZ 102620).

***Bufo mazatlanensis* Taylor**

Bufo mazatlanensis Taylor, Univ. Kansas Sci. Bull., 26:492, November 27, 1940 (type locality, two miles east of Mazatlán, Sinaloa).

Remarks.—See Zweifel (1960:93) for a brief summary of the taxonomy of *Bufo mazatlanensis*. It is variable in dorsal coloration and tubercle size throughout its range, but no detailed study of geographic variation has been completed.

Specimens were taken in both the wet and dry seasons. Calling males were found on July 29, in roadside ponds north of Mazatlán. The males usually call from the bank of the pond at the water's edge. A few females were collected on the road that same night but none were noted near the water. The first amplexing pair was collected about 8 days later near Villa Unión. Choruses were heard throughout July and August and amplexing pairs were observed as

late as August 16. The breeding season probably continues through the remainder of the rainy season.

Distribution in Sinaloa.—Common throughout, below an elevation of about 1000 meters. See Fig. 22.

Specimens examined.—Aguapepe (CAS 89955-57); 1 mi. NE Ahome, S Río Fuerte (UAZ 10893); 1.5 km. SE Camino Real, Río Piaxtla (° KU 63658); 8 km. N Carrizalejo, 460 m. (° KU 78097); 0.2 mi. W Chupaderos (CSCLB 1826-27); 1 km. S Concepción, 75 m. (° KU 63657); Concordia (° KU 78289-92); 4.3 mi. NE Concordia (CSCLB 1838); 4.5 mi. NE Concordia (LACM 6156-57; UAZ 11758); 4.7 mi. NE Concordia (CSCLB 1815-16); 9.4 mi. NE Concordia (CSCLB 1837); 27.2 mi. NE Concordia (CSCLB 1821-22); 3.5 mi. E Coyotitán (LACM 6165) 2.1 mi. N. Culiacán (CSCLB 1834); 14 mi. N Culiacán (CSCLB 1874); 1.3 mi. NE Culiacán (CSCLB 1871-73); 39-40 mi. SE Culiacán (UAZ 14368-69); 54.4 mi. SE Culiacán (UAZ 11699, 11748-54, 11756, 11758, 11763-64); 54 km. SSE Culiacán (° KU 37638-43, 37741); 2 mi. S Culiacán (LACM 25415); 7.5 mi. S Culiacán (LACM 6175); 7.6 mi. S Culiacán (LACM 6176); 18.8 mi. S Culiacán (LACM 6177); 2 km. S El Dorado, 6 m. (° KU 73801); 8 km. N El Fuerte, Río Fuerte, 160 m. (° KU 78079-81); 12 mi. N El Fuerte (CSCLB 1823-24); 6 km. NE El Fuerte, 150 m. (° KU 78082-96, 78098-116, 78282-86); Elota (° KU 78287); 12.6 mi. SE Escuinapa (UAZ 11803); 59 km. S Escuinapa (° KU 73799-800); Guamúchil (UCLA 14808, 14828-30); 8 mi. NW Guamúchil (CSCLB 1832); 10 km. SSE Cuasave (° KU 41365-69); Isla Palmito de la Virgen (° KU 73802); 1-3 mi. E La Cruz (LACM 6166-68); 5 mi. E La Cruz (LACM 6170-72); 1 mi. E Los Mochis (CSCLB 1814, 1833); 7.9 mi. NW Los Mochis turnoff (on hwy. 15) (UAZ 11688-92); 9.9 mi. NW Los Mochis turnoff (on hwy. 15) (UAZ 11667-87, 11701-17); 11.7 mi. N Los Mochis turnoff (on hwy. 15) (UAZ 9460-61, 9465); Matatán, 165 m. (° KU 73804); Mazatlán (° KU 33936; SDSC 1766-69); Mazatlán, beachroad (UAZ 14384); 1.1 mi. N Mazatlán (CSCLB 1835); 1.9-5.7 mi. N Mazatlán (UAZ 11785-86, 11797); 2.5 mi. N Mazatlán (UAZ 11628, 11798); 4.3 mi. N Mazatlán (LACM 6150-54); 5.5 mi. N Mazatlán (LACM 6141); 6.7 mi. N Mazatlán (UAZ 11787-88); 7 mi. N Mazatlán (CSCLB 1831; LACM 6142); 8 mi. N Mazatlán (UAZ 11790, 11792-94, 11799, 11800); 8.3 mi. N Mazatlán (LACM 6143-44); 9 mi. N Mazatlán (LACM 6145); 10.9 mi. N Mazatlán (CSCLB 1789-92); 11 mi. N Mazatlán (UAZ 11696-98, 11789, 11791); 12.5 mi. N Mazatlán (UAZ 11795-96); 13.8 mi. N Mazatlán (UAZ 11718-31); 14.9 mi. N Mazatlán (UAZ 11700); 16 mi. N Mazatlán (LACM 6138); 17.7 mi. N Mazatlán (LACM 6149); 18.1 mi. N Mazatlán (LACM 6146); 20.4 mi. N Mazatlán (LACM 6148); 27 mi. N Mazatlán (LACM 6180-82); 27.1 mi. N Mazatlán (LACM 6147); 30 mi. N Mazatlán (UAZ 11757); 55 mi. N Mazatlán (CSCLB 1817-20, 1828-30); 5.3-11.7 mi. SE Mazatlán (UAZ 11693-95); 5.4 mi. SE Mazatlán (UAZ 11759); 1 mi. NW Mazatlán (LACM 6174); 0.6 mi. N [on hwy. 15] Nayarit state line (CSCLB 1793-1813); 1 mi. N Palmillas (LACM 25414); 8 mi. S Palmillas (LACM 25412-13); 14.2 mi. WNW Pericos, Rancho de los Pocitos, ca. 50 ft. (UAZ 14386); Rosario, 150 m. (° KU 73803); 8 km. SSE Rosario (° KU 29809-10); 4 mi. N San Blas, 400 ft. (JRM 1126-28, 1135); San Ignacio (LACM 6169); 1.5 km. ENE San Lorenzo (° KU 47907-13); San Miguel, Río Fuerte (° KU 44538-43); 0.6 mi. W Santa Lucía (LACM 6179); Teacapán (LACM 6183-94); 15.2 mi. N Terreros (LACM 6173); 5 km. NE [Las] Trancas (° KU 78288); 9.5 mi. S [on hwy. 15] Tropic of Cancer (CSCLB 1836); nr. Tropic of Cancer [on hwy. 15] (CSCLB 1825); Villa Unión (° KU 29808, 29832); 4 mi. NE Villa Unión (LACM 6155); 7.4 mi. NE Villa Unión (LACM 6158); 9.4 mi. NE Villa Unión (LACM 6159); 12.8 mi. SE Villa Unión (LACM 6163-64); 13 mi. SE Villa Unión (LACM 6162); 16.3 mi. SE Villa Unión (LACM 6160-61); 1.5 km. NW Villa Unión, 15 m. (° KU 68712).

Literature records.—10 mi. W Concordia; Costa Rica (Porter, 1964:240); Costa Rica (Smith and Van Gelder, 1955:145); Coyotitán; 2 mi. N, 5 mi. N, 5 mi. S, 16-18 mi. NW Culiacán (Porter, 1964:240); El Dorado (Fugler and

Dixon, 1961:8; Porter, 1964:240); 1 mi. NE El Fuerte; 5 mi. N, 7 mi. N, 9 mi. N, 29 mi. N El Quelito; Escuinapa; 3 mi. SE, 18 mi. SE, 26 mi. SE Escuinapa (Porter, 1964:240); 7 mi. W Guamúchil (Riemer, 1955:20); Guasave; Los Mochis; 10, 11, 13 mi. N Los Mochis (Porter, 1964:240); Mazatlán (Smith and Taylor, 1948:44; Langebartel and Smith, 1954:126; Porter, 1964:240); 3, 10, 13, 15-20, 39 mi. N, 2 mi. E, 2 mi. NW, 3.5 mi. NNW Mazatlán (Porter, 1964:240); 5-11 mi. N Mazatlán (Riemer, 1955:20); Rosario (Langebartel and Smith, 1954:126); 3 mi. SE Rosario; 2 mi. SE San Lorenzo (Porter, 1964:240); 1 mi. SE Villa Unión; 2 mi. W. Villa Unión (Porter, 1964:241).

Additional records.—N bank Río Baluarte, 3 mi. N of bridge (CAS 99289-301); 11.1 mi. S Río Baluarte (CAS 99445); 4.5 mi. S Caitime (FAS 8587); 0.2 mi. S Río Cañas (CAS 99634-35); Concordia, 400 ft. (TCWC 12480-83); 10.1 mi. E Concordia (CAS 99612); 11 mi. NE Concordia (SM 10686-94); 16.3 mi. E Concordia (CAS 99609); 17.0 mi. E Concordia (CAS 99607); 17.1 mi. E Concordia (CAS 99606); 17.4 mi. E Concordia (CAS 99605); nr. Coyotitán (AMNH 67948-64); 2 mi. N Culiacán (AMNH 59245); 53.4 mi. N Culiacán (FAS 14195); 3 mi. S Culiacán (UF 17120); 5 mi. S Culiacán (AMNH 60442); 40-45 mi. S Culiacán (FAS 14576); 16-18 mi. NW Culiacán (AMNH 67965-66); 1.3 mi. N El Dorado (CAS 99657); 1.6 mi. N El Dorado (CAS 99658); 10 mi. N El Dorado (SM 10831); 1.3 mi. S Río Elota (CAS 99636-43); 2.4 mi. N Escuinapa (CAS 99600); 5.1 mi. N Escuinapa (CAS 99602); 7.8 mi. N Escuinapa (CAS 99603); 11.8 mi. N Escuinapa (CAS 99604); 7 mi. NW Escuinapa (SM 10889-95); 0.2 mi. S Escuinapa (CAS 99446-47); 3.1 mi. S Escuinapa (CAS 99448); 4.4 mi. S Escuinapa (CAS 99449); 9.9 mi. S Escuinapa (CAS 99450); 17.9 mi. S Escuinapa (CAS 99451); nr. Guasave, Río Sinaloa (AMNH 64225, 67967-69); E Guasave (FAS 11666); 1 mi. E Guasave (FAS 11658); west half La Cruz rd. (CAS 99647-52); Los Mochis (CAS 99439-40; FAS 14112); N Los Mochis, Río Fuerte at hwy. 15 (AMNH 64220-24); 15 mi. N Los Mochis (SM 10880-84); 11 mi. NE Los Mochis (UIMNH 40617); 13 mi. NE Los Mochis (UIMNH 40607-16); nr. Madero (UMMZ 102632-33); Mazatlán (CAS 99599; MCZ 44288-89, 45681); N Mazatlán (AMNH 13253); 1 mi. N Mazatlán (SM 10695); 3 mi. N Mazatlán (AMNH 59244; SDSNH 19894-903); 6.7 mi. N Mazatlán (CAS 99381); 8.2 mi. N Mazatlán (CAS 99382); 8.3 mi. N Mazatlán (CAS 99383); 8.4 mi. N Mazatlán (CAS 99384); 8.5 mi. N Mazatlán (CAS 99386); 8.6 mi. N Mazatlán (CAS 99387); 8.8 mi. N Mazatlán (CAS 99388-91); 9.0 mi. N Mazatlán (CAS 99392); 9.6 mi. N Mazatlán (CAS 99394); 10.3 mi. N Mazatlán (CAS 99397); 12.3-14.1 mi. N Mazatlán (CAS 99405); 20.6 mi. N Mazatlán (CAS 99407); 21.5 mi. N Mazatlán (CAS 99408); 21.8 mi. N Mazatlán (CAS 99409-10); 21.9 mi. N Mazatlán (CAS 99411); 22.4 mi. N Mazatlán (CAS 99418-20); 22.6 mi. N Mazatlán (CAS 99423); 61.0 mi. N Mazatlán (CAS 99430); 78.2 mi. N Mazatlán (CAS 99438); 4 mi. NE Mazatlán (SM 9752); 2 mi. E Mazatlán, 50 ft. (TCWC 12479); 2.3 mi. E Mazatlán (FAS 7905); 2.3 mi. N, 1.5 mi. W Mazatlán (FAS 8581); 49 mi. NNW Mazatlán, nr. Río Piaxtla (AMNH 67970-72); 10.2-10.8 mi. SE Navolato (CAS 99681-82); 9 mi. NW Piaxtla (SM 10832-37, 10885-86); 12.4 mi. S Río Presidio (CAS 99441); 33.8 mi. S Río Presidio (CAS 99442); Rosario (USNM 46942-46, 47446); 8 mi. NW Rosario (SM 10896-99); Villa Unión (AMNH 72639); 24.8 mi. E hwy 15, Villa Unión (CAS 99318).

Bufo occidentalis Camerano

Bufo occidentalis Camerano, Atti R. Acad. Sci. Torino, 14:887, December 31, 1878 (based on 3 syntypes from México).

Remarks.—Three females are 76, 80, 86 and seven males are 39-74 (57.7) in snout-vent length. Seven juvenile toads have snout-vent lengths of less than 39. The tympanum is large and distinct, but covered with thick skin, in all toads examined. The tympanum is

indiscernible externally, except in large adults, which seem to have fewer warts over the tympanum. Supraorbital crests are absent in the smallest toads, but become more evident with an increase in snout-vent length. The color pattern, shape of the parotoid glands, and the habitat were the primary bases for the identification of the juveniles.

Two specimens have been reported from the coastal lowlands near Mazatlán and Presidio. The specimen (AMNH 13253) reported by Kellogg (1932:67) is *Bufo mazatlanensis*. A second specimen was listed by Günther (1885-1902:254) and Kellogg (1932:64) as coming from Presidio, Sinaloa. No other specimens have been collected on the coastal plain. Duellman (1961:28) mentioned specimens from near 900 meters, the lowest altitudinal limit of the species in Michoacán. Other locality information indicates that the species inhabits pine and oak forests in México. It seems likely that Günther's specimen, if it is *Bufo occidentalis*, was collected to the east of Presidio in the foothills of the Sierra Madre Occidental rather than on the coastal plain, and that Presidio was the port or origin of shipment of the specimen rather than the collecting locality.

Distribution in Sinaloa.—Known from several localities in pine-oak forest between 1100 and 2000 meters near Santa Lucía. See Fig. 23.

Specimens examined.—4 mi. E [by hwy. 40] El Palmito [Durango] (CSCLB 1786); 2.6 km. SW El Palmito (Durango), 2015 m. (° KU 78302-03); 2.2 km. NE Santa Lucía, 1150 m (° KU 78296-98); 19.2 km. NE Santa Lucía, 1940 m. (° KU 78299-301, 78304-12); Santa Rita (LACM 6198); 4.8 mi. E Santa Rita (LACM 6196); 0.9 mi. W Santa Rita (LACM 6197); 1.2 mi. W Santa Rita (LACM 6195); 47.2 mi. NE Villa Unión (CSCLB 1787).

Literature records.—El Batel, 5100 ft. (Riemer, 1955:21); Plomosas (Kellogg, 1932:67); Presidio [?] (Günther, 1885-1902:254; Kellogg, 1932:64).

Additional record.—9.6 mi. SW El Palmito (UMMZ 123027).

***Bufo punctatus* Baird and Girard**

Bufo punctatus Baird and Girard, Proc. Acad. Nat. Sci. Philadelphia, 6:173, 1854 (based on a specimen from Río San Pedro [Devil's River], Val Verde Co., Texas).

Remarks.—*B. punctatus* has been taken at scattered localities: on the coastal plain near Guamúchil, Navolato, and Mazatlán, and in the mountains at El Batel and Plomosas. Taylor (1938:508) found a specimen beneath a rock near Mazatlán. In other parts of its range the toad usually is found in arid situations, and is active during or after rains.

Distribution in Sinaloa.—Probably occurs throughout the state. See Fig. 18.

Specimens examined.—None.

Literature records.—El Batel; Guamúchil (Riemer, 1955:22); about 3 mi. SE Mazatlán (Taylor, 1938:508); Plomosas; Presidio [?] (Riemer, 1955:22).

Additional records.—36 mi. N Mazatlán (UIMNH 39474); 2 mi. E. Mazatlán (FMNH 102426); 14.2 mi. E Navolato (CAS 99659).

Family Hylidae

Diaglena spatulata (Günther)

Tripriion spatulatus Günther, Ann. Mag. Nat. Hist., ser. 5, 10:279, October, 1882 (type locality, Presidio, México).

Diaglena spatulata, Cope, U. S. Nat. Mus. Bull., 32:12, 1887.

Remarks.—Twenty-five males have snout-vent lengths of 66-87 (74.7), tibia lengths of 24.5-29.5 (27.8), foot lengths of 33.1-41.5 (38.5), head-casque lengths of 23.5-29.2 (25.9), head-casque widths (over the tympanum) of 15.3-19.6 (16.9), interorbital widths of 12.2-16.5 (14.0), third finger-pad widths of 2.6-3.6 (3.2), fourth toe-pad widths of 2.1-3.1 (2.8), and greatest tympanum widths of 3.0-4.1 (3.6). In two females (KU 75283, 75285) the above measurements are, respectively: 82, 84; 20.9, 31.2; 44.3, 43.1; 28.2, 29.4; 19.1, 19.9; 16.5, 16.8; 3.5, 3.7; 2.9, 3.1; 4.3, and 4.0. The testes are white in two males examined (KU 75273, 75281). All males have black nuptial pads on the thumbs, and vocal pouches distended with two vocal pouch openings located posterior and slightly lateral to the tongue attachment. Both females contain eggs.

One of the objectives of field work by the second author was to learn something concerning the breeding biology of the amphibian fauna of the state. One of the more difficult species to study was *D. spatulata*. Single males were collected in early July from temporary rain ponds near Concordia, southeast of Villa Unión, and near Coyotitán. Males collected near Concordia on July 1, and near Villa Unión on July 7, were found away from the water and apparently had just arrived at the vicinity of the ponds. Calling males were first heard on July 12 near Coyotitán. *Diaglena* called from the shallow edges of a large rain pond, together with a large chorus of *Bufo mazatlanensis* and *Smilisca baudinii*. No females were seen. For several nights thereafter the pond was revisited, as were several other potential breeding sites, but to no avail.

On August 20, a remarkable incident occurred. McDiarmid had been collecting in the La Cruz area continuously for three nights. There had been a steady rain of two or three hours duration on August 18, but no rain on the 19th. We arrived at the La Cruz road about 8 p. m. on August 20. The sky was cloudy and overcast and

the temperature slightly cooler than the previous night. There was no indication of rain that afternoon, although it may have rained that morning. We began collecting frogs of several species from choruses congregated at roadside ponds. The second pond visited contained several hundred *Diaglena*. Males were calling from about 35 centimeters above the edge of the water or on rocks in the water. No males were observed calling from the water. There appeared to be established calling sites around the pond. Most of the calling males were spaced about 50 centimeters apart on the bank. Several amplexing pairs were noted swimming in the water; amplexus is axillary. Some of the pairs were put in gallon jars and remained in amplexus for several days. We encountered many more *Diaglena* hopping toward the pond as we returned to the road. When the lights of the field vehicle were turned on, amphibians were seen everywhere on the road. The high density of frogs extended for nearly 5 miles. *Diaglena* were very abundant; an estimate of a thousand individuals is considered conservative. The road was dry at the time. Although no males were calling from the road, twelve pairs in amplexus were collected as they hopped along the pavement. The ditches on each side of the road were full of water 50 to 100 centimeters deep. Breeding in the same ditches with *Diaglena* were several other amphibians, including: *Scaphiopus couchii*, *Bufo kelloggi*, *Bufo mazatlanensis*, *Hypopachus oxyrrhinus*, *Gastrophryne olivacea*, *Phyllomedusa dacnicolor*, *Pternohyla fodiens*, and *Smilisca baudinii*. The following night we returned to the area only to find the breeding ponds deserted. Except for the eggs and tadpoles there was no sign of the previous night's activity.

On July 8, 1963, the first author collected 17 specimens (KU 75273-89) in rain pools in association with *Scaphiopus couchii*, *Pternohyla fodiens*, *Smilisca baudinii*, *Phyllomedusa dacnicolor*, and *Hyla smithi*. Some males were calling and one pair was found in amplexus. No specimens have been collected later than August 20.

Peters (1955:1) reviewed the current knowledge of frogs of the genus *Diaglena* and pointed out that breeding activity of *D. reticulata* in Michoacán apparently is correlated with the first heavy rain of the year. Duellman (1960:59) mentioned choruses of *D. reticulata* immediately following torrential rains. The enormous breeding population of this supposedly rare hylid that was encountered near La Cruz suggests that the paucity of specimens is due to poor timing on the part of collectors. While the exact ecologic stimulus for breeding remains unknown, we suspect that a

combination of sufficient rain, cool weather, and overcast sky initiates reproductive activity.

Distribution in Sinaloa.—Known only from the lowlands of Sinaloa from about 60 miles south of Culiacán to near Villa Unión. See Fig. 24.

Specimens examined.—2.1 mi. NE Concordia (CSCLB 1876, 1881-86); 4 km. SE Concordia (° KU 73835-36); 5 km. SW Concordia (° KU 75282-89, 73837-40); 3.5 mi. E Coyotitán (LACM 6242); 7.5 mi. E Coyotitán (LACM 6243-47); 89 km. S Culiacán (° KU 73841-44); La Cruz to 5 mi. E La Cruz (LACM 6248-98); Mazatlán (SDSC 1774); 4.2 mi. N Mazatlán (CSCLB 1878); 7 mi. N Mazatlán (CSCLB 1146); 8 mi. N Mazatlán (CSCLB 1877); 16.2 mi. N Mazatlán (CSCLB 1879); 16.7 mi. N Mazatlán (CSCLB 1880); 9 km. NE Villa Unión (° KU 75273-81); 9.4 mi. NE Villa Unión (LACM 6239); 13 mi. SE Villa Unión (LACM 6241); 16.3 SE Villa Unión (LACM 6240).

Literature records.—Nr. Mazatlán (Peters, 1955:1); Presidio (Günther, 1885-1902:293; Kellogg, 1932:138); nr. Presidio (Taylor, 1942b:58); Venodio [Venadillo], 4000 ft. [?] (Kellogg, 1932:138).

Additional records.—22.8 mi. S El Salado (FAS 17019; UIMNH 62383); Mazatlán (MCZ 44304); 9 mi. N Mazatlán, 100 ft. (AMNH 58694; MVZ 58803, 58807); 19 mi. N Mazatlán (AMNH 62154); 74.5 mi. N Mazatlán (FAS 14688); 18.6 mi. NNW Mazatlán (UMMZ S-1938-9, 115322).

Hyla arenicolor Cope

Hyla arenicolor Cope, Jour. Acad. Nat. Sci. Philadelphia, 6:84, July, 1866 (based on a specimen from northern Sonora).

Remarks.—Kellogg (1932:159) listed one specimen of *Hyla arenicolor* from Sinaloa. Bogert and Oliver (1945:314) implied that this species occurs in Sinaloa, but did not cite definite records. The occurrence of this species in the surrounding states of Sonora, Chihuahua, Durango, and Nayarit suggests that it is probably more widespread in Sinaloa than our records indicate.

Distribution in Sinaloa.—Higher elevations in southern part of state. See Fig. 25.

Specimens examined.—44 mi. NE Villa Unión (CSCLB 1751-56); 47.2 mi. NE Villa Unión (CSCLB 1648).

Literature record.—Plomosas (Kellogg, 1932:159).

Additional record.—Sinaloa [State?] (USNM 84410-11).

Hyla smaragdina Taylor

Hyla smaragdina Taylor, Copeia, no. 1:18, March 30, 1940 (type locality, six kilometers east of Cojumatlán, Michoacán).

Remarks.—Twenty-eight frogs collected on July 11 and two on July 25, 1963 (included in the series KU 75295-333, 78380-82) are yellowish green, pinkish tan, brown, or rusty brown with dark brown or black specks uniformly distributed from between the eyes to the anus. The lips are dark brown below a line connecting the nostril

and the anterior edge of the eye. The iris is rose-gold to pinkish gold with tiny black flecks; the pupil is horizontally elliptical. The belly is yellowish white. The hands are darker dorsally than the dorsum, and the toe pads are yellow. The unexposed parts of the thigh are golden brown with no flecks, and those parts of the tibia and foot are similar but paler in color.

One gravid female (KU 75304) obtained on July 11, 1963, has a snout-vent length of 28.4 and a tibia length of 13.7. Forty-two males (KU 68719, 75295-303, 75305-33, 78380-82) have snout-vent lengths of 22.7-25.6 (24.2) and tibia lengths of 10.8-12.2 (11.7). The testes are unpigmented.

Metamorphosing tadpoles (KU 78988-89), collected on August 8 and 9, 1963, agree with the description given by McDiarmid (1963: 7-8), except that the brown reticulations and blotches on the caudal musculature and lines are more distinct than indicated in his illustration (Fig. 3, p. 8).

Distribution in Sinaloa.—Known only from the vicinity of Santa Lucía in the pine-oak forest. See Fig. 25.

Specimens examined.—27.2 mi. E Concordia (CSCLB 582-611); Copala (° KU 95807-13); Potrerillos, 1550 m. (° KU 78988-89); Santa Lucía, 1100 m. (° KU 75295-333); 2.2 km. NE Santa Lucía, 1150 m. (° KU 78380-82); 1.5 km. E Santa Lucía, 1300 m. (° KU 68719).

Additional record.—Santa Lucía, 3600 ft. (KU 80321-23).

Hyla smithi Boulenger

Hyla smithi Boulenger, Zool. Rec. Reptilia and Batrachia, 38:33, 1902 (type locality, Cuernavaca, Morelos).

Remarks.—Forty-two specimens (excluding KU 73867, 78400, 78404-06) from Sinaloa were compared with 97 specimens from Oaxaca. Females in both samples are slightly larger than males, and the specimens of both sexes from Oaxaca are slightly larger than those from Sinaloa. The samples are similar in tibia length, eye diameter, tympanum diameter, and third finger pad diameter. In both samples some specimens have an unmarked dorsum, some have small dark flecks, and some have distinct brown spots on the pale yellow ground color. Two differences in coloration were observed between these samples. The pale, yellowish white dorsolateral stripe extends to the groin in frogs from Sinaloa, but in the frogs from Oaxaca the stripe terminates posteriorly near the middle of the body or slightly posterior to the middle; rarely does the stripe extend to the groin. The ventral surfaces of the frogs from Sinaloa were uniformly white or pale yellow, whereas in the Oaxacan frogs

the belly was pale yellow and the ventral surfaces of the legs and throat were deeper yellow.

On July 27, 1963, several *Hyla smithi* were collected near Villa Unión. An egg mass (KU 78987) was deposited in a plastic bag by a mated pair. The embryos of 29 preserved fertilized eggs (KU 78987) are 0.9-1.1 (1.0); the vitelline membranes are closely adherent to the eggs; the outer envelope is 1.3-2.0 (1.7) in diameter.

This common frog is usually found in rain pools in the southern lowlands of Sinaloa. The males usually call from vegetation in the water or around the edge. *Hyla smithi* was found in the same pool with *Phyllomedusa dacnicolor*, *Pternohyla fodiens*, *Rana pipiens*, *Bufo marinus*, *Bufo kelloggi*, and *Natrix valida* in July, 1963.

Distribution in Sinaloa.—Recorded from several localities in the lowlands, but not from the arid northwest, and from Polomosas at an elevation of 760 meters. See Fig. 26.

Specimens examined.—4 km. NE Concordia (* KU 73858); 3.7 mi. E Concordia (CSCLB 1715); 10 km. SW Concordia (* KU 73859-64); N Culiacán (CSCLB 647-49); 15.5 mi. N (by hwy. 15) Río Elota (LACM 6310-11); 34 km. SE Escuinapa (* KU 73870-74); La Cruz (LACM 6299-300); 7.3 km. SW Matatán, 155 m. (* KU 78383-84, 78407); Mazatlán (CSCLB 1717); 1.9-5.7 mi. N Mazatlán (UAZ 16063); 3.3 mi. N Mazatlán (UAZ 16064); 4.5 mi. N Mazatlán (UAZ 16024-33); 7.1 mi. N Mazatlán (CSCLB 1732); 9.2 mi. N Mazatlán (CSCLB 1716); 55 mi. N Mazatlán (CSCLB 1730-31); 2.4 mi. SE Mazatlán (UAZ 16061); 8.2 mi. SE Mazatlán (UAZ 16062); Plomosas, 760 m. (* KU 73875-77); San Ignacio, 210 m. (* KU 73865-69; LACM 6307-09); 0.5 km. S Santa Lucía (CSCLB 1643); Teacapán (* KU 73878; LACM 6313, 6523-25); Villa Unión, 15 m. (* KU 78400-06); 3 mi. NE Villa Unión (LACM 6301-02); 8.4 mi. NE Villa Unión (LACM 6303-06); 9.5 km. NE Villa Unión (* KU 75334); 26 mi. NE Villa Unión (CSCLB 1722-29); 2.3 mi. E Villa Unión (CSCLB 1644-47); 3.7 km. E Villa Unión, 30 m. (* KU 78385-99, 78987).

Literature records.—El Dorado (Fugler and Dixon, 1961:7); 2 mi. E Mazatlán (Taylor, 1937:357).

Additional records.—Chele, ca. 300 ft. (UMMZ 110915 [7 spec.]); 11 mi. NE (by road) Copala (UIMNH 40530-31); 3.2 km. SW Copala (KU 95814-44, 95850); 7.6 mi. N Culiacán, Hacienda Simon (UMMZ 120252); 8.5 mi. NW Culiacán (AMNH 59272); El Dorado (UIMNH 43079-89); El Venadillo (UMMZ 123028); Mazatlán (FAS 8569-77; USNM 147980-81); 9.2 mi. S Mazatlán (UIMNH 38444-90); 59 mi. S Mazatlán (FMNH 107023); 2.5 mi. N, 1.5 mi. W Mazatlán (FAS 9006-47); 3 mi. SE Rosario (UIMNH 7288); 12 mi. NE San Benito, 1000 ft. (KU 91409); 20.2 mi. NNW Sinaloa, 200 ft. (UMMZ 115257); 6 mi. NNW Teacapán (KU 91408).

Phrynohyas venulosa (Laurenti)

Rana venulosa Laurenti, Specimen medicum, exhibens synopsis reptilium . . ., (based on Seba, 1734, Locupletissimi rerum naturalium thesauri accurata descriptio, . . ., I:115, pl. 72, fig. 4) p. 31, 1768 (type locality, "habitat in Indies"); validated by fiat, International Commission of Zoological Nomenclature, Opinions and Decisions, 1958:169.

Phrynohyas latifasciata Duellman, Misc. Publ. Mus. Zool., Univ. Michigan, 96:24, February 21, 1956 (type locality, Presidio, Sinaloa).

Phrynohyas venulosa: validated by fiat, International Commission of Zoological Nomenclature, Opinions and Decisions, 1958:169.

Remarks.—Eight specimens, seven males and a female (one pair in amplexus), were collected south of Escuinapa on August 3. The males were located in the water by their calls. The pond was about 25 centimeters deep and surrounded by secondary vegetation.

On the afternoon of September 2, near Teacapán, another *Phrynohyas* was heard calling from a coconut palm during a light rain. The following day a second male called from a strangler fig tree in dense forest. Both eluded capture. Judging from the two diurnal encounters and field experience with this frog elsewhere, we assume the *P. venulosa* is arboreal most of the time and descends to the ground only to breed. The only other specimens known from Sinaloa were collected near Presidio by Forrer (Boulenger, 1882: 327-28).

A study of the genus *Phrynohyas* in Mexico and Central America (McDiarmid, 1968) forms the basis for assigning the Sinaloan frogs to *P. venulosa*.

Distribution in Sinaloa.—Known from two localities in the southern lowlands. See Fig. 25.

Specimens examined.—9.4 mi. SE Escuinapa (LACM 6315-19, 7245).

Literature record.—Presidio (Boulenger, 1882:327-28).

Phyllomedusa dacnicolor Cope

Phyllomedusa dacnicolor Cope, Proc. Acad. Nat. Sci. Philadelphia, 16:181, September 30, 1864 (type locality, Colima, Colima).

Remarks.—Fifty-four males have snout-vent lengths of 60-77 (68) and tibia lengths of 23-29 (26). Thirty-three females have snout-vent lengths of 46-92 (67) and tibia lengths of 18-38 (28). Sexual dimorphism in snout shape, as described by Duellman (1957a:30), was evident in all specimens examined.

In the rainy season this large hylid is usually abundant near temporary rain pools throughout the lowlands of Sinaloa. Several were taken from trees along a small stream near Carrizalejo, on the night of June 18, in association with *Smilisca baudinii*, *Rana pipiens*, *Leptodactylus occidentalis*, *Bufo mazatlanensis* and *Lepidodeira splendida ephippiata*. *Phyllomedusa dacnicolor* was found with *Pternohyla fodiens*, *Bufo kelloggi*, *B. marinus*, *Hyla smithi*, *Rana pipiens*, and *Natrix valida valida* at a large roadside rain pool near Villa Unión. All males observed calling were doing so from trees or branches around or above the ponds. *Phyllomedusa* is one of the few amphibians active during the dry season. Thirteen speci-

mens were taken on the road north of Mazatlán during the first week of April and three specimens were found in December at Mazatlán. A specimen was removed from the stomach of a *Leptophis diploptoris* near Terreros.

Distribution in Sinaloa.—Throughout the lowlands, below 500 meters. See Fig 27.

Specimens examined.—9 mi. NW Acaponeta [Nayarit] (LACM 6334); 8 km. N Carrizalejo, 460 m. (° KU 78117-31); 1 km. S Concepción, 75 m. (° KU 63675); Concordia (UNM 10017-18); 2.1 mi. E Concordia (CSCLB 1551); 3 mi. E Concordia (CAS 91921-24); 3.7 mi. E Concordia (CSCLB 1552); 4.3 mi. E Concordia (CSCLB 1560); 5 km. SW Concordia (° KU 75372-76); Culiacán (CSCLB 1561-62); 15.8 mi. N Culiacán (CSCLB 1559); 5.4 mi. N, 1.3 mi. NE Culiacán (CSCLB 1870); 51 km. SSE Culiacán (° KU 37772); 5.5 mi. S Culiacán (LACM 6333); Elota (° KU 78408); 15.5 mi. N Río Elota (LACM 6328); 9.4 mi. SE Escuinapa (LACM 6335); 8.6 mi. S Espinal (CSCLB 1538); Guamúchil (UAZ 12866); Isla Palmito del Verde, middle (° KU 73891); 6 mi. E La Cruz (LACM 6327); 5 km. NE Las Trancas (° KU 78413-16); 5 km. N Los Mochis (° KU 73888-89); 7.3 km. SW Matatán, 150 m. (° KU 78446-54); Mazatlán (CAS 89711-12; CSCLB 1543-45, 1547-50, 1563-71; LACM 6515; UAZ 12835); S Mazatlán (JFC 62:51-54); 1 mi. N Mazatlán (LACM 6337-39); 3.3 mi. N Mazatlán (UAZ 12857-64, 12867); 5 mi. N Mazatlán (CSCLB 1542, 1546); 5.9 mi. N Mazatlán (UAZ 13359); 7.1 mi. N Mazatlán (CSCLB 1540); 9.2 mi. N Mazatlán (LACM 6320); 2 mi. SE Mazatlán (UAZ 12832); 13.7 mi. SE Mazatlán (UAZ 12833); 2.5 mi. S Mazatlán (UAZ 12865); 2.6 mi. S Mazatlán, Urias (UAZ 12836); 4 km. SW Navolato, 6 m. (° KU 73880); 8 mi. S Palmillas (LACM 25621); 14.2 mi. WNW Pericos turnoff [on hwy. 15], Rancho de los Pocitos (UAZ 13363-65); 1.4 mi. N Río Piaxtla (CSCLB 1539); 0.2 mi. SE Rancho Huanacastle (LACM 6336); 3.5 mi. N Rosario (CSCLB 1553-57); 4 mi. N San Blas, 400 ft. (JRM 1108-10); 5 km. SW San Ignacio, 200 m. (° KU 78409-12); Teacapán (° KU 73890; LACM 6537-39); Villa Unión, 15 m. (° KU 73881-87, 75366-67, 78418-45; LACM 6329-32; SU 15571-74, 15585); 3 mi. NE Villa Unión (LACM 6326); 4 mi. NE Villa Unión (LACM 6321); 9 km. NE Villa Unión (° KU 75368-71); 8.8 mi. NE Villa Unión (LACM 6322); 9.4 mi. NE Villa Unión (LACM 6323); 2.3 mi. E Villa Unión (CSCLB 1541); 3.7 km. E Villa Unión, 60 m. (° KU 78417); 16.3 mi. SE Villa Unión (LACM 6324-25); 5.9 mi. S Villa Unión (CSCLB 1558).

Literature records.—Costa Rica (Smith and Van Gelder, 1955:145); El Dorado (Fugler and Dixon, 1961:7); 14 mi. SE Escuinapa, 100 ft. (Davis and Dixon, 1957b:147); Mazatlán (Kellogg, 1932:144; Taylor, 1938:515; Martín del Campo, 1941:760; Smith and Taylor, 1948:72); N Mazatlán (Kellogg, 1932:144; Lewis and Johnson, 1956:277); 2 mi. E Mazatlán, 50 ft. (Davis and Dixon, 1947b:147); Presidio; Rosario (Kellogg, 1932:144; Smith and Taylor, 1948:72); San Blas (Smith and Taylor, 1948:72); San Francisquito (Kellogg, 1932:144).

Additional records.—N bank Río Baluarte, 3 mi. N bridge (CAS 99286-87); 9 mi. S Río Baluarte (CAS 99443); 9.3 mi. S Río Baluarte (CAS 99444); 0.8 mi. S Río Cañas (CAS 99633); Chele, ca 300 ft. (UMMZ 110916 [7 spec.]); Concordia (AMNH 73778); 1.1 mi. E Concordia (CAS 99615); 11 mi. NE Concordia (SM 9210-12); 12 mi. NE Concordia (SM 9989-90); 3.2 km. SW Copala (KU 95870); Costa Rica (UIMNH 34890-91); Culiacán, 270 ft. (UMMZ 118813; USNM 153770); 2 mi. N Culiacán (AMNH 59282); 7.6 mi. N Culiacán, Hacienda Simon (UMMZ 120260); 7.8 mi. N Culiacán (FAS 12497); 30-35 mi. S Culiacán (FAS 14599); El Dorado (AMNH 70825-26); 0.2 mi. N El Dorado (CAS 99656); 10 mi. N El Dorado (SM 12040-44); 1 mi. NE El Fuerte (FMNH 71442-63); 8 mi. NNE El Fuerte (FMNH 71464); El Venadillo (UMMZ 123031); Escuinapa (AMNH 860-62); 11.7 mi. N

Escuinapa (UF 16550); 15 mi. SE Escuinapa, Hacienda La Campana, 300 ft. (UMMZ 118814 [5 spec.]); 9.1-14.1 mi. S Escuinapa (FAS 13956-60); 3.6 mi. E Guasave (on Verdura road) (CAS 99033-42); W half La Cruz rd. (CAS 99653); Los Mochis (FAS 10639-43); 13 mi. NNE Los Mochis (UIMNH 40566-68); Mazatlán (USNM 153773-74); N Mazatlán (AMNH 13126); 1 mi. N Mazatlán (SM 9194-209); 1.8 mi. N Mazatlán (UF 12854); 3 mi. N Mazatlán (MCZ 32575-76; USNM 151798-801; 3.2 mi. N Mazatlán (CAS 99380); 4 mi. N Mazatlán (AMNH 6205-06); 5 mi. N Mazatlán (SM 12051-55); 10 mi. N Mazatlán (MCZ 32573); 10.3 mi. N Mazatlán (CAS 99398); 10.4 mi. N Mazatlán (CAS 99399); 12 mi. N Mazatlán (UF 12855); 18 mi. N Mazatlán (AMNH 59281); 21 mi. N Mazatlán (MCZ 32571-72); 24 mi. N Mazatlán (MCZ 32565-70); 78.1 mi. N Mazatlán (CAS 99437); 1 mi. E Mazatlán (UIMNH 32769); 2.5 mi. E Mazatlán (FAS 8579); 0.4 mi. SE Mazatlán (MCZ 32574); ca. 2 mi. SE Mazatlán (FMNH 105263; UIMNH 25394-403); 2 mi. SE Mazatlán (FMNH 112751, 112754, 112757, 117466-68, 117476, 117478, 117481-84); 2.3 mi. N, 1.5 mi. W Mazatlán (FAS 7734-43); 25 mi. NW Mazatlán (MCZ 32950); 5-8 mi. NNW Mazatlán, 50-100 ft. (UMMZ 115302 [3 spec.]); 23.3 mi. NNW Mazatlán, 150 ft. (UMMZ 115303); 9 mi. NW Piaxtla (SM 11665-66, 12045-50); Rosario (UIMNH 7073, 62656-64); 8 mi. WNW Rosario (UMMZ 112850-51); Villa Unión, Río Presidio (UMMZ 102615); 3 mi. SE Villa Unión (SM 12056-61).

Pternohyla fodiens Boulenger

Pternohyla fodiens Boulenger, Ann. Mag. Nat. Hist., ser. 5, 10:326, figs., juveniles) of *Pternohyla fodiens* from Sinaloa were compared with three males of *Pternohyla dentata* Smith from Aguascalientes. In addition to the characters that Smith (1957:1) listed as differentiat-

Remarks.—Thirty-nine specimens (32 males, two females, and five

October, 1882 (type locality, Presidio, W. México).

ing the two species, males of *Pternohyla fodiens* have black throats speckled with white (white tips of the ventral granules), and the paired vocal pouches are joined medially. The three males of *P. dentata* have the vocal pouches darker in color than the belly but paler than the light interspaces of the dorsum, and the pouches are separated by the white throat skin, which is as granular as the belly.

The males, females and juveniles of *P. fodiens* have snout-vent lengths of 38-62 (47.5), 60, 61, and 35-41 (38.8), and tibia lengths of 15.0-23.6 (19.1), 24.0, 28.7, 14.8-16.4 (15.5), respectively. The three males of *P. dentata* have snout-vent lengths of 52, 52 and 56 and tibia lengths of 18.7, 18.8, and 20.0.

Males usually call from the base of bushes or in grass, well back from the edge of the ponds. Amplexing pairs were collected on August 20 near La Cruz. Tadpoles were collected the following day from a pond eight to ten centimeters in depth. Thousands of tadpoles, all of which appeared to be newly hatched and about 10 mm. in length, were all that remained from the previous night's breeding activities. Most of the larvae were floating in clusters with their tails directed downward at the surface of the pond.

When a cluster was disturbed, the larvae would disperse, some swimming away and others sinking to the bottom. Jelly envelopes, some containing undeveloped eggs, were scattered over the bottom of the pond. The tadpoles clustered at the surface may have been feeding on surface scum. Three large series were collected and allowed to develop. Three days later the larvae lost their external gills.

Distribution in Sinaloa.—Throughout the lowlands, below 250 meters. See Fig. 28.

Specimens examined.—8.9 mi. N Acaponeta [Nayarit] (LACM 6408); 2.1 mi. NE Concordia (CSCLB 1608); 4 km. NE Concordia (° KU 73901); 3.7 mi. NE Concordia (CSCLB 1611-16); 4.7 mi. NE Concordia (CSCLB 1617-22); Culiacán (CSCLB 1601-05); 19.7 mi. S Culiacán (LACM 6405); 19.8 mi. S Culiacán (LACM 6406); 20.2 mi. S Culiacán (LACM 6404); 12 mi. NE El Fuerte (CSCLB 1606); 2.9 mi. N Elota (CSCLB 1623); 12 mi. N (by hwy. 15) Río Elota (LACM 6400); 15.5 mi. N (by hwy. 15) Río Elota (LACM 6401-02); 3.4 km. SE Escuinapa (° KU 73902-08); 1-3 mi. E La Cruz (LACM 6394-95); 5 mi. E La Cruz (LACM 6397-99); 10 mi. E La Cruz (LACM 6396); Matatán, 170 m. (° KU 73897-900); Mazatlán (CSCLB 1607; SDSC 1758-65); 5 mi. N Mazatlán (CSCLB 1625-38); 7.1 mi. N Mazatlán (CSCLB 1639-41); 8 mi. N Mazatlán (CSCLB 1610); 15.9 mi. N Mazatlán (LACM 6409); 55 mi. N Mazatlán, Río Piaxtla (CSCLB 1642); 7.3 km. SW Matatán, 155 m. (° KU 78455-56); Rosario, 150 m. (° KU 73896); 4 mi. N San Blas, 400 ft. (JRM 1105-07); San Ignacio (LACM 6391-93); 5 km. SW San Ignacio, 200 m. (° KU 78457); 1.5 km. ENE San Lorenzo (° KU 47904-05); Teacapán (LACM 6516-22); 0.8 mi. S Terreros (LACM 6409); Villa Unión (° KU 75383-96; LACM 6373-75); 3 mi. NE Villa Unión (LACM 6390); 9.5 km. NE Villa Unión (° KU 75397); 7.4 mi. NE Villa Unión (LACM 6376-82); 9.4 mi. NE Villa Unión (LACM 6383); 3.7 km. E Villa Unión, 60 m. (° KU 78458-63); 2.3 mi. E Villa Unión (CSCLB 1624); 10 mi. SE Villa Unión (LACM 6385-86); 16.3 mi. SE Villa Unión (LACM 6387-89); 18 mi. SE Villa Unión (LACM 6384).

Literature records.—Concordia, 400 ft. (Davis and Dixon, 1957b:147); Costa Rica (Smith and Van Gelder, 1955:145); El Dorado (Fugler and Dixon, 1961:7); 2 mi. E. Mazatlán (Taylor, 1938:514); Presidio; Rosario, 250 ft. (Kellogg, 1932:137).

Additional records.—23.3 mi. S Caitime (FAS 8590-91); 0.8 mi. S Río Cañas (CAS 99632); 1.0 mi. E Concordia (CAS 99620); 1.1 mi. E Concordia (CAS 99616); 4.4 mi. E Concordia (CAS 99614); 26.4 mi. N Culiacán (FAS 12632-33); 25 mi. S Culiacán (AMNH 60441); 58-63 mi. S Culiacán (FAS 12646-58); 7-8 mi. W Culiacán (FAS 12626); El Dorado (AMNH 70827); 1 mi. NE El Fuerte (UIMNH 40558-61); W part La Cruz rd. (CAS 99654); 13 mi. NE Los Mochis (UIMNH 40553-57); Mazatlán (FAS 7804-07; MCZ 44311-16; UIMNH 30676-81); 9 mi. N Mazatlán (UIMNH 40552); 35-40 mi. S Mazatlán (FAS 15354-57); 3.5 mi. NNW Mazatlán (UMMZ 115299); 19.6 mi. NNW Mazatlán (UMMZ 115298); 10.2-10.8 mi. SE Navolato (CAS 99680); Rosario (UIMNH 62707-710).

Smilisca baudinii (Duméril and Bibron)

Hyla baudinii Duméril and Bibron, *Erpétologie générale*, 8:564, 1841 (based on a specimen from México).

Smilisca baudinii, Cope, *Bull. U. S. Nat. Mus.*, 34:379, 1889.

Remarks.—Twenty-seven males have snout-vent lengths of 51-72

(62.5) and tibia lengths of 25.8-33.0 (29.8). The corresponding measurements for eight females are 45-78 (58.0) and 23.8-37.0 (29.2). One juvenile has a snout-vent length of 34 and a tibia length of 16.6. See Duellman and Trueb (1966:293) for additional notes on the Sinaloan population of this species.

Smilisca baudinii is one of the first frogs to begin breeding at the onset of the rainy season. Large choruses were heard as early as June 29 near Concordia. Males call from the shore or from low bushes around temporary ponds. Gravid females were collected at breeding ponds as early as July 7. Amplexing pairs were seen in the water and perched on limbs a few feet above the water.

On July 1, observations were made (at a breeding pond located about 10 miles NE of Villa Unión) which emphasized the spatial isolation existing between calling males of different species breeding at the same pond. The pond was about ten meters in diameter and was nearly circular. The shore was grassy except for a large tree at one side and some shrubs in another place. Small scattered bushes grew about 6 meters from the water's edge. Individual males of four species were calling from specific sites around the pond. *Bufo mazatlanensis* called from the open grassy shore near the water. About 30 males of *Phyllomedusa dacnicolor* were calling from limbs and leaves high in the tree above the water. Several jumped eight to ten meters into the pond when disturbed. Another frog, *Pternohyla fodiens*, was calling well away from the water, usually from the ground at the base of a bush or from a depression. Several *Smilisca* were calling from shore near the shrubs or from the lower branches of the shrubs. At no place around the pond were any two species calling from the same site, thus enhancing the separation of contemporary breeding populations.

Distribution in Sinaloa.—Throughout the state below 800 meters, most commonly in the southern lowlands. See Fig. 29.

Specimens examined.—8 km. N Carrizalejo, 460 m. (* KU 78133); 4 km. NE Concordia (* KU 73914); 3.7 mi. NE Concordia (CSCLB 1657-63); 4.5 mi. NE Concordia (LACM 6345-49); 5 km. SW Concordia (* KU 75438-39); 6 km. E Cosalá, 460 m. (* KU 73910); 3.5 mi. E Coyotitán (LACM 6361); N Culiacán (CSCLB 1664-66); 51 km. SSE Culiacán (* KU 37792); El Dorado (* KU 60392); 15.5 mi. N Río Elota (LACM 6366); 9.4 mi. SE Escuinapa (LACM 6367-70); Isla Palmito del Verde, middle (* KU 73916-17); 5 mi. E La Cruz (LACM 6363-65); 11.1 mi. NW (by hwy. 15) Los Mochis turnoff [on hwy. 15] (UAZ 13331); Matatán, 170 m. (* KU 73913); 7.3 km. SW Matatán, 155 m. (* KU 78464, 78466-70); Mazatlán (CAS 89707; SDSC 1756-57, 1771-72); 1.9-5.7 mi. N Mazatlán (UAZ 13338, 13414-15); 4.3 mi. N Mazatlán (LACM 6342-44); 5 mi. N Mazatlán (CSCLB 1649); 5.5 mi. N Mazatlán (LACM 6340); 7.1 mi. N Mazatlán (CSCLB 1652-54); 8.8 mi. N (by hwy. 15) Mazatlán (UAZ 13411); ca. 11 mi. N (by hwy. 15) Mazatlán

(UAZ 13412-13); 11.1 mi. N (by hwy. 15) Mazatlán (UAZ 13332); 15.9 mi. N Mazatlán (LACM 6341); 16 mi. N Mazatlán (CSCLB 1655); 17.5 mi. N Mazatlán (LACM 6371); 27.9 mi. N Mazatlán (LACM 6372); 8 mi. S Palmillas (LACM 25613); Rosario, 150 m. (* KU 73911-12; CSCLB 1651); 8 km. SSE Rosario (* KU 37625); 4 mi. N San Blas, 400 ft. (JRM 1111); San Ignacio (LACM 6362); 5 km. SW San Ignacio, 200 m. (* KU 78465); 1.5 km. ENE San Lorenzo (* KU 47917-24); Teacapán (* KU 73915; LACM 6526-36); Villa Unión (* KU 78471; LACM 6350-51); 8 km. N Villa Unión, 140 m. (* KU 80689-90); 5.7 km. NE Villa Unión (* KU 75434-37); 9.4 mi. NE Villa Unión (LACM 6352); 25 mi. NE Villa Unión (CSCLB 1656); 12.8 mi. SE Villa Unión (LACM 6360); 13 mi. SE Villa Unión (LACM 6359); 16.3 mi. SE Villa Unión (LACM 6354-58); 18 mi. SE Villa Unión (LACM 6353).

Literature records.—Costa Rica (Smith and Van Gelder, 1955:145); El Dorado (Fugler and Dixon, 1961:7); N Mazatlán; Plomosos (Kellogg, 1932:162); 2 mi. N Presidio (Taylor, 1938:515).

Additional records.—2.6 mi. S Río Cañas (CAS 99631); 15.5 mi. E Concordia (CAS 99611); 16.5 mi. E Concordia (CAS 99608); Costa Rica (UIMNH 34887-89); N Culiacán (UF 12858); Río Culiacán (AMNH 64205); 25 mi. S Culiacán (AMNH 60440); El Dorado (AMNH 70828-29); 1 mi. NE El Fuerte (FMNH 71468); 5.0 mi. N Escuinapa (CAS 99601); 13 mi. NNE los Mochis (UIMNH 40536-37); Mazatlán (MCZ 44308-09); 3 mi. N Mazatlán (MCZ 32564); ca. 4 mi. N Mazatlán (AMNH 12562); 36 mi. N Mazatlán (UIMNH 38364); 4 mi. NE Mazatlán (SM 10237); 2.3 mi. N, 1.5 mi. W Mazatlán (FAS 7725-33); 3.5 mi. NNW Mazatlán (UMMZ 115197); Rosario (UIMNH 62706); 3 mi. E Rosario (UIMNH 7360-76); 6 mi. NNW Teacapán (KU 91410); 5.7 mi. W Villa Unión (AMNH 59284).

Family Microhylidae

Gastrophryne olivacea mazatlanensis (Taylor)

Microhyla mazatlanensis Taylor, Univ. Kansas Sci. Bull., 29:355, October 15, 1943 (type locality, two miles east of Mazatlán, Sinaloa).

Microhyla carolinensis mazatlanensis: Hecht and Matalas, Amer. Mus., Novitates, 1315:5, April 1, 1946.

Microhyla olivacea mazatlanensis: Langebartel and Smith, Herpetologica, 10:126, May 5, 1954.

Gastrophryne olivacea mazatlanensis: Fugler and Dixon, Michigan St. Univ., Mus. Publ., 2(1):8, July 20, 1961.

Remarks.—Hecht and Matalas (1946:4) reported intergradation between *Microhyla carolinensis* and *M. mazatlanensis* in Sonora, México, and as a result considered *mazatlanensis* to be a subspecies of *carolinensis*. Twenty-two *Gastrophryne olivacea* from Sinaloa agree with the original description for *Microhyla mazatlanensis* Taylor (1943:355-357) with the following exceptions: the lateral black line is absent or is reduced to a single spot on the shoulder in some; the sides are dark brown below the lateral black line, becoming paler ventrally; the inguinal spot and the limb bars, which form a continuous line when the leg is folded, have faint pale centers in individuals from northern Sinaloa; the scattered black dorsal spots tend to form a pattern of lines diverging posteriorly in specimens

from southern Sinaloa and are scattered, forming an indistinct pattern, in frogs from northern Sinaloa; the flanks are pale ventrally with a slight peppering of pigment or are faintly mottled with pale brown.

The specimens from Sinaloa were compared with 20 specimens from Sonora (20 to 50 kilometers east of Kino), and with 161 frogs from Texas. The Sonoran specimens have brownish flanks; an indistinct row of black spots borders the flanks dorsally and posterior to the eye in some individuals, but spots are absent in others. The brown inguinal spots seem slightly smaller, but darker and more conspicuous, than those of the Sinaloan frogs. The limb bars are either solid, composed of many fused dark brown spots, or reduced to two to four dark brown spots. Dorsal brown spots are present anteriorly, or they are absent. The belly is creamy white with the edges, the chest, and lower jaw mottled with brown, or with a faint peppering of dark pigment. The flanks are distinctly mottled with brown.

The Texan frogs have small inguinal spots or lack them entirely. The limb spots, if present, are small, brown to brownish black, separated or fused, and enclose a pale tan area. The dark brown lateral area that is present in frogs from Sinaloa may be absent or indistinct. The dorsal spots are smaller and fewer than in Sonoran frogs, or are absent. The belly is clear with only a trace of mottling laterally. The flanks are unmarked or only faintly mottled.

From the characters of the pattern and coloration examined, it is evident that the population in western Sonora differs from the populations in Sinaloa and Texas in having distinctly mottled sides, mottling on the lower jaw, chest, and edges of the belly, and distinct dark brown inguinal and leg spots. Other characters are intermediate between the Sinaloan and Texan populations.

Wake (1961:88-89), on the basis of specimens secured in southern Arizona, elevated *mazatlanensis* to specific status on the assumption that the single specimen reported by Hecht and Matalas (1946:4) is a hybrid and does not represent an intergrading population. If the specimen reported by Hecht and Matalas (1946:4) is a hybrid, then the Sinaloan population would be *G. mazatlanensis*. Until more material from eastern Sonora and western Chihuahua is available, we refer the Sinaloan specimens to *Gastrophryne olivacea mazatlanensis*. Regardless of the specific status of the frogs west of the continental divide, those from northwestern coastal Sonora possibly represent a taxon distinct from that in Sinaloa.

Single males were encountered at night in early July, immediately following heavy rains. On August 18, several calling males were collected in a pond near La Cruz. A few nights later a large series of both sexes was collected in the same area. The breeding ponds were all temporary rain-filled pools, usually on the forest floor. The water was dirty brown and contained much floating debris. The majority of males were calling from the water. The tiny frogs would hang on floating debris, arch their backs and call; sometimes the black and white mottled vocal pouch was all that was visible of the songster. The call begins with a peep and continues as a high-pitched buzz of about two seconds duration. Males calling from the shore usually were concealed in deep grass or in a depression. All amplexing pairs were taken in shallow water near shore.

Distribution in Sinaloa.—Throughout the lowlands, below 250 meters north of Villa Unión. See Fig. 30.

Specimens examined.—5 km. SW Concordia (* KU 75461); 16 mi. N Coyotitán (LACM 6429); 32 km. N Culiacán (* KU 73928-32); 12 mi. N (by hwy. 15) Río Elota (LACM 6457); 15.5 mi. N (by hwy. 15) Río Elota (LACM 6458-63); 5 mi. E La Cruz (LACM 6436-56); 10 mi. E La Cruz (LACM 6430-35); 10.9 mi. N La Cruz turnoff [Las Teposanas] on hwy. 15 (LACM 6428); 5 km. N Los Mochis (* KU 73922-27); 2.3 mi. NE (by hwy. 15) Villa Unión (CSCLB 1875); 9 km. NE Villa Unión (* KU 75451-60); 0.8 mi. S Villa Unión (CSCLB 1721).

Literature records.—El Dorado (Fugler and Dixon, 1961:8); 13 mi. NE Los Mochis (Chrapliwy, *et al.*, 1961:89); Mazatlán (Hecht and Matalas, 1946:6); 2 mi. E Mazatlán (Taylor, 1938:516); 18.6 mi. NNW Mazatlán (Wake, 1961:90).

Additional records.—1 mi. NE El Fuerte (FMNH 71465-67); 6 mi. S Los Mochis (SDSNH 19892-93); Mazatlán (USNM 147964-65).

Gastrophryne usta usta (Cope)

Engystoma ustum Cope, Proc. Acad. Nat. Sci. Philadelphia, 18:131, 1866 (type locality, Guadalajara, Jalisco).

Gastrophryne usta: Stejneger, Proc. Biol. Soc. Washington, 23:166, December 29, 1910.

Gastrophryne usta usta: Lynch, Trans. Kansas Acad. Sci., 68:397, November 10, 1965.

Remarks.—Two males and three females have snout-vent lengths of 25.0, 25.7, 26.9, 27.0, and 25.3 (USNM 73267), respectively. All females contain eggs. The five frogs examined have a narrow, mid-dorsal line that is faintly cream-colored and that resembles the mid-dorsal line in frogs illustrated by Taylor and Smith (1945; plate 32, figs. 2 and 4); however, there is no trace of a fine line on the posterior surface of the femur, tibia or foot. All five frogs have two well-developed metatarsal tubercles.

On June 30, a single male was located as it called from beneath

a rock in an arroyo northeast of Concordia. The call was about two seconds in duration and was issued every three or four minutes. The following night a male and female were taken from a pool in the arroyo. Two other males were collected as they called from beneath a small log at the edge of a pond on July 7. A female taken at the same time was gravid. Another series of males in chorus was secured in August at Teacapán.

The call is a soft, high-pitched baaaaa. After some time it was possible to distinguish between the call of *G. usta* and that of *G. olivacea*, which is lower in pitch and slightly louder. The characteristic peep preceding the *mazatlanensis* call was not perceived from *usta* and may be lacking.

The ranges of the two species of *Gastrophryne* overlap near Mazatlán. The two species have not been taken sympatrically and probably are ecologic replacements of each other in southern Sinaloa. *Gastrophryne usta* has been collected in the same pond with *Smilisca baudinii*, *Phyllomedusa dacnicolor*, *Pternohyla fodiens*, *Hyla smithi*, *Diaglena spatulata*, *Bufo mazatlanensis*, and *Hypopachus oxyrrhinus*.

Distribution in Sinaloa.—Recorded from the coastal lowlands from near Mazatlán southward. See Fig. 30.

Specimens examined.—4 km. NE Concordia (° KU 73918-19); 4.5 mi. NE Concordia (LACM 6464-65); 34 km. SE Escuinapa (° KU 73920-21); Teacapán (LACM 6468-74); Venodio [Venadillo] (° USNM 73267); 16.3 mi. SE Villa Unión (LACM 6467); 18 mi. SE Villa Unión (LACM 6466).

Literature records.—Presidio (Parker, 1934:149); Venodio [Venadillo] (Kellogg, 1932:188; Smith and Taylor, 1948:94).

Hypopachus oxyrrhinus oxyrrhinus Boulenger

Hypopachus oxyrrhinus Boulenger, Ann. Mag. Nat. Hist., ser. 5, 11:344, May, 1883 (type locality, Presidio de Mazatlán, Sinaloa).

Hypopachus oxyrrhinus oxyrrhinus: Shannon and Humphrey, Herpetologica, 14:89, July 23, 1958.

Remarks.—Sixteen specimens examined have dark brown pigment on the side of the head from above the nostril and outer edge of the eyelid, ventrally and posteriorly to the groin. The dark pigment forms a sharp but irregular border dorsally, then fades gradually into the pale ventral coloration. The dark pigment contains color flecks that increase in size ventrally, becoming large round white spots on the belly. These frogs resemble *H. oxyrrhinus ovis* in this aspect of their coloration, but none has an irregular dark line from between the eyes to the groin (Taylor, 1940c:521, plate 62, figs. C and D). Also, the Sinaloan frogs, which have snout-vent lengths of 36-49 (41) and foot lengths of 21-28 (24), are larger than *H. o. ovis* as defined by Smith and Taylor (1948:95).

The first specimen of *Hypopachus* was collected in late June as it called from a hole in the bank of a slow, rain-fed stream. Heavy rain that afternoon initiated the breeding season for several species of frogs which were then collected for the first time. Three gravid females were taken from a pond southeast of Villa Unión where several males were found calling from hoof depressions around the edge of the pond. No amplexing pairs were seen that night. Other males were calling from concealed sites in grass near the Río Elota. The call is a loud Waaaaa, lower in pitch than *Gastrophryne*, and lasting two or three seconds. Amplexing pairs were noted swimming in the water on two occasions in mid-August.

Distribution in Sinaloa.—Known from the coastal lowlands south of Espinal. See Fig. 31.

Specimens examined.—2.1 mi. NE Concordia (CSCLB 1709-11); 4 km. NE Concordia (° KU 73935-38); 3.7 mi. NE Concordia (CSCLB 1673-1707); 4.5 mi. NE Concordia (LACM 6475); 10 km. SW Concordia (° KU 73939); 16 mi. N Coyotitán (LACM 6487); 6 mi. N (by hwy. 15) Río Elota (LACM 6493-95); 15.5 mi. N (by hwy. 15) Río Elota (LACM 6496-99); 9.4 mi. SE Escuinapa (LACM 6545-47); 34 km. SE Escuinapa (° KU 73940-43); 1-3 mi. E La Cruz (LACM 6488); 5 mi. E La Cruz (LACM 6489-92); 7.3 km. SW Matatán, 155 m. (° KU 78497-99); 7.1 mi. N Mazatlán (CSCLB 1708); 3 mi. S Rosario (LACM 6503); 9 km. NE Villa Unión (KU 75465-68); 16.3 mi. SE Villa Unión (LACM 6476-86).

Literature records.—8.1 and 8.8 mi. N Mazatlán (Shannon and Humphrey, 1958:88); Presidio (Boulenger, 1883:344; Kellogg, 1932:185).

Additional records.—8.0 mi. S Río Balurate (CAS 99629-30); 9 km. NE Concordia (KU 95939-44); 1.0 mi. E Concordia (CAS 99621); 1.1 mi. E Concordia (CAS 99619); 12.4 km. SW Concordia (KU 95945).

Family Ranidae

Rana catesbeiana Shaw

Rana catesbeiana Shaw, General Zoology, 3:106, pl. 33, 1802 (based on a specimen from North America; type locality restricted to South Carolina by Kellogg, Bull. U. S. Nat. Mus., 160:197, March 31, 1932).

Remarks.—Two recently metamorphosed frogs have snout-vent lengths of 35.7 and 43.4. The tips of the toes are pointed; the sub-articular tubercles of the hind feet are small and rounded; dorsolateral folds are absent; the tympanum is distinct and approximately the same size as the eye in both specimens.

One of the frogs was taken on August 4, 1962, from a roadside pond in association with *Phyllomedusa dacnicolor*, *Leptodactylus occidentalis*, *Gastrophryne olivacea mazatlanensis*, and *Bufo marinus*.

In 1956, *Rana catesbeiana* was introduced near Los Mochis in anticipation of its use as a harvestable food item (Ibarra, 1963:19).

Since its introduction, the bullfrog has spread throughout the irrigation ponds and ditches of the agricultural region around Los Mochis. Males were heard calling on several nights along the highway south of Los Mochis. The frog is well established and probably will continue to spread whenever and wherever suitable habitat becomes available.

Distribution in Sinaloa.—Known only from the vicinity of Los Mochis and Guasave. See Fig. 23.

Specimens examined.—Los Mochis (CSCLB 1600); 5 km. N Los Mochis (° KU 73944); 6.5 km. E Los Mochis (° KU 62363); 24.3 mi. S (by hwy. 15) Los Mochis (LACM 6416).

Additional records.—3.6 mi. E Guasave (CAS 99050); Los Mochis turnoff (on hwy. 15) (FAS 14105-09); 15 mi. N Los Mochis (SM 10625).

Rana pipiens Schreber

Rana pipiens Schreber, Der Naturforscher, Halle, 18:185, pl. 4, 1782 (based on a specimen from Raccoon, Gloucester county, New Jersey).

Rana forreri Boulenger, Ann. Mag. Nat. Hist., ser. 5, 11:343, May, 1883 (type locality, Presidio de Mazatlán, Sinaloa).

Remarks.—*Rana pipiens* has been collected from near sea level in tropical thorn woodland to about 1700 meters in tropical deciduous forest. This species is frequently found near irrigated fields, roadside pools in the lowlands, and creeks, rivers, or ponds at the higher elevations. The leopard frog is another species which has benefitted from agricultural development in Sinaloa, having become abundant in the irrigation ditches near Los Mochis.

Distribution in Sinaloa.—Throughout the state, below 1700 meters. See Fig. 32.

Specimens examined.—8 km. N Carrizalejo, 460 m. (KU 78158-77); 1 km. S Concepción, 75 m. (KU 63676); Concordia (UNM 10014-16); 7.2 mi. NE Concordia (CSCLB 1599); 6 km. E Cosalá, 460 m. (KU 73949); Coyotitán (JFC 62:16-17); 4 mi. N Culiacán (JMS osteo. coll.); 80 mi. N Culiacán (LACM 6420); 21.4 mi. S Culiacán (LACM 6426); El Burrion (JFC 62:39-44); 6 km. NE El Fuerte, 150 m. (KU 78154-55); 15.4 mi. N Río Elota (JMS osteo. coll.); 9 mi. S Escuinapa (LACM 25688); 6 km. ESE Guasave (KU 48981-82); 3.3 mi. S Guasave (UAZ 16268); 17.4 mi. NW (by rd.) Guasave (on rd. to Plaza Visnaga) (UAZ 9451-52); Isla Palmito de la Virgen, 15 m. (KU 73950); 1.3 mi. S La Cruz turnoff (on hwy. 15) (JFC 62:27-29, 70); Los Mochis (CSCLB 1598); 14.1 mi. S Los Mochis (UAZ 16271-75); 6 km. W Los Mochis, 3 m. (KU 78156-57); 11.1 mi. NW Los Mochis turnoff [on hwy. 15] (UAZ 16270); 34.1 mi. NW Los Mochis turnoff [on hwy. 15] (UAZ 16269, 16276-79); Mazatlán (CSCLB 1597); 1 mi. W Pánuco (CSCLB 1596); 14.2 mi. WNW Pericos turnoff [on hwy. 15], Rancho de los Pocitos (UAZ 16262-67); Plomosas, 760 m. (KU 73951-58); 4 mi. N San Blas, 400 ft. (JRM 1119-24); San Miguel (KU 44613, 44616); Santa Lucía, 1100 m. (KU 75444); 1.2 mi. NE Santa Lucía (CSCLB 1758-59); E Santa Lucía (KU 44627-29); 2 km. E Santa Lucía (KU 44624-26); 2.8 mi. W Santa Lucía (CSCLB 1595); Teacapán (LACM 6540-44); 79.2 mi. N Terreros (LACM 6425); 17.6 mi. S Terreros (JMS osteo. coll.); 18.1 mi. S Terreros (JMS osteo. coll.); Villa Unión (CSCLB 1594; LACM 6423-24).

Literature records.—50 mi. NE Choix (Kellogg, 1932:212); El Carrizo (Lewis and Johnson, 1956:277); El Dorado (Fugler and Dixon, 1961:8); Mazatlán (Martin del Campo, 1941:760); nr. Mazatlán (Kellogg, 1932:212; Taylor, 1938:516); 3 mi. E Mazatlán (Taylor, 1938:516); Presidio (Boulenger, 1883:343; Kellogg, 1932:212); nr. Presidio (Taylor, 1938:516); Rincón de Urías (Kellogg, 1932:212).

Additional records.—Chele, ca. 300 ft. (UMMZ 110913); Concordia (UMMZ 102621, 102639 [3 spec.]); 1.1 mi. E Concordia (CAS 99623); Culiacán (AMNH 58378-81); ca. 10 mi. N Culiacán (UIMNH 38149-51); 18-23 mi. S Culiacán (FAS 12495); 24.2 mi. S Culiacán (UF 17119); 14 mi. SW El Batel (AMNH 59224); 1 mi. NE El Fuerte (FMNH 71476-78); Río Fuerte at hwy. 15 (AMNH 64152-53); 37.6 mi. N Guamúchil (AMNH 67558-59); Guasave, Río Sinaloa (AMNH 64154); 3.6 mi. E Gusave (CAS 99043-49); 6 mi. S Los Mochis (SDSNH 19886-90); Mazatlán (MCZ 8630); nr. Mazatlán (FMNH 107802; USNM 47445); N Mazatlán (AMNH 12568, 13127-28); 9 mi. NW Piaxtla (SM 10426, 10430, 10439); 10 mi. S Presidio (UIMNH 32181-82); Rosario (UIMNH 62511); 1.3 mi. N Santa Lucía (MCZ 32590); 24.8 mi. E hwy. 15 [Villa Unión] on hwy. 40 (CAS 99310-12).

Rana pustulosa Boulenger

Rana pustulosa Boulenger, Ann. Mag. Nat. Hist., ser. 5, 11:343, May, 1883 (type locality, Ventanas, Durango).

Remarks.—We have examined six frogs and four tadpoles. The frogs have the following measurements: snout-vent length 49.9-75.4 (56.1); tibia length 28.3-43.9 (31.3); head length 19.7-30.0 (22.2); head width 17.3-26.8 (19.5). The tibia length/snout-vent length is 0.54-0.58 (0.557); head length/snout-vent length is 0.39-0.41 (0.396); head width/snout-vent length is 0.33-0.35 (0.347); head width/head length is 0.84-0.89 (0.875). The tadpoles, two of which were metamorphosing when preserved on June 23, 1955, agree closely with the descriptions and illustrations given by Taylor (1942a:44-45, pl. I, fig. 1, pl. III, fig. 4) and Zweifel (1955:251, fig. 22). The tadpoles were found in the rapids of a canyon stream.

The proximity of the type locality to Sinaloa, and the range of the species to the south, suggest that *Rana pustulosa* probably occurs in the mountains of southeastern Sinaloa. Two specimens (USNM 84404-05) were sent to the U. S. National Museum in November, 1921, by the Departamento de Exploracion Biologia Republica Mexicana. One of these (USNM 84405) was sent to the Museum of Comparative Zoology on February 21, 1944, and identified as *Rana sinaloae* (MCZ 25756). Zweifel (1954a:135-36) discussed the National Museum specimen (84404, not 34404 as published by Zweifel) and pointed out that it is either *Rana pustulosa* or *sinaloae* but definitely not *R. pipiens* (the only other logical possibility for the area). Examination of both specimens indicates that the frogs probably are *R. pustulosa*. Although the specimens are listed as coming from

Mazatlán we suspect they were collected at higher elevation in the Sierra Madre Occidental and subsequently shipped to México City from Mazatlán. An examination of the original tags indicates that the Mazatlán referred to is the one in Sinaloa.

Dunn (1922:222) recorded a single specimen of *R. pustulosa* from Mazatlán that, upon later examination, was referred to *Rana montezumae* by Oliver (1937:7-8). Since *R. montezumae* otherwise is known only from the southern part of the Mexican plateau, since the specimen examined by Oliver was "badly rubbed," since Mazatlán represents a locality and habitat separate and distinct from those previously known for the species (Duellman, 1961:54-55), *R. montezumae* is not here included in the fauna of the state.

Distribution in Sinaloa.—Known only from the vicinity of Santa Lucía in the southern highlands. See Fig. 33.

Specimens examined.—Mazatlán [probably incorrect] (MCZ 25756; USNM 84404); 3 mi. N Santa Lucía (° MCZ 32591-94); 1.2 mi. NE Santa Lucía (° CSLB 1760); 1.5 km. E Santa Lucía (° KU 69159; N = 4); 5.1 mi. SW Santa Lucía (° CSLB 652).

Rana sinaloae Zweifel

Rana sinaloae Zweifel, Bull. So. California Acad. Science., 53:131, December 31, 1954 (type locality, fourteen miles, by road, southwest of El Batel, Sinaloa, 4200 feet).

Remarks.—A series of 24 specimens agrees with the original description. The measurements are as follows: snout-vent length, 25.8-76.8 (46.8); head width 10.2-28.9 (17.2); head length 9.7-26.5 (16.2); tibia length 13.5-46.8 (25.6); tympanum diameter 1.6-5.9 (3.2). The tibia length/snout-vent length is 0.48-0.62 (0.536); the tympanum diameter/head width is 0.16-0.21 (0.189), which agrees with data given by Zweifel (1954a:133), but is lower than those reported by Duellman (1958b:10) and by McDiarmid (1963:9).

Rana sinaloae occurs in tropical deciduous forest, usually along mountain streams.

Distribution in Sinaloa.—Known only from the vicinities of Plomosas and Santa Lucía, from about 750 to 1950 meters elevation. See Fig. 34.

Specimens examined.—Plomosas, 760 m. (° KU 73960-65); Santa Lucía, 1100 m. (° KU 75445-50; CSLB 646); 0.6 mi. NE Santa Lucía (CSCLB 653-54); 2.2 km. NE Santa Lucía, 1150 m. (° KU 78492-96; 1.5 km. E. Santa Lucía (° KU 44632-37); 21 km. E Santa Lucía (° KU 44631); 7.2 mi. W Santa Rita (LACM 6427).

Literature record.—10 mi. NE (by rd.) El Batel, 6400 ft. (Zweifel, 1954a:132).

Additional record.—3.2 km. SW Santa Lucía, 4000 ft. (KU 95948-49).

Class REPTILIA

Order TESTUDINES

Family Kinosternidae

Kinosternon integrum Le Conte

Kinosternon integrum Le Conte, Proc. Acad. Nat. Sci. Philadelphia, 7:183, 1854 (type locality, México).

Remarks.—Three specimens identified as *K. hirtipes* by Taylor (1938:529) were later reidentified by Norman Hartweg (personal communication) as *K. integrum*. Examination of 55 specimens of *K. integrum* from Sinaloa and nine specimens of *K. hirtipes* from Chihuahua and Durango has revealed at least three characters which serve to separate these two confusing species. In *K. hirtipes* the plastron is narrower relative to the carapace, the gular is shorter relative to the suture separating the humerals and pectorals, and the thighs of males bear patches of cornified scales posteriorly. In *K. integrum* the plastron is wider, the gular is longer, and there are no cornified scales on the thighs of males. To our knowledge, *K. integrum* is the only species of *Kinosternon* known definitely from Sinaloa.

The measurements for 55 specimens are as follows: carapace length 36-180 (132), carapace width 33-113 (88), carapace width/carapace length 0.62-0.92 (0.68). Excluding seven individuals with carapace lengths of less than 100 mm. the ratio is 0.62-0.75 (0.67) for the remaining 48 specimens.

Kinosternon integrum was the turtle most commonly encountered during the field work. Mud turtles are found in all river drainages in the state and are taken often in roadside ponds, ditches, and on the road at night. Hatching turtles were found in late July, August, and September.

Distribution in Sinaloa.—Found in association with permanent water throughout the state, up to an elevation of about 1100 meters. See Fig. 35.

Specimens examined.—2.5 km. N Badiraguato, 230 m. (° KU 83423); 1.5 km. SE Camino Real (° KU 63633-36); 1 km. S Concepción (° KU 63612-32); 1 mi. W Copala (CSCLB 1992); Concordia (UNM 9998-10009); Culiacán (CSCLB 1993-96); 5.5 mi. N Culiacán (CSCLB 1998); 12 km. W Cuspaderos [Chupaderos?] (° KU 78978); El Dorado (° KU 45398); 5.8 mi. S Escuinapa (CSCLB 1999); 7.3 km. SW Matatán, 155 m. (° KU 78974-76); North Mazatlán (JFC 63:140); Río Presidio Bridge (SU 18263); Rosario (LACM 6550); 4.8 km. NE San Miguel (° KU 63637-46); Santa Lucía, 1100 m. (° KU 75648-53, 78977; CSCLB 1997); 5 km. SW Santa Lucía, 660 m. (° KU 80771); Teacapán (LACM 6553-57); 13 km. NNE Vaca, 400 m. (° KU 80772-73); Villa Unión (SU 22292); 9.5 km. NE Villa Unión (° KU

48557-60); 8.4 mi. NE Villa Unión (LACM 6548); 10.2 mi. NE Villa Unión (LACM 6549).

Literature records.—Mazatlán (Boulenger, 1889:42; Günther, 1885-1902: 15); Presidio (Boulenger, 1889:42; Taylor, 1938:529).

Additional records.—Concordia (UMMZ 102627-31); Culiacán (AMNH 82143); 7.6 mi. N Culiacán (UMMZ 121922); El Dorado (AMNH 90765); 20 mi. S, 14 mi. E Escuinapa (MVZ 68971); Guasave (AMNH 82142); Mazatlán (USNM 12607-08, 13388-89); 5 mi. N Mazatlán (SM 11425, 11427-32, 11456); 20 mi. S Mazatlán (AMNH 17867); ca. 13 mi. NE Palmar [de Sepúlveda], tributary of Río Bacubirito (UMMZ 122242); Presidio (FMNH 123640); Rosario (UIMNH 7052-58); 0.9 mi. N San Benito, tributary of Río Mocerito (UMMZ 122235-39); Villa Unión (UMMZ 102625-26); 4 mi. S. Villa Unión (UMMZ 118040-41); 1 mi. NW Villa Unión (AMNH 94721-22).

Family Emydidae

Chrysemys scripta hiltoni (Carr)

Pseudemys scripta hiltoni Carr, Amer. Mus. Novitates, 1181:1, Figs. 1-3, July 30, 1942 (type locality, Guirocoba, 28 miles southeast of Alamos, 1485 feet, Sonora).

Chrysemys scripta [hiltoni]: McDowell, Proc. Zool. Soc. London, 143:274, September 1964.

Remarks.—Ten specimens obtained from the Río Fuerte and nearby lagoons in northern Sinaloa, 5-7 March, 1961, are typical *hiltoni*. Their measurements are: carapace length 125-295 (180), carapace width 100-215 (130), and shell depth 45-150 (70). The series includes two males. Marginal black spots are distinct on all specimens.

Distribution in Sinaloa.—Probably occurs throughout the Río Fuerte drainage system. See Fig. 36.

Specimens examined.—4.8 km. NE San Miguel, Río del Fuerte, 90 m. (° KU 63600-09).

Additional record.—7 mi. N Los Mochis (SM 10585).

Chrysemys scripta ornata (Gray)

Emys ornata Gray, Synopsis reptilium, p. 30, 1831 (type locality, Mazatlán, Sinaloa).

Pseudemys scripta ornata: Carr, Herpetologica, 1:135, December 30, 1938.

Chrysemys scripta [ornata]: McDowell, Proc. Zool. Soc. London, 143:274, September 1964.

Remarks.—Three specimens from southern Sinaloa are typical *ornata*, with no indication of black smudge-like marks on the marginals that are characteristic of *hiltoni*. Measurements of an adult male, female, and juvenile are respectively: carapace length 151, 300, 34; carapace width 120, 235, 31; shell depth 54, 120, 18. Intergradation between *ornata* and *hiltoni* may occur in north-central Sinaloa.

This turtle inhabits roadside ponds, tanks, and wells in the lowlands of southern Sinaloa. They were seen sunning on the banks or on floating debris in both the wet and dry seasons. Field observations indicate that *ornata* is more terrestrial than *hiltoni*. Specimens have been collected on the road at night near Escuinapa, and encountered wandering overland in early spring near Teacapán. Two females contained well developed ova on April 26; nesting activities were observed on May 18 near Teacapán (Scott, 1962:19).

Distribution in Sinaloa.—Coastal drainage systems of southern Sinaloa below 200 meters. See Fig. 36.

Specimens examined.—1.5 km. SE Camino Real (* KU 63610); 1 km. S Concepción (* KU 63611); 7.3 km. SW Matatán, 155 m. (* KU 78979); Rancho Huanacastle (LACM 6551); 1 mi. N Teacapán (LACM 6552).

Literature records.—Mazatlán; Presidio (Boulenger, 1889:81).

Additional records.—2 mi. N Escuinapa (FAS 15911); 5 mi. N Mazatlán (SM 10578-82); ca. 5.5 mi. SW Villa Unión (UMMZ 113090).

Rhinoclemys pulcherrima pulcherrima (Gray)

Emys pulcherrima Gray, Cat. Shield Reptiles Brit. Mus., Pt. I Testudinata, p. 25, Table 25, Fig. 1, December 1, 1855 (based on a specimen from México).

Geoemyda pulcherrima pulcherrima: Wettstein, Sitzb. Akad. Wiss. Wien, math-nat. Kl., Abth. 1, 143:18, 1934.

Rhinoclemys pulcherrima [pulcherrima]: McDowell, Proc. Zool. Soc. London, 143:267, September 1964.

Remarks.—Two individuals (KU 75656, 43617) have the following measurements: carapace 101.9×85.0 , 94.5×83.3 ; plastron 92.3×56.6 , 87.3×51.2 (hind lobe); depth 42.8, 41.9; length anterior lobe of plastron 20.0, 18.9; length posterior lobe 26.6, 26.9; length bridge 45.1, 40.7. In both specimens the lateral borders of the carapace are strongly bowed, a distinct median keel is present dorsally, the posterior edge of the plastron is deeply notched, the gular is triangular with its anterior corners protruding beyond the plastron edge, there are three light lines anterior to the eye, and the plastron is yellow laterally with a brown stripe occupying the median half. Other characters agree with Gray (1855:25) and Günther (1885-1902:6-7).

Although *Rhinoclemys pulcherrima* apparently is abundant to the north and south of Sinaloa (Bogert and Oliver, 1945:396) only a few specimens have been collected in the state. Nothing is known concerning the specific habitat of this species. Two turtles (KU 43617; CSCLB 2000) were found crossing a road in July; a third (KU 75656) was obtained from natives in the same month.

Distribution in Sinaloa.—Inhabits canyons and arroyos at intermediate elevations on the Pacific versant of the Sierra Madre Occidental. See Fig. 37.

Specimens examined.—7.5 mi. E Concordia (CSCLB 2000); 1.5 km. W Coyotitán (° KU 43617); Santa Lucía, 1100 m. (° KU 75656).

Literature record.—Presidio de Mazatlán (Günther, 1885-1902:6).

Additional record.—"Vicinity of Los Mochis" (UMMZ 120422).

Terrapene nelsoni klauberi Bogert

Terrapene klauberi Bobert, Amer. Mus. Novitates, 1226:2, 1943 (type locality, Rancho Guirocoba, about 18 miles southeast of Alamos, Sonora).

Terrapene nelsoni klauberi: Milstead and Tinkle, Copeia, No. 1:184, March 20, 1967.

Remarks.—Inquiry among the inhabitants at Terreros led to the discovery of this turtle, heretofore unknown from the state. A single plastron and carapace was found on a steep hillside near Terreros. William W. Milstead kindly examined this specimen and provided the identification. The specimen is a male with the following characteristics: total length, 135; posterior lobe of plastron length, 81; interabdominal suture, 28; interfemoral, 14; interanal, 39; posterior lobe ratios—interabdominal, 0.34; interfemoral, 0.17; interanal, 0.48 (all measurements by Milstead).

The specimen was found on an isolated rocky peak that reaches a height of about 600 meters; the hillside is covered by a low-canopy forest. Numerous burrows were found on the southeastern slope of the peak, some of which were attributed to *Terrapene*. Additional collecting in the foothills along the eastern border of the state and on other isolated peaks on the coastal plain should turn up additional specimens.

Distribution in Sinaloa.—Known only from an isolated peak in the central lowlands. See Fig. 37.

Specimen examined.—About 4 mi. W Terreros (JMS osteo. coll. 911).

Family Testudinidae

Gopherus agassizii (Cooper)

Xerobates agassizii Cooper, Proc. California Acad. Sci., 2:120, 1863 (type locality, Mountains of California near Fort Mojave, Kern County, California).

Gopherus agassizii: Stejneger, N. Amer. Fauna, 7:161, 1893.

Remarks.—Bogert and Oliver (1945:398-9), on the basis of four specimens of *Gopherus agassizii* from Alamos, Sonora, reported that the population inhabiting the Río Fuerte drainage has become partly

differentiated from *G. agassizii* in Arizona and California. The Alamos specimens differed from other specimens of *Gopherus* in the ratios of plastron width and length, shell depth and plastron length, and hind foot diameter and head width. One specimen was reported from Sinaloa (Loomis and Geest, 1964:203).

Distribution in Sinaloa.—Known only from the northern foothills. See Fig. 37.

Specimens examined.—None.

Literature record.—3.8 mi. NE El Fuerte (Loomis and Geest, 1964:203).

Family Cheloniidae

Caretta caretta *gigas* Deraniyagala

Caretta gigas Deraniyagala, Ceylon Journ. Sci. sect. B, 28:61, 1933 (type locality, Ceylon).

Caretta caretta gigas: Deraniyagala, Tetrapod reptiles of Ceylon, 1:164, 1939.

Remarks.—This widely distributed species has been reported only from the southern coast and from adjacent Baja California.

Distribution in Sinaloa.—Known only from the coast at Mazatlán. See Fig. 38.

Specimens examined.—None.

Literature records.—Mazatlán (Boulenger, 1889:186); Sinaloa [state only] (Anonymous, 1966:25).

Chelonia mydas *carrinegra* Caldwell

Chelonia mydas carrinegra Caldwell, Contrib. in Sci., Los Angeles County Mus., 61:4, December 7, 1962 (type locality, waters adjacent to Isla Angel de la Guarda, Gulf of California, Baja California).

Remarks.—Green sea turtles have been taken in the Gulf of California and Pacific Oceans from Sonora southward to Michoacán, México. This species apparently is abundant (Carr, 1961:68) and a valuable food source in some portions of the state.

Distribution in Sinaloa.—In waters off the coast. See Fig. 38.

Specimens examined.—None.

Literature records.—Sinaloa [state only] (Anonymous, 1966:19); Bahía de Ohura; Topolobampo (Carr, 1961:68).

Eretmochelys imbricata (Linnaeus)

Testudo imbricata Linnaeus, Systema naturae, ed. 12, p. 350, 1766, (type locality, American seas).

Eretmochelys imbricata: Fitzinger, Systema reptilium, fasc. 1:30, 1843.

Remarks.—This species has been reported as common in estuaries

along the southern coast (Scott, 1962:17). The name used herein follows Smith and Taylor (1950b:16, footnote).

Distribution in Sinaloa.—Known only from the southern coast. See Fig. 38.

Specimens examined.—None.

Literature records.—Teacapán (Scott, 1962:17).

Lepidochelys olivacea (Eschscholtz)

Chelonia olivacea Eschscholtz, Zool. Atlas, pt. 1, p. 2, 1829 (based on a specimen from Manila Bay, Philippine Islands).

Lepidochelys olivacea: Girard, United States Exploring Expedition . . . , 20 (Herpetology):435, 1858.

Remarks.—This species has been reported from several localities on the Pacific coast, and ranges as far northward as Tiburon Island, Sonora (Bogert and Oliver, 1945:417).

Distribution in Sinaloa.—Entire Pacific coast. See Fig. 38.

Specimen examined.—Mazatlán (JMS osteo. coll. 1310).

Literature records.—Sinaloa [state only] (Anonymous, 1966:35); Mazatlán; Tamboritos; Teacapán (Carr, 1961:69); Teacapán (Scott, 1962:17).

Additional record.—Mazatlán (USNM 12609).

Family Dermochelyidae

Dermochelys coriacea (Linnaeus)

Testudo coriacea Linnaeus, Systema naturae, ed. 12, vol. 1, p. 350, 1766 (type locality, unknown).

Dermochelys coriacea: Blainville, Bull. Sci., Soc. Philom., Paris, p. 119, 1816.

Remarks.—The leather back turtle has been taken occasionally in the Gulf of California (Caldwell, 1962:25). Although there are no known records from the coast of Sinaloa, a record from Guaymas, Sonora (Smith and Taylor, 1950b:13) suggests its presence in the state. *Dermochelys* is included here in the herpetofauna of Sinaloa, pending evidence to the contrary.

Distribution in Sinaloa.—In waters off the coast.

Specimens examined.—None.

Literature record.—Sinaloa [state only] (Anonymous, 1966:13).

Order SQUAMATA

Suborder SAURIA

Family Gekkonidae

Coleonyx variegatus fasciatus (Boulenger)

Eublepharis fasciatus Boulenger, Cat. Liz. Brit. Mus., 1:234, 1885 (type locality, Ventanas, Durango).

Coleonyx variegatus fasciatus: Conant, Amer. Mus. Novitates, 2205:6, January 29, 1965.

Remarks.—Only five specimens of *Coleonyx* have been collected in Sinaloa. Edward H. Taylor found a specimen beneath a pile of logs south of Presidio and referred it to *Coleonyx fasciatus* (Taylor, 1935b:203-05, 1938:517; Klauber, 1945:182-84, 205). A second specimen (UIMNH 57847), collected at night on the highway in the same area, exhibits the coloration typical of *C. fasciatus*. Three other specimens are known from north of Culiacán; two were taken at night on the road and a third (SU uncataloged) was found beneath a rock. Conant (1965:4-6) considered his specimen (AMNH 87617) to be intermediate between *C. variegatus sonoriensis* and *C. fasciatus* and accordingly reduced *fasciatus* to subspecific status. The other two lizards from the same area confirm his findings.

Distribution in Sinaloa.—Probably throughout the lowlands of the state. See Fig. 39.

Specimen examined.—11 mi. S Guamúchil (CSCLB 2002).

Literature records.—18 mi. NW Culiacán (Conant, 1965:4); 10 mi. S Presidio (Klauber, 1945:182; Smith and Taylor, 1950b:43; Taylor, 1935b:203).

Additional records.—7.4 mi. S junc. hwy. 15 and 40 (UIMNH 57847); 21 mi. N Río Culiacán [hwy. 15] (SU uncataloged, field number FWB 2140).

Gehyra mutilata (Wiegmann)

Peropus mutilatus Wiegmann, Nova Acta Acad. Leop.- Carol., 17:238, 1835 (type locality, Manila, Philippine Islands).

Gehyra mutilata: Boulenger, Catalogue Lizards Brit. Mus., 1:148, 1885.

Remarks.—Two females agree with the redescription by Smith and Necker (1943:197-99) based on one adult and one juvenile of undetermined sex. The snout-vent lengths are 48, 56; tail 50, 33 (partially regenerated); supralabials 7/7, 8/8 to center of eye; infra-labials 7/7 to center of eye. Both specimens were captured from the side of a building on June 4, 1962. The name *Gehyra mutilata* is used following Boulenger (1885a:148) and Bustard (1965:260).

Gehyra mutilata has been introduced into western México at several seaport towns. The climbing ability and secretive habits of these lizards make them likely candidates for stowaway transport with ship cargos. The original colonists probably came from the Philippine Islands (Taylor, 1922:64). These lizards are seen in abundance at night throughout the older parts of Mazatlán. Specimens were found by careful searching of walls and buildings along the beach front. Individuals are especially plentiful around lights where they feed on insects attracted to the light.

Distribution in Sinaloa.—Known only from Presidio and Mazatlán, but probably present elsewhere on the seacoast in association with human habitation. See Fig. 39.

Specimens examined.—Mazatlán (° KU 73653-54; JFC 62:34-35; LACM 3244-49, 6564-66; UAZ 4569-79, 10242, 10244, 10246, 10254, 10283); N Mazatlán (CSCLB 1976).

Literature records.—Mazatlán (Martín del Campo, 1941:761; Smith and Taylor, 1950b:52); Presidio (Boulenger, 1885a:150; Smith and Taylor, 1950b:52).

Additional records.—Mazatlán (SM 11295-310; UIMNH 46846; USNM 153771-72).

Hemidactylus frenatus Schlegel

Hemidactylus frenatus Schlegel, in Duméril and Bibron, *Erpétologie Générale* . . . 3:366, 1836 (based on two specimens from Timor and Java; type locality restricted to Java by Loveridge, *Bull. Mus. Comp. Zool.*, Harvard College, 98 (1):127, January, 1947; type locality further restricted to Batavia, Java by Taylor, *Univ. Kansas Sci. Bull.*, 35:1549, September 10, 1953).

Remarks.—Two females were collected in Los Mochis on September 8, 1963, by C. H. Lowe, Jr. They have the following characters: snout-vent length 20, 39; lamellae beneath fourth toe 10, 10; granules between eyes 37, 40; internasal scale 1, 1; scales in row between nasals posterior to internasals 5,4; supralabials 9-8, 9-9; infralabials 12-12, 12-12; postmentals in mutual contact medially and also contact infralabials 2-2, 2-1. Both specimens have 8 rows of enlarged dorsal tubercles at midbody; 2 paravertebral rows with 19-16, 18-20 tubercles; 6 lateral rows with 21, 21-22 tubercles that converge anteriorly and posteriorly. Tails are incomplete with 6, 6 scales in anterior caudal rows. Both specimens agree with *Hemidactylus frenatus* from Zihuatanejo and Acapulco, Guerrero, in all characters examined. It is likely that *Hemidactylus* was introduced into Los Mochis within the last 25 years, probably from an active Mexican port such as Acapulco.

Distribution in Sinaloa.—Known only from Los Mochis. See Fig. 39.

Specimens examined.—Los Mochis (UAZ 11939-40).

Phyllodactylus homolepidurus homolepidurus Smith

Phyllodactylus homolepidurus Smith, *Univ. Kansas Sci. Bull.*, 22:121, November 15, 1935 (type locality, five miles southwest of Hermosillo, Sonora).

Phyllodactylus homolepidurus homolepidurus: Dixon, *Sci. Bull.*, Research Center, New Mexico State Univ., 64(1):40, March 1964.

Remarks.—Dixon (1964:42) stated that he knew of no records of

Phyllodactylus homolepidurus outside of the "rock outcroppings of sandstone, schist, and granite within a 130 mile radius of Hermosillo, Sonora." Three specimens examined by us are from northern Sinaloa, thus representing a considerable extension of the known range southward.

These specimens have, respectively: 14, 12, 14 rows of dorsal tubercles; 5, 6, 6 tubercles at base of tail; 20, 19, 19 tubercles between axilla and groin; 32, 32, 33 paravertebral tubercles; 13, 13, 13 lamellae beneath fourth toe; 23, 25, 20 interorbital scales; 26, 28, 28 scales across snout between third labials; 7, 7, 7 scales bordering postmentals; 8, 7, 7 scales bordering internasals; 64, 62, 61 scales from posterior gular region to anus; and 14, 15, 14 scales between nostril and eye.

These data confirm a decrease from north to south in number of lamellae beneath fourth toe and of scales bordering postmentals, and an increase from north to south in number of scales across snout at third labials and of scales between nostril and eye—as demonstrated by Dixon (1964:39) for specimens in central and northern Sonora. However, our specimens have more scales bordering the internasals, and fewer interorbital scales, than expected from north-south trends in these characters as reported by Dixon.

Phyllodactylus tuberculosus is known from northern Sinaloa, near Los Mochis (KU 67538-40). Although the ranges of *P. homolepidurus* and *P. tuberculosus* apparently overlap, these species may be ecologically separated in this area.

Distribution in Sinaloa.—Northern coastal lowlands. See Fig. 39.
Specimens examined.—Topolobampo (CSCLB 1518-1520).

Phyllodactylus tuberculosus saxatilis Dixon

Phyllodactylus tuberculosus saxatilis Dixon, Sci. Bull., Research Center, New Mexico State Univ., 64(1):31, March 1964 (type locality, eight miles northeast of Villa Unión, 200 ft., Sinaloa).

Remarks.—Fifty-four specimens of *Phyllodactylus* are referred to *P. tuberculosus saxatilis* following Dixon (1964:31-36). Dixon recorded three species of *Phyllodactylus* in northwestern México: *P. homolepidurus homolepidurus* in central Sonora; *P. tuberculosus saxatilis* in southern Sonora, Sinaloa, central Nayarit, and northern Jalisco; and *P. lanei rupinus* in southern Nayarit and northern Jalisco. Difficulty was experienced in allocating specimens from Sinaloa to one of the above species because of the extensive overlap in the ranges of variation of certain meristic characters. With respect

to eleven meristic characters, all but nine of the specimens have six or more characters that are within the range of variation for all three species.

The specimens that we examined have the following characters: rows of dorsal tubercles, 12-16 ($13.6 \pm .11$); rows of tubercles at base of tail, 4-7 ($5.6 \pm .10$) (excluding KU 67515, 75480); tubercles between axilla and groin, 17-22 ($18.9 \pm .17$) (excluding KU 67537); paravertebral tubercles, 26-38 ($31.4 \pm .37$) (excluding KU 29531, 67537); lamellae beneath fourth toe, 11-15 ($13.1 \pm .11$); interorbital scales, 16-29 ($22.0 \pm .38$); scales across snout between third labials, 22-29 ($25.7 \pm .38$) (excluding KU 67516); scales bordering postmentals, 5-10 ($7.0 \pm .15$); scales bordering internasals, 6-9 ($6.9 \pm .08$); scales from posterior gular region to anus, 59-78 ($66.5 \pm .52$); scales between nostril and eye, 11-16 ($13.4 \pm .15$). These characters are equivalent to those used by Dixon (1964).

Sinaloan specimens examined closely resemble specimens of *P. t. saxatilis* (Dixon, 1964:31-36) in the number of tubercles between axilla and groin, rows of tubercles at base of tail, lamellae beneath fourth toe, interorbital scales, scales across snout between third labials, scales bordering internasals, scales between nostril and eye, and scales from posterior gular region to anus. The specimens closely resemble *P. h. homolepidurus* (Dixon, 1964:40-42) in the rows of dorsal tubercles, and the number of scales bordering postmentals. The specimens closely resemble *P. lanei rupinus* (Dixon, 1964:67-71) in the number of paravertebral tubercles.

The Sinaloan specimens were compared with 26 specimens of *P. h. homolepidurus* (KU 67464-89 from Sonora) and with four specimens of *P. lanei rupinus* (three, KU 63371-73, from Jalisco; one, KU 63370, from Nayarit). Characteristically, specimens of *P. h. homolepidurus* are paler and more uniform in dorsal coloration than are specimens of *P. t. saxatilis* from Sinaloa. The four specimens of *P. l. rupinus* are more like *P. t. saxatilis*. Otherwise, no consistent differences can be determined in the dorsal pattern. Specimens of *P. h. homolepidurus* usually have a creamy white belly with pale yellow lateral patches. The yellow patches are almost indistinguishable in some *homolepidurus*, faintly present in only two *saxatilis* (both from southern Sinaloa), and absent in all of the *rupinus*. Specimens of *P. t. saxatilis* can be readily separated from *P. h. homolepidurus* when the dorsal tubercles at mid-body are compared in lizards of similar snout-vent length. The tubercles of *saxatilis* are larger, more distinctly keeled, and the base is oval in shape, while in

homolepidurus the tubercles are smaller and lower (due to the less distinct keel) and the base is usually circular in shape. Accordingly, the allocation of these specimens to *P. t. saxatilis* seems reasonable.

Phyllodactylus tuberculosus is nocturnal in habit and is frequently encountered on rocky hillsides, near caves, beneath stone bridges, and in road culverts. One specimen (LACM 6570) was found at night on the highway where the road passed through a rocky ridge.

Distribution in Sinaloa.—Probably occurs throughout the state, although specimens are lacking from some areas in the northern highlands. See Fig. 40.

Specimens examined.—24 km. NW Acaponeta [Nayarit], 75 m. (* KU 67515); 20 km. N, 5 km. E Badiraguato, 240 m. (* KU 83398); E base Cerro Pocitos, 17.5 mi. W Pericos junc. (UAZ 4375, 4377); 16 km. NNE Choix, 520 m. (* KU 73655); 4 km. NE Concordia (* KU 73662); 15 km. NE Concordia, 240 m. (* KU 75477-82); 21 km. NE Concordia (* KU 75483-84); 5 mi. N Culiacán (CSCLB 1989); 13.9 mi. N Culiacán (CSCLB 1988); 15.8 mi. N Culiacán (CSCLB 1987); 32 km. SE Elota 120 m. (* KU 67525-37); 37 km. S Escuinapa (* KU 73663); 13 km. SW Escuinapa, 15 m. (* KU 67516); Labrados (CAS 64979); 22 km. N Los Mochis (* KU 67538-39); 26 km. N Los Mochis (* KU 67540); Matatán, 170 m. (* KU 73657-61); 7 km. SW Matatán, 155 m. (* KU 78508); Mazatlán (CSCLB 1985-86); 33.2 mi. N Mazatlán (LACM 6570); 3 mi. S Palmillas (LACM 25689-90); 2 km. S Pericos (* KU 37754); Río Piaxtla, 1 mi. W. hwy. 15 (CSCLB 1990-91); 8 km. SSE Rosario, 35 m. (* KU 29531); 1 km. W Rosario, 35 m. (* KU 29532); Santa Lucía, 1100 m. (* KU 75485-86); 2 km. E Santa Lucía, 1700 m. (* KU 40428-29); 3 km. E Santa Lucía, 1700 m. (* KU 40430); 44 km. ENE Sinaloa, 180 m. (* KU 69922); 19.6 mi. NE hwy. 15 [Villa Unión] on hwy. 40 (LACM 6567-69); 13 km. ENE Villa Unión, 60 m. (* KU 67514, 67518-25); 16 km. ENE Villa Unión, 140 m. (* KU 67517).

Literature records.—5 mi. SW Copala; 8 mi. NW Culiacán; 10 mi. SE Elota; 4 mi. NW Elota; 28 mi. NW Elota (Dixon, 1964:35); Mármol (Lewis and Johnson, 1956:277); Mazatlán (Smith, 1935a:126; Van Denburgh, 1898:460); 18.5 mi. N Mazatlán; 1 mi. E. Mazatlán (Dixon, 1964:35-36); 2 mi. E Mazatlán (Smith, 1935a:126; Taylor, 1938:517); Presidio (Boulenger, 1885a:80; Dixon, 1964:36).

Additional records.—19.5 mi. N Culiacán (FAS 15863); 8 mi. NW Culiacán (UMMZ 117366); El Dorado (AMNH 90766-67); 23 mi. S Guamúchil (FAS 15864).

Family Iguanidae

Anolis nebulosus (Wiegmann)

Dactyloa nebulosa Wiegmann, Herpetologia Mexicana, p. 47, 1834 (type locality, México).

Anolis nebulosa: Bocourt, Mission Scientifique au Mexique et dans L'Amérique Centrale. Reptiles, Livr. 2:68-69, 1873.

Remarks.—The characters used to distinguish *Anolis nebulosus* (Wiegmann) from *A. nebuloides* Bocourt often are applicable to some populations but not to others. Duellman (1961:61-63) synthesized the available information for both species and presented characters which distinguish the two species in Michoacán. A

general application of these characters to anoles from Sinaloa resulted in allocation of these lizards to *A. nebulosus*. The characters used were: dorsal scales slightly smaller than ventral scales; throat fan bright orange in adult males. The smoothness and low keeling of snout scales is variable in the Sinaloan lizards.

The color of the dewlap is probably the most significant character in *Anolis* systematics, especially for distinguishing between *A. nebulosus* and *A. nebuloides*. Fifty-seven specimens of *Anolis* from Sinaloa were examined; the dewlap color for 14 males was orange in life. Lewis and Johnson (1956:278) reported seven *Anolis* from Mármol, Sinaloa with "large, red" dewlaps. Taylor (1938:518) described three specimens from southern Sinaloa as having dewlaps "grayish or with a pinkish tinge." Zweifel and Norris (1955:233) listed *Anolis* with pale pink gular pouch areas from southern Sonora. In Sinaloa it has been noted that the orange dewlap of living *Anolis nebulosus* turns reddish or pinkish after the animals have been preserved. This color change may account for some of the reports of lizards with red or pink dewlaps from the state. If, however, there is an anole with a red dewlap in Sinaloa, it seems probable to us that this lizard would represent a species distinct from *Anolis nebulosus*. All specimens examined during this study had, in life, an orange dewlap and are here referred to *Anolis nebulosus*.

Variation in dorsal color pattern is most evident in the females, which usually have a light middorsal stripe with straight, irregular or serrate edges. Some females have a brown middorsal stripe, heavily serrate, bordered with tan.

This lizard is much more obvious in the forest during the dry season than during the rainy season. Most specimens were collected in the lower levels of the forest, usually on limbs of low trees and shrubs. Several individuals were found at night asleep at the tip of branches or on tall grass.

Distribution in Sinaloa.—Known from most of the state except the dry northern lowlands. See Fig. 41.

Specimens examined.—E base Cerro Pocitos, 17.5 mi. W Pericos junc. (UAZ 4378-81); 16 km. NNE Choix, 520 m. (° KU 73670-71); 1 km. S Concepción, 76 m. (° KU 63677); 5.5 mi. NE Concordia (LACM 6573); 6 km. E Cosalá, 460 m. (° KU 73672-73); N Culiacán (CSCLB 2035); 19 km. N Culiacán (° KU 40437); 14 mi. N Culiacán (CSCLB 2038); 36.8 mi. N Culiacán (CSCLB 2031-32); 46 mi. S. Culiacán (CSCLB 2040); Escuinapa (UCLA 14843); La Cruz (LACM 6572); Mazatlán (LACM 6579); 5 km. NNW Mazatlán (° KU 29537); 8 km. NNW Mazatlán (° KU 63375-76); 3 mi. S Palmillas (LACM 25691); 5 km. SW El Palmito (Durango), 1850 m. (° KU

75500-02); 1.5 km. S Pericos (° KU 37731); 1 km. E San Blas (° KU 38066); San Ignacio, 210 m. (° KU 73674-75; LACM 6574-78); 5.5 km. NE San Lorenzo, 150 m. (° KU 83399); Santa Lucía, 1100 m. (° KU 75499; CSCLB 2039); near Santa Lucía (° KU 40438-46); 1 km. NE Santa Lucía, 1150 m. (° KU 78509); 2.2 km. NE Santa Lucía (via hwy. 40), 1930 m. (° KU 78516-18, 78520); 2 km. E Santa Lucía (° KU 40431-35, 44640); 1-2 mi. W Santa Rita (LACM 6580); Teacapán (LACM 6581); 54 mi. N Tropic of Cancer (LACM 6571); 13 km. NNE Vaca, 400 m. (° KU 80702); 8 km. N Villa Unión, 140 m. (° KU 80691-94); 12 km. N Villa Unión, 120 m. (° KU 80695-701); 1 mi. S, 26 mi. E Villa Unión (CSCLB 2036-37); 3 km. W Villa Unión (° KU 29534).

Literature records.—El Dorado (Fugler and Dixon, 1961:9); Mármol (Lewis and Johnson, 1956:278); Mazatlán (Martín del Campo, 1941:761; Taylor, 1938:518); 17 mi. N Mazatlán (Tanner and Robison, 1959:76); Presidio (Boulenger, 1885b:77); near Presidio (Taylor, 1938:518).

Additional records.—Chele, ca. 300 ft. (UMMZ 110909); 11 mi. NE Concordia (SM 11693-98); 2 mi. WSW Copala, 500 ft. (TCWC 12787); 4 mi. E Coyotitán (AMNH 69703); 14 mi. SW El Batel (AMNH 75868); El Dorado (AMNH 90768-71); Elota (AMNH 96592); 4 mi. W Elota (AMNH 62334); Escuinapa (AMNH 1550); 1.3 mi. S La Cruz rd. (JFC 62:2); Mazatlán (USNM 25152, 40041); near Mazatlán (USNM 47253); 10 mi. N Mazatlán (MCZ 61461-67); 17 mi. N Mazatlán (MCZ 61453-60); 30 mi. N Mazatlán (MVZ 66197); 32 mi. N Mazatlán, 350 ft. (TCWC 12788-89); 36 mi. N Mazatlán (FAS 11584-86); 2 mi. E Mazatlán, 50 ft. (TCWC 12786); about 5 mi. [E] Mazatlán (UMMZ 102593-94); 7.1 mi. SE Mazatlán (UIMNH 6655); 9.2 mi. S Mazatlán (UIMNH 40698); 12.1 mi. N Pericos (UIMNH 40697); 9 mi. NW Piaxtla (SM 11665-66); Plomosas (USNM 47693-96); 15 mi. S Presidio (UIMNH 20194); Rincón de Urías (AMNH 20733-36); Rosario (USNM 47697-98); Venodio (USNM 73268); 5 mi. E Villa Unión (UMMZ 113060); 3 mi. SE Villa Unión (SM 11684-92); 10 mi. S Villa Unión (MCZ 61468-70).

Anolis utowanae Barbour

Anolis utowanae Barbour, Copeia, no. 1:12, April 12, 1932 (type locality, about 10 miles north of Mazatlán, Sinaloa).

Remarks.—Repeated efforts to collect additional specimens of this lizard have failed. On three different occasions trips were made to the area of the type locality without results. Comparison of the holotype with other anoles from Sinaloa reaffirms the distinctiveness of *A. utowanae*. The dewlap color is unknown.

Distribution in Sinaloa.—Known only from the type locality. See Fig. 42.

Specimen examined.—About 10 mi. N Mazatlán (MCZ 31035).

Callisaurus draconoides bogerti Martín del Campo

Callisaurus draconoides bogerti Martín del Campo, Anales del Instituto Biología, México, Tome XIV:619, 1943 (type locality, Isla de los Chivos, en el Puerto de Mazatlán, Sinaloa).

Remarks.—Fugler and Dixon (1961:9) summarized the nomenclatural history of this species in Sonora and Sinaloa, and referred the lowland populations from southern Sinaloa through Sonora to *Callisaurus draconoides bogerti* and the montane Guirocoba—

Alamos populations (Sonora) to *C. d. brevipes*. Our data support this arrangement for Sinaloan specimens (Table 3). The ratio of hind leg length into snout-vent length was about the same in the Sinaloan material examined as was the ratio of fourth toe length into snout-vent length. The one specimen from Isla San Ignacio had a lower fourth toe to snout-vent ratio than the other two populations. If the one Isla San Ignacio specimen is considered, a decrease in ventral scales and an increase in femoral pores is indicated from south to north in the lowlands. Although this insular specimen supports this trend in variation for the above two characters, disagreement is found in fourth toe lamellae and the ratio noted above. Several possibilities exist to explain these differences: the insular population may be expected to differ in certain (or all) characters from the mainland population depending on the duration of its isolation; and differences in the methods of securing data may have resulted in a higher lamellar count and lower ratio. Another and perhaps more plausible explanation for this disagreement is that the number of toe lamellae is correlated with the substrate of the habitat and hence variable from deme to deme and of no systematic value.

Five specimens from the vicinity of El Fuerte are referred to *C. d. brevipes* on the basis of the data in Table 3. Note that in ventral scales and femoral pores the greatest difference in the two subspecies is between adjacent populations.

There has been some confusion as to the systematic relationships between *bogerti* in Sinaloa and the coastal race in Sonora referred to *bogerti* (Fugler and Dixon, 1961:9) and *brevipes* (Langebartel and Smith, 1954:128). Males from near Guaymas and Hermosillo, Sonora, have the same breeding colors found in the Sinaloan populations of *bogerti*. A male from Teacapán (LACM 6584) has two lateral dark bars covered with a bright green wash. The green extends posteriorly and laterally to the insertion of the hind legs. There is an orange-brown wash anterior to the green that extends onto chest and forelegs; it is darkest anterior to the bars. The chin and throat are dusky orange, darkest in the gular area. An adult female (LACM 6585) has a bright orange spot in front of the body bars, a yellow wash through the bars and onto the hind legs and base of the tail. The chin is white with lateral gray streaks and bright orange gular spot. We have not examined live material referred to *brevipes*. It appears that the coastal race in Sinaloa

TABLE 3.—A Comparison of Data for *Callisaurus draconoides bogerti* and *C. d. brevipes* in Sonora and Sinaloa.

SPECIES	Locality	Number of specimens	Ventral scales	Fourth toe lamellae	Total femoral pores
<i>C. d. bogerti</i>	Vicinity of Mazatlán	28	82-95 (85.5)	27-35 (31.5)	17-30 (24.8)
<i>C. d. bogerti</i>	* El Dorado	21	76-92 (84.6)	26-34 (29.0)	13-19 (15.2) [= 30.4]
<i>C. d. bogerti</i>	Isla San Ignacio	1	83	35	32
<i>C. d. brevipes</i>	Vicinity of El Fuerte	5	76-82 (78.6)	30-35 (33.0)	23-26 (24.4)
<i>C. d. brevipes</i>	**	9	75-82 (78.2)	30-33 (31.7)	11-15 (12.8) [= 25.6]

* Data from Fugler and Dixon, 1961:10.

** Data from Bogert and Dorson, 1942:175.

is the same as the coastal Sonoran population. This tentative conclusion may be revised by Benjamin H. Banta, who is presently working on lizards of the genus *Callisaurus*.

Distribution in Sinaloa.—Occurs in beach habitat along the coast to Teacapán. See Fig. 43.

Specimens examined.—N. Mazatlán (CSCLB 2018-30; JFC 62:30-32; LACM 6582-83); 1.5 km. N Mazatlán (° KU 40366-84, 68722-25); 5 km. NNW Mazatlán (° KU 29652-56); Playa Visnaga (UAZ 9505-19); Isla San Ignacio, 3 m. (° KU 69923); 1 mi. N Teacapán (LACM 6584-86).

Literature records.—Costa Rica (Smith and Van Gelder, 1955:145); La Boca (Fugler and Dixon, 1961:9); Mazatlán (Martín del Campo, 1941:761; Van Denburgh, 1898:461); Mazatlán, Isla de los Chivos (Martín del Campo, 1941:761).

Additional records.—Altata (UMMZ 118967); 6 mi. W Baca del Rico [= La Boca?] (SM 11410-15); El Dorado (AMNH 90779-85; LSU 6441-42); 9 mi. SW El Dorado (SM 11416-24); Mazatlán (SM 10213-23; UF 20621; UMMZ 102569); Mazatlán, Isla de los Chivos (AMNH 64715-17); 4 mi. W Mazatlán (MVZ 59011).

Callisaurus draconoides brevipes Bogert and Dorson

Callisaurus draconoides brevipes Bogert and Dorson, Copeia, no. 3:173-75, October 8, 1942 (type locality, Guirocoba, 18 miles southeast Alamos, Sonora).

Remarks.—Lizards of this subspecies, discussed in the account of *Callisaurus draconoides bogerti*, are frequently encountered along the sandy washes and arroyos of northeastern Sinaloa. On June 16, 1963, five specimens were obtained along the Río Fuerte in deciduous thorn woodland dominated by *Acacia* and *Prosopis*. *Holbrookia* was common in the same area.

Distribution in Sinaloa.—Known only from the area drained by the Río de Choix and Río Fuerte above El Fuerte. See Fig. 43.

Specimens examined.—8 km. N El Fuerte, Río Fuerte, 160 m. (° KU 78521); 6 km. NE El Fuerte, Río Fuerte, 155 m. (° KU 78522-25).

Literature record.—Río de Choix, Río Fuerte (Bogert and Dorson, 1942:173).

Additional records.—2 mi. N Choix (FMNH 71479-80); 4 mi. NNE El Fuerte (FMNH 71481); 8 mi. NNE El Fuerte (FMNH 71482-84).

Ctenosaura hemilopha (Cope)

Cyclura (*Ctenosaura*) *hemilopha* Cope, Proc. Acad. Nat. Sci. Philadelphia, 1863, p. 105 (type locality, Cape San Lucas, Baja California).

Remarks.—In a revision of the genus *Ctenosaura*, Bailey (1928: 8-9) listed six species as occurring in western México: *C. acanthura*, *C. hemilopha*, *C. brachylopha*, *C. pectinata*, *C. brevirostris*, and *C. parkeri*. Bailey distinguished these species utilizing characters of the median dorsal scales, head length, and numbers of scale rows between the whorls of spinous caudal scales. Smith (1935a:134-142)

and Smith and Taylor (1950b:73-76) allocated *C. brachylopha*, *C. breviostris* and *C. parkeri* to the synonymy of *C. pectinata*. Specimens of *C. acanthura* reported from western México were designated as *C. pectinata* (Smith and Taylor, 1950b:74, footnote). Smith and Taylor (1950b:73, 75) characterized *C. hemilopha* as possessing a single row of small scales between the fourth and fifth rows of enlarged caudal spines, and having a range including southern Baja California and central Sonora to northern Sinaloa. They characterized *C. pectinata* as possessing three rows of small scales between the fourth and fifth proximal rows of enlarged caudal spines, and having a range from southern Sinaloa southward to the Isthmus of Tehuantepec, Oaxaca. Other authors have followed Smith and Taylor in distinguishing between *C. hemilopha* and *C. pectinata* in Sinaloa (Smith and Van Gelder, 1955:145; Fugler and Dixon, 1961:11). Bailey (1928:8-9) stated that the median enlarged dorsal scales are interrupted at the sacrum in *hemilopha* and complete to the end of the tail in *C. pectinata*.

In an effort to clarify the relationships between these two species in Sinaloa, we examined more than 150 specimens of *Ctenosaura* from western México. All specimens of *C. hemilopha* examined from throughout its range have the dorsals interrupted over the sacrum. Of 99 specimens of *pectinata* examined, 46 per cent possessed a complete row of enlarged dorsal scales, whereas 54 per cent had enlarged dorsal scales interrupted over the sacrum. This condition might suggest a clinal trend in dorsal scales from interrupted series in the north to a complete series in the south. However, there was no geographic trend in the dorsal scale row character in *C. pectinata* from Sinaloa to Colima, both conditions occurring throughout this region. In Sinaloa, 36 of 50 specimens of *C. pectinata* examined for this character have the enlarged dorsal scales interrupted over the sacrum. Individuals in a large series of *C. similis* from Costa Rica have a complete row of dorsal scales. If *similis* were included in the above analysis, a clinal gradient is indicated for this character from Sonora, México, to Panamá.

The number of small scale rows between the fourth and fifth caudal whorls varies in the specimens examined. Damaged specimens were not included in the following counts. Twenty-six of 54 specimens (48%) of *C. hemilopha* have a single row of small scales preceding the fifth caudal whorl; 28 specimens (52%) have two rows of scales preceding the fifth caudal whorl. In Sinaloa, 14 specimens (56%) of *hemilopha* have one row of small scales and

11 specimens (44%) have two rows of small scales preceding the fifth caudal whorl. A total of 92 *C. pectinata* examined includes 34 specimens (37%) with two rows of small scales, 53 specimens (58%) with three rows of small scales, and 5 specimens (5%) with four rows of small scales preceding the fifth enlarged caudal whorl. In Sinaloa, 30 specimens (50%) of *pectinata* have two rows of scales, 29 specimens (48%) have three rows, and 1 specimen (2%) has four rows. Thus, the number of rows of small scales preceding the fifth caudal whorl seemingly increases from north to south. As with the other character discussed, there is considerable overlap in counts for *hemilopha* and *pectinata* in Sinaloa.

Little is known concerning the amount of sexual dimorphism or the degree of ontogenetic change in either of these scale characters. Neither character serves to separate the two species in Sinaloa. A re-evaluation of these characters as diagnostic criteria for distinguishing species of *Ctenosaura* is warranted in view of our findings. Because of the lack of knowledge of variation in other characters in the genus *Ctenosaura* (a necessary precursor to an understanding of specific relationships), and because of the scope of this paper we continue to recognize two species of *Ctenosaura* in Sinaloa based primarily on differences in color patterns. We suspect a detailed study of *Ctenosaura* would indicate that a single species ranges from southern Sinaloa, México, along the Pacific coast to Tehuantepec and perhaps southward to Panamá. A second species is found in Baja California, Sonora, and northern Sinaloa. The eastern Mexican population may be distinct or represent a race of the Pacific coastal population.

A large series of *C. hemilopha* was examined from southern Sonora. The coloration and pattern of this population are evident continuously through Sonora into northern Sinaloa; specimens from the vicinity of El Fuerte, Topolobampo, Guamúchil, Terreros, and Pericos have the same coloration as the Sonoran sample. Specimens from about 20 miles north of Culiacán southward throughout the rest of the state are characteristic of specimens referred to *C. pectinata*. An apparent gap of about 12 miles between ranges of the two forms is not real, because the highway from which much of the collecting is done, passes through a flat area with extensive agricultural activity; the lack of habitat close to the road rather than an actual gap in range accounts for the hiatus. The taxonomic status of the two remains uncertain, pending efforts to obtain specimens from this area of potential contact; meanwhile, we retain them

as distinct species. There are suggestions of morphological character differences that correlate with color pattern, but evaluation of these characters requires further study.

Adult males of *C. hemilopha* exhibit the following coloration: top of head light tan, sides and neck darker gray; white stripe from angle of lower jaw to tympanum; a black spot and two black bars on shoulders and back, increasing in width posteriorly, separated by light gray to white bands; first bar with lateral arms extending anteriorly to near tympanum, below first spot; posterior two-thirds of body gray, speckled with dark brown or black; chin, gular area, forelegs, and pectoral region black ventrally; belly and hind legs tan or dirty white with scattered black spots; hind legs dorsally speckled black, with three irregular narrow white bars on thigh; dorsal crest scales lower than *pectinata*.

Lowe and Norris (1955:90) suggested that "either one should recognize one widespread and variable monotypic form, *Ctenosaura hemilopha*, or recognize a polytypic species with four subspecies of varying degrees of differentiation." It is their opinion that four subspecies should be recognized, primarily on the basis of "highly significant differences in color pattern." They recognized two insular subspecies (*insulana* and *conspicuososa*); *C. h. hemilopha* from Sonora, northern Sinaloa, and southwestern Chihuahua, México; and *C. h. interrupta* from southern Baja California.

The name *hemilopha* was first used in reference to a population of *Ctenosaura* from Cape San Lucas, Baja California, by Cope in 1863. The name *interrupta* was originally used by Bocourt in 1882 for a population in Baja California (later restricted to Cape San Lucas by Smith and Taylor, 1950a:322). Therefore, if subspecies are recognized, *hemilopha* (the oldest available name) would apply to the Baja California (peninsula) population. This would leave the population in Sonora, northern Sinaloa, and southwestern Chihuahua without a trivial name.

We follow the first alternative of Lowe and Norris (1955:90) in recognizing one widespread variable monotypic form, *Ctenosaura hemilopha*, until more evidence becomes available to warrant subspecific designations, and until the relationships between *hemilopha* and *pectinata* are clarified.

Ctenosaura hemilopha is found in rocky areas throughout its range. The lizards are often seen in trees in areas where no rocky retreats are available.

Distribution in Sinaloa.—Known from the northern third of the state. See Fig. 44.

Specimens examined.—Ahome (* LACM 8645); E base Cerro Prieto, 17.5 mi. W Pericos junction (* UAZ 4206); 16 km. NNE Choix, 520 m. (* KU 73676); 26 km. NNE Choix, 510 m. (* KU 68751); 52 km. N Culiacán (* LACM 28705); 52.5 km. N Culiacán (* LACM 28706-07); 36.8 mi. N Culiacán (* CSCLB 1981); 43.4 mi. N Culiacán (CSCLB 2125-26); 53.2 mi. N Culiacán (* UAZ 1521, 1524); 92 km. N Culiacán (* LACM 28708); 42.8 mi. NW Culiacán (* UAZ 1523); 6 km. NE El Fuerte, 150 m. (* KU 77797-808, 78982); 40 mi. SE Guamúchil (* CSCLB 2148); 9 mi. S Guamúchil (* LACM 25703); Rancho Rosalito (* KU 45397); 1.1 mi. NE Topolobampo (* UAZ 1522); 0.5 mi. E Topolobampo (* CSCLB 2136); 13 km. NNE Vaca, 400 m. (* KU 80703-05).

Additional records.—5 mi. NNE El Fuerte (ASDM 793); Higuera de Zaragoza (SDSNH 18192-93); Hiqueres (UCLA 12945); Mocerito (USNM 33571-72); 3.5 mi. N Palmar de Sepulveda (UMMZ 123850).

Ctenosaura pectinata (Wiegmann)

Cyclura pectinata Wiegmann, Herpetologia Mexicana, p. 42, pl. 2, 1834 (type locality, México, by inference; type locality restricted to Colima, Colima, by Bailey, Proc. U. S. Nat. Mus., 73:25, 1928).

Ctenosaura pectinata: Gray, Catalogue of Lizards . . . Brit. Mus., p. 191, 1845.

Remarks.—Adult males of *C. pectinata* exhibit the following coloration: head mostly black, sometimes with scattered light scales; dorsum dark grayish brown with five to seven middorsal blotches; pale blotches middorsally on neck and shoulders between dark blotches; hind legs and base of tail black dorsally; ventral surface of forelegs, chest and belly straw to gray in color; hind legs uniform gray ventrally; chin mottled gray on greenish white background, with a black gular stripe; two to five narrow lateral-ventral black bars, interrupted on the midline. See the account of *C. hemilopha* for additional remarks.

Ctenosaura pectinata is common in varied habitat from sea level to about 300 meters wherever the topography or vegetation provides adequate cover or retreats. Individuals are common in rock piles and on stone walls in Mazatlán. Several specimens were dug from burrows along ravines near Rosario. Apparently these lizards take to the trees only where adequate ground cover is not available. The bright green hatchlings were first observed in July and are abundant in August. The young are unmarked except for black tail bands, present also on the adults. A female, measuring 135 mm. in snout-vent length, had lost almost completely the juvenile green coloration and had attained the typical adult pattern (Scott, 1962:21).

Distribution in Sinaloa.—Throughout the southern lowlands to north of Culiacán. See Fig. 44.

Specimens examined.—Camino Real (° AMNH 69681, 69685-86); 1 km. S Concepción, 75 m. (° KU 63743-48, 63750); 5 km. NE Concordia (° KU 33908); 9.9 mi. N Culiacán (° AMNH 86815); 19 km. N Culiacán (° LACM 28709); 15.8 mi. N Culiacán (° CSCLB 2120-22); 30 km. N Culiacán (° LACM 28710); 32 km. N Culiacán (° LACM 28711); 27 km. N, 1 km. NE Culiacán (° LACM 28712); 27 km. N, 2 km. NE Culiacán (° LACM 28713); 10.5 mi. NW Culiacán (° AMNH 75870); 19.2 mi. NW Culiacán (° UAZ 1535); El Dorado (° AMNH 90773; ° KU 61454-60); 6 mi. N Elota (° UAZ 15048); 10 mi. S Elota (° UAZ 11495); 38.4 mi. NW Elota (° UAZ 1536); Escuinapa (° UCLA 12944); 1.5 km. NW Escuinapa (° KU 33909); 6 mi. N Espinal (° CSCLB 2123-24); Isla Palmito del Verde, middle (° KU 73677); Isla Palmito de la Virgen, 5 m. (° KU 73693); Mazatlán (° KU 63382-85, 63387; ° CSCLB 2118-19); between Mazatlán and Elota (° LACM 4979-81); N Mazatlán (JFC 62:22-23); 4 mi. N Mazatlán (° AMNH 15356, 15359-60); 5 mi. N Mazatlán (° CSCLB 2128); 6 mi. N Mazatlán (° UAZ 1534); 25 mi. E Mazatlán (° AMNH 84576); 1.5 km. SE Mazatlán (° KU 29514, 29517); 5.4 mi. SE Mazatlán (° UAZ 1537); 1.5 km. S Pericos (° KU 37762); Rosario (° LACM 6593); 10 km. SE Rosario (° KU 33907); San Francisquito (° AMNH 15379); San Ignacio (° LACM 6592); 25 km. SW San Ignacio (° LACM 25200); 21.2 mi. S San Lorenzo (° UAZ 15047); Teacapán (° LACM 6589-91, 7247); Villa Unión (° UAZ 12315); 11 mi. S Villa Unión (° UCLA 14481); 1 mi. S, 26 mi. E Villa Unión (° CSCLB 1982).

Literature records.—Costa Rica (Smith and Van Gelder, 1955:145); Culiacán (Bailey, 1928:24; Smith, 1949:36); El Dorado (Fugler and Dixon, 1961:11); Escuinapa (Bailey, 1928:16); Mazatlán (Bailey, 1928:24; Burt, 1935:169; Lewis and Johnson, 1956:278; Martín del Campo, 1941:761; Smith, 1939a:23; Smith, 1949:36; Van Denburgh, 1898:461); near Mazatlán; near Presidio; 10 mi. S Presidio (Smith, 1935a:134; Taylor, 1938:517); Sinaloa [state only] (Bailey, 1928:24).

Additional records.—10 mi. NW Acajoneta (Nayarit), 50 ft. (TCWC 12532); Concordia (UIMNH 56580); 11 mi. NE Concordia (SM 10168); 11 mi. N Culiacán, 150 ft. (TCWC 12535); 3 mi. W El Dorado (SM 11753-55, 11762, 11767-69); Elota, 200 ft. (UMMZ 114691-92); 3.7 mi. SSE Elota, 200 ft. (UMMZ 114690); Escuinapa (AMNH 1585-95); 44.5 mi. N Escuinapa (FAS 15531); 9 mi. SE Escuinapa (UIMNH 6667); 5 mi. NW Escuinapa (UIMNH 6668); 12 mi. NW Escuinapa (UIMNH 6670); Mazatlán (AMNH 15369; CAS 95811; MCZ 31589; SDSNH 7225; SM 10169-70); N Mazatlán (AMNH 20663-68); 4 mi. N Mazatlán (AMNH 15353-55, 15357-58, 15361-62; FMNH 75694); 5 mi. N Mazatlán (USNM 146622-24); 10.7 mi. N Mazatlán (FAS 11412); 14 mi. N Mazatlán (UMMZ 118974); 20 mi. N Mazatlán (AMNH 75869); 34 mi. N Mazatlán (UIMNH 41576); 37.5 mi. N Mazatlán (FAS 13570); 11 mi. N, 1.2 mi. E Mazatlán (UMMZ 112732-33); 37.4 mi. S Mazatlán (FAS 7744); 25.4 mi. NW Mazatlán (UF 12842); 5 mi. SE Piaxtla (SM 11771); 9 mi. NW Piaxtla (SM 11770); 10 mi. S Presidio (UIMNH 20228-29); 3 mi. SE Rosario (UIMNH 6669); San Francisquito (AMNH 15378); Santa Rosa UMMZ 118975); Isla Venados, N [NW] Mazatlán (SDSNH 41224); Villa Unión (SU 22297).

Dipsosaurus dorsalis sonoriensis Allen

Dipso-saurus dorsalis sonoriensis Allen, Occ. Papers Mus. Zool., Univ. Michigan, 259:4, April 3, 1933 (type locality, Hermosillo, Sonora).

Remarks.—Only a single specimen of *Dipsosaurus* has been reported from Sinaloa since the original description (Bogert and Oliver, 1945:401). Several additional specimens have been taken

on the floodplain of the Río Fuerte north of Los Mochis. Nine females have the following characters: supralabials 7-10 (mode 8); infralabials 8-9 (mode 9); total femoral pores 36-45 (40.5); snout-vent length 85-118 (104). Five males have the following characters: supralabials 8-10 (mode 8); infralabials 8-10 (mode 9); total femoral pores 40-41 (40.6); snout-vent length 88-135 (113). Most specimens have one row of small scales separating the nasal and rostral. The two largest males (snout-vent length 130, 135 mm.) have two rows of small scales between the nasal and rostral. The specimens agree closely in color pattern with the original description and with specimens at hand from the vicinity of the type locality.

Distribution in Sinaloa.—Known only from the floodplain of the Río Fuerte in the northern lowlands. See Fig. 42.

Specimens examined.—Ahome (° LACM 8646); 4 mi. N Los Mochis turn-off (° LACM 25716-26); San Miguel, Río del Fuerte, 110 m. (° KU 40448); 2.5 km. N Topolobampo (° CSCLB 1521).

Literature record.—Ahome (Bogert and Oliver, 1945:401).

Additional records.—1 mi. NE Ahome, S bank Río Fuerte (UAZ 9525); 22 mi. NNE Los Mochis (UIMNH 40427); 2.6 mi. SE Playa Visnaga (UAZ 9523).

Holbrookia maculata elegans Bocourt

Holbrookia elegans Bocourt, Mission scientifique au Mexique . . ., Etudes sur les reptiles, livr. 3:164, pl. 17 bis, figs. 8, 8a, 1874 (type locality, Mazatlán, Sinaloa).

Holbrookia maculata elegans: Smith and Taylor, Bull. U. S. Nat. Mus., 199:84, October 26, 1950.

Remarks.—Smith (1935b:192) characterized specimens of *Holbrookia maculata elegans* from southern Sinaloa as having tails shorter than the body (longer in specimens from Sonora), larger femoral pores, pink gular spots and more strongly angular and conspicuous dorsal spots in females, and very little blue surrounding the lateral black spots of males. Lewis and Johnson (1956:278) reported females from between Culiacán and Mazatlán as having relatively smaller femoral pores, pink chin coloration in only one, and bright blue-green bordering the lateral black bars of males.

Twenty-seven males from Sinaloa have the following measurements: dorsal scales from parietal to posterior edge of femur 138-158 (146.2); total femoral pores 22-31 (27.4); lamellae beneath fourth toe 21-30 (25.1); ventrals from gular fold to anus 58-76 (65.2); snout-vent length 27-66 (48.2); tail length 25-88 (53.0); snout-vent/tail 0.78-1.08 (0.92). Comparable measurements for 18 females are respectively: 139-157 (146.9); 17-33 (25.7); 22-28 (24.7); 57-71 (65.9); 29-61 (50.4); 29-60 (49.2); 0.91-1.03 (0.98). Specimens

from four localities north of Guasave, Sinaloa, have fewer dorsal scales and femoral pores, about the same number of lamellae beneath the fourth toe, a similar number of ventrals, and a relatively shorter tail in males than specimens from the rest of the state.

Ventral color pattern of live males is as follows: two dark blue or black bars bordered with light blue; light orange anterior to bars continuous to insertion of forelimbs; bright yellow posterior to bars, continuous to hind limbs and anterior part of thighs; chin gray or white, with orange (pink in preservative) gular spot covering about 15 scales; tail white. Ventral color of females is as follows: bars much fainter than males, without blue borders; light orange anterior to bars and bright yellow posterior to bars, extending onto femur; chin gray and white or white with orange gular spot; tail light orange. The orange gular coloration may be correlated with breeding activity and exhibit seasonal variation.

Axtell (personal communication) distinguishes female *H. m. elegans* from females of *H. m. thermophila* by differences in ground color, distinctness of the dorsal blotches, relative proportions of the dorsal blotches, and the relative size of the femoral pores. In material from Sonora and Sinaloa available to us, the paravertebral blotches are more sharply defined and are relatively wider in *elegans* than in *thermophila*. There are no constant differences in other characters examined. Axtell considers specimens from Guirocoba, Alamos, and Camoa (Sonora) to be intergrades between the two subspecies. Until more evidence regarding the intergradation zone becomes available, all specimens from Sinaloa are referred to *Holbrookia maculata elegans*.

Most specimens were found in open areas along trails, in river beds, and on the beach. Females collected between July 3 and July 19 contained eggs. Two recently hatched individuals (LACM 6606-07) were collected on August 15, 1962.

Distribution in Sinaloa.—Lowlands throughout the state, to elevation of 520 meters. See Fig. 45.

Specimens examined.—16 km. NNE Choix, 520 m. (° KU 73682-83); Colonia de la Reforma, 19.7 mi. W Techa junc. (UAZ 4361); 19 km. N Culiacán (° KU 40450-55); 23 mi. E Culiacán (CSCLB 1977); 48 mi. S Culiacán (SU 19356); 6 km. NE El Fuerte, 155 m. (° KU 78619-20); 18 mi. S El Fuerte (JRM 1129); 40 km. N El Limón (° KU 40449); Guamúchil (UAZ 14366); 11 mi. S Guamúchil (CSCLB 2104); La Cruz, 9 m. (° KU 73678; LACM 6601); 4 mi. N Los Mochis turnoff (LACM 25712-14); 7.3 km. SW Matatán, 155 m. (° KU 78616); near Mazatlán (LACM 6602); 7 mi. N Mazatlán (LACM 25711); 10 mi. N Mazatlán (LACM 8624); 7 mi. E Mazatlán (UNM 10049); 1.5 km. SE Mazatlán, 3 m. (° KU 29657-61); 2 mi. S Obispo (LACM 6600); Playa Visnaga (UAZ 10492); 1 mi. W highway 15 along Río Piaxtla (CSCLB 1978); Rancho de los Pocitos, 14.2 mi. WNW Pericos junc. (UAZ

4358-60, 14364-65); San Ignacio, 210 m. (° KU 73679-81; LACM 6603-05); 1.5 km. WNW San Lorenzo (° KU 48743-45); 1 mi. W Terreros (LACM 6608); 1.5 mi. N Topolobampo (CSCLB 1979); 3.9 mi. NE Topolobampo (UAZ 1729-30, 1807); 16 km. SE Topolobampo, 6 m. (° KU 69924); 13 km. NNE Vaca, 400 m. (° KU 80712-15); 12 km. N Villa Unión, 120 m. (° KU 80706-11); 10 km. NE Villa Unión (° KU 48739-40); 9.4 mi. NE Villa Unión (LACM 6606-07).

Literature records.—Bacubirito (Schmidt, 1922:715); 30 mi. S Culiacán (Lewis and Johnson, 1956:278); Escuinapa (Schmidt, 1922:715; Smith and Taylor, 1950b:84); near Mármol (Lewis and Johnson, 1956:278); Mazatlán (Bocourt, 1874; Cope, 1868:310; Schmidt, 1922:715; Smith and Taylor, 1950b:84; Van Denburgh, 1898:461); N Mazatlán (Lewis and Johnson, 1956:278); Presidio (Smith and Taylor, 1950b:84); near Presidio (Smith, 1935b:191; Taylor, 1938:517); Rosario (Schmidt, 1922:716; Smith and Taylor, 1950b:84).

Additional records.—4 mi. NNE El Fuerte (FMNH 71489); 8 mi. NNE El Fuerte (FMNH 71487-88); 25 mi. NW Elota (MVZ 58983); 5 mi. NW Escuinapa (UIMNH 6684-88); 12.3 mi. S Guamúchil (FAS 14481); 23 mi. S Guamúchil (UIMNH 41606-07); 43 mi. SE Guasave (SM 11569-72); 20.2 mi. S Los Mochis (FAS 10474); near Mazatlán (USNM 47260-61); N Mazatlán (AMNH 20650); 1.3 mi. N Mazatlán (FAS 14480); 12 mi. N Mazatlán (MVZ 58981-82); 11 mi. N, 1.5 mi. E Mazatlán (UMMZ 112629); 37.4 mi. S Mazatlán (FAS 7745); 2.3 mi. N, 1.5 mi. W Mazatlán (FAS 7722); 12.1 mi. N Pericos (UIMNH 40153); Presidio (UIMNH 20361-62); Rosario (USNM 47682-86); 6 mi. W Topolobampo (SM 11568); 3 mi. SE Villa Unión (SM 11223); 10 mi. S Villa Unión (MCZ 61471).

Iguana iguana rhinolopha Wiegmann

[*Iguana*] *H[ypsiplophus] rhinolophus* Wiegmann, Herpetologia Mexicana, 1:44, 1834 (type locality, México).

Iguana igvana [sic] *rhinolopha*: Van Denburgh, Proc. Acad. Nat. Sci. Philadelphia, p. 461, 1897.

Remarks.—Adult iguanas were observed on several occasions sunning in the tops of trees along the rivers in southern Sinaloa. Large males (more than 1500 mm. in total length) have extensive areas of orange color on their head and dewlap. Females contain well developed ova in February and March. Two females are 120 and 205 mm. and four males are 88, 117, 210, and 220 mm. in snout-vent length. Iguanas are very abundant in some parts of Sinaloa. More than 500 specimens, mostly juveniles, were brought to us by local people at Teacapán between August 29 and September 5, 1962.

Distribution in Sinaloa.—Known only from the lowlands north to Costa Rica. See Fig. 42.

Specimens examined.—1 km. S Concepción, 75 m. (° KU 63751-55); 13.8 mi. S Escuinapa (UAZ 12314); 7.3 km. SW Matatán, 155 m. (° KU 78621); Río Presidio (UAZ 14860); Rancho Huanacastle (LACM 6611); 8.4 mi. S Rosario (UAZ 1953); Teacapán (LACM 6612-13); Villa Unión (SU 22737).

Literature records.—Costa Rica (Smith and Van Gelder, 1955:145); Mazatlán (Boulenger, 1885b:191; Smith and Taylor, 1950b:72; Van Denburgh, 1898:461); Presidio (Boulenger, 1885b:191; Smith, 1935a:133; Smith and Taylor, 1950b:72).

Additional records.—Barrón, Río Presidio (SDSNH 41225-26); El Dorado (AMNH 90772); Escuinapa (AMNH 1544); Mazatlán (USNM 7179); N

Mazatlán (AMNH 20669-79); 5 mi. N Mazatlán (SDSNH 41227); 73 mi. S Mazatlán (FAS 8716); near Presidio (FMNH 117780-81); 10 mi. S Presidio (UIMNH 20403-04); Rincón de Urías, E Mazatlán (AMNH 15363-64).

Phrynosoma solare Gray

Phrynosoma solaris Gray, Catalogue Lizards Brit. Mus. Nat. Hist., p. 229, 1845 (type locality, California).

Remarks.—Five specimens agree with the diagnosis given by Reeve (1952:907) with the exception that the ventral scales are not distinctly keeled. Measurements are as follows: (two males) snout-vent length 72, 40; tail 40, 14; tail/snout-vent length 0.56, 0.35; (three females) snout-vent 78, 61, 34; tail 31, 28, 11; tail/snout-vent length 0.40, 0.46, and 0.32. Horned lizards, known from areas of thorn woodland, reach their southern limit of distribution in central Sinaloa.

Distribution in Sinaloa.—Northern part of the state (north of Terreros). See Fig. 46.

Specimens examined.—Ahome (UCLA 13907, 13910-12); 6 km. NE El Fuerte, 150 m. (° KU 77809); 11 mi. S Guamúchil (CSCLB 1980); 10 km. S, 38 km. E Sinaloa, 240 m. (° KU 69925); Terreros (LACM 6614); 1 mi. W Terreros (LACM 6615); 4 mi. W Terreros (LACM 6616); 13 km. NNE Vaca, 400 m. (° KU 80716-18).

Literature records.—Ahome (Bogert and Oliver, 1945:401; Smith and Taylor, 1950b:104); Sierra de Choix (Reeve, 1952:910; Smith and Taylor, 1950b:104).

Additional records.—8 mi. NNE El Fuerte (FMNH 71485-86); 5 mi. N Guasave, 100 ft. (TCWC 12455); near Mocerito (UMMZ 125221); Río Sinaloa (MVZ 21012); 2 mi. S Sinaloa (UMMZ 125220).

Sceloporus bulleri Boulenger

Sceloporus bulleri Boulenger, Proc. Zool. Soc. London, p. 729, pl. 48, fig. 3, December 4, 1894 (type locality, La Cumbre de los Arrastrados, Jalisco).

Remarks.—Twenty-eight males have the following characteristics: dorsal scales 38-45 (40.5); middorsal scales in black collar 3-5.5 (4); total femoral pores (excluding KU 44746) 31-40 (35.7); snout-vent length 42-102 (63.6); tail length 81-130 (93.7) (N = 7; KU 44756, 75542, 78627, 78633, 78638-40); snout-vent/tail 0.62-0.68 (0.66). Ten males have the white anterior edge of the black collar broken middorsally; in 18 the white edge is complete. The corresponding characteristics of 12 females are, respectively: 36-42 (39.6); 3-6 (4); 30-37 (33.3); 48-91 (64.8) (excluding KU 78634); 85-135 (103.3) (N = 3; KU 75540, 78628, 78643); 0.61-0.67 (0.65). The white anterior edge is broken medially in 5, unbroken in 7.

The color of an adult male (LACM 6672) is as follows: top of head brownish olive with spots of pale green; collar velvet black,

with pale green anterior edge, broken middorsally; middorsal scales pale brownish green, grading into pale green laterally and into blue of belly; dorsal and lateral scales of tail pale blue with brown edges; legs brown dorsally; mental and anterior gulars pale blue; throat royal blue with invasions of black from sides of lower jaw; chest black; two royal blue lateral patches, joined by black anteriorly, separated posteriorly by dirty white; ventral surface of legs dirty white, yellowish white along femoral pores and outer edges of vent.

Specimens have been found on the sides of wooden buildings and on logs during June, July, and August in pine-oak forest above 1000 meters elevation.

Distribution in Sinaloa.—Known only from the mountains (above 1000 meters) in the vicinity of Santa Lucía and El Palmito [Durango]. See Fig. 47.

Specimens examined.—5 km. SW El Palmito, 1850 m. (° KU 75534-43); 1 km. NE Santa Lucía, 1155 m. (° KU 78626-27); 2.2 km. NE Santa Lucía, 1555 m. (° KU 78628-31); 10 km. NE Santa Lucía, 1950 m. (° KU 75533); 19.2 km. NE Santa Lucía, 1940 m. (° KU 78632-43); 1.5 km. E Santa Lucía, 1750 m. (° KU 44746-52, 44754); 2 km. E Santa Lucía, 1720 m. (° KU 44753, 44755-56); Santa Rita (LACM 6668-71); 4.8 m. E Santa Rita (° LACM 6672).

Literature record.—El Batel, 5100 ft. (Zweifel, 1954b:145).

Additional records.—37 mi. E Concordia (UIMNH 41621-22); 8 mi. W El Palmito (AMNH 94810-17); 10.3 mi. W El Palmito (UAZ 11984).

Sceloporus clarkii boulengeri Stejneger

Sceloporus boulengeri Stejneger, N. Amer. Fauna, 7:180, pl. 1, figs. 5a-c, 1893 (type locality, Presidio, about 50 miles [south] from Mazatlán, Sinaloa).

Sceloporus clarkii boulengeri: Burt, Trans. Amer. Micr. Soc., 54:171-72, April, 1935 (part).

Remarks.—*Sceloporus clarkii boulengeri* has been recognized by most authors despite some confusion with other lizards (Burt, 1935:172; Taylor, 1938:520) and some disagreement about the taxonomic value of certain characters (Bogert and Oliver, 1945:347). Intergradation between *boulengeri* and *clarkii* occurs near Alamos (Bogert and Oliver, 1945:348) and Navojoa (Langebartel and Smith, 1954:130), Sonora.

Little sexual dimorphism is evident in the following characters of 140 specimens: snout-vent length, 33-126 (83.2); dorsal scales 28-37 (32.7) (excluding KU 29586, 37631, 63683); femoral pores (total), 13-27 (18.6) (excluding KU 29586, 77823, 80728). There are two rows of lorilabials below the suboculars in 126, one row in six, one right and two left in three, and two right and one left in

three (excluding KU 29575, 37631). The frontoparietals are in contact medially in 23; separated in 115 (excluding KU 29586, 63694).

As a measure of variation in *Sceloporus clarkii* in Sinaloa, the total femoral pores and number of dorsal scales were analyzed statistically for samples from Vaca, El Fuerte, Culiacán, Mazatlán, and Concepción. The total femoral pores of the Culiacán and Mazatlán samples are significantly different from each other and the other three populations (Fig. 8). The result suggests a possible

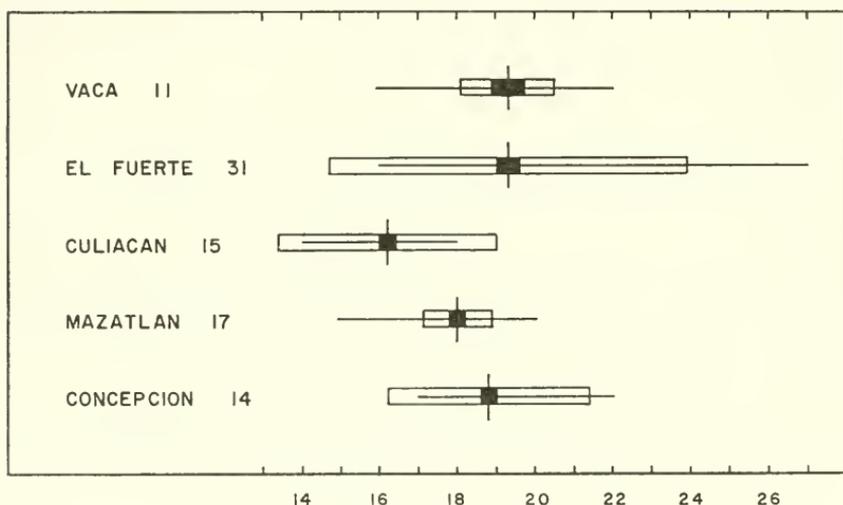


FIG. 8. Variation in the number of femoral pores in five samples of *Sceloporus clarkii boulengeri* in Sinaloa. The horizontal line represents the range of variation; the vertical line, the mean; the solid rectangle, two standard errors on either side of the mean; open rectangle, two standard deviations on either side of the mean. The samples include both sexes.

cline in southern Sinaloa in this character, with a sharp break between Culiacán and El Fuerte. Some workers might separate Sinaloan *Sceloporus clarkii* into two subspecies based on this character. No significant differences in the number of dorsal scales are indicated (Fig. 9). Analysis of variation in other characters demonstrates that there is little or no geographic correlation with variation of these characters. Our data support Smith's contention (1939c:132) that *Sceloporus clarkii boulengeri* exhibits a wide latitude of variation.

Tanner and Robison (1959:77), on the basis of three specimens, described *Sceloporus clarkii uriquensis* from Urique, Chihuahua. They diagnosed this subspecies as having the nasal separated from

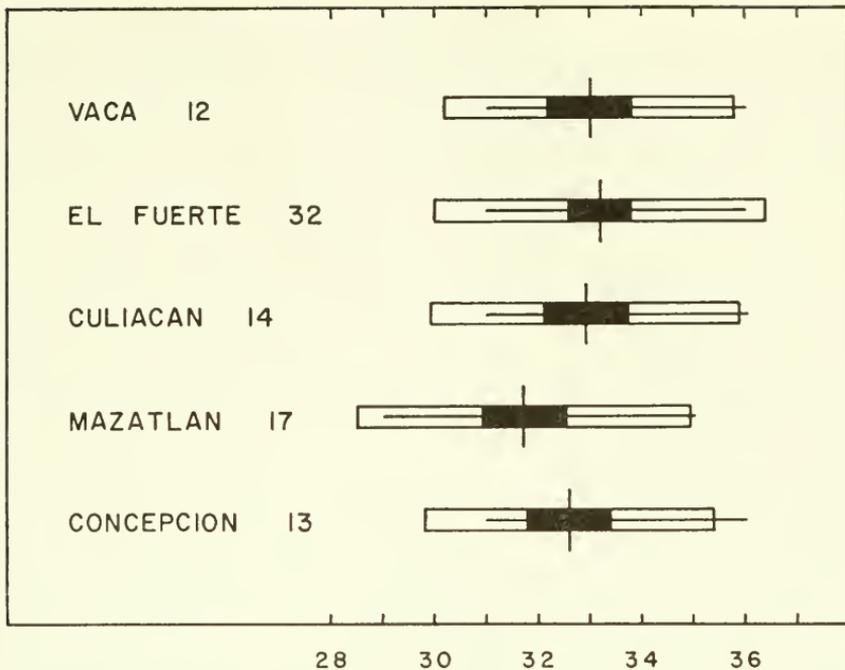


FIG. 9. Variation in the number of dorsal scales in five samples of *Sceloporus clarkii boulengeri* in Sinaloa. The horizontal line represents the range of variation; the vertical line, the mean; the solid rectangle, two standard errors on either side of the mean; open rectangle, two standard deviations on either side of the mean. The samples include both sexes.

the lorilabials, only one scale between the subocular and labials, only four supraoculars, and postmentals reduced to four. Tanner and Robison also stated that the Urique specimens do not have the dorsolateral stripes characteristic of *boulengeri*.

Three male topotypes (KU 56215-17), examined by us, have the nasal in contact with the lorilabials in one and not in two; they have 2, 3, and 2/1 rows of lorilabials between subocular and labials; two specimens have 5 supraoculars, one has six (or at least five, depending on whether small anterior plates are counted). The postmentals were counted in the manner indicated by Smith (1946:180) and Peters (1964:274). The three topotypes and 135 (of 139) Sinaloan specimens have two postmentals. Four specimens representing four different localities from El Fuerte to Rosario have three postmentals. Tanner and Robison evidently counted postmentals in the manner indicated by Smith (1939c:23). In any case, our data show no decrease in northern Sinaloa or at Urique; of 140 specimens examined only nine have a reduction of supraoculars

(one or both sides) and four of those reductions were from the vicinity of El Fuerte. Several specimens from Sinaloa do not exhibit the dorsolateral striping assumed to be characteristic of *boulengeri* (Tanner and Robison, 1959:77). Smith (1939c:130-31) indicated that females of *S. clarkii boulengeri* have dorsolateral stripes but males "become more or less uniform light straw color above" (p. 131). The type specimen of *uriquensis* is an adult male.

On the basis of a more complete understanding of the variation in *Sceloporus clarkii boulengeri* in Sinaloa, the intermediate condition in some characters of specimens from the Río Fuerte drainage, the probable continuum of distribution of *S. clarkii* throughout the Río Fuerte drainage (including Urique), and the latitude of variation of *Sceloporus clarkii uriquensis* (as shown by the three topotypes discussed), we find extensive overlap in the characters utilized by Tanner and Robison to diagnose the Urique specimens. Therefore, we place *Sceloporus clarkii uriquensis* Tanner and Robison in the synonymy of *Sceloporus clarkii boulengeri* Stejneger.

Sceloporus clarkii boulengeri is arboreal and commonly found on trunks of coconut palms along the coast. The lizards are wary and often retreat to the upper branches when disturbed. Taylor (1938: 520) found *S. c. boulengeri* in "large trees that stood isolated in pasture fields" near Presidio and Mazatlán. Langebartel and Smith (1954:130) recorded *boulengeri* in "dense cactus and thorny scrub thickets of the west coast." Lewis and Johnson (1956:278-79) found *boulengeri* 10-15 feet above the ground in mesquite trees near El Carrizo (northern Sinaloa), and in thorny broadleaf trees and acacias and along fence rows north of Mazatlán. Newly hatched young were found at Teacapán in early September.

Distribution in Sinaloa.—Relatively abundant throughout the state. See Fig. 48.

Specimens examined.—Ahome (UCLA 13909, 13920-22, 13928-32); 1 mi. NE Ahome (UAZ 9389); 1.5 km. SE Camino Real, Río Piaxtla, 120 m. (° KU 63692); E base Cerro Pocitos, 17.5 mi. W Pericos junc. (UAZ 4373); 16 km. NNE Choix, 520 m. (° KU 73696-98); Colonia de la Reforma, 19.7 mi. W Techa junc. (UAZ 14363); 1 km. S Concepción, 77 m. (° KU 63678-91); 8.3 mi. ENE Concordia (UAZ 14255-57); 6 km. E Cosalá, 460 m. (° KU 73699-701); Culiacán (LACM 8637-39); N Culiacán (CSCLB 2078-81); 7.8 mi. N Culiacán (CSCLB 2100-01); 19 km. N Culiacán, 120 m. (° KU 40401-02, 40405-06); 55 km. N Culiacán (° KU 40400); 46 mi. S Culiacán (CSCLB 2073); 18 km. NW Culiacán, 30 m. (° KU 67541-46); 53 mi. NW, 1 mi. E Culiacán (UAZ 2335-37); 53 mi. NW, 2.7 mi. E Culiacán (UAZ 2339); 32 km. SSE Culiacán (° KU 37632); 6 km. NE El Fuerte, 150 m. (° KU 77811-36, 77842); 8 km. NE El Fuerte, 160 m. (° KU 77837-41); 36 mi. NW Elota (UAZ 2338, 2340, 2465); 5 km. SW El Palmito, 1850 m. (° KU 75568); Escuinapa (LACM 8640-44); 5 km. NW Escuinapa, 150 m. (° KU 73707);

2.7 mi. N Guamúchil (CSCLB 2072); 3 mi. NW Guamúchil (UAZ 14346-54); 8 mi. N Guamúchil (SU 18258); 14 mi. N Guamúchil (CSCLB 2074); 6 km. W Guasave, 15 m. (* KU 67547-51); Isla Palmito de la Virgen, 5 m. (* KU 73702-06); Isla Palmito del Verde, middle (* KU 73708-16); La Cruz (LACM 6625); Los Mochis (CSCLB 2088-90); 12 mi. NW Los Mochis (UAZ 14344-45); 7.3 km. SW Matatlán, 155 m. (* KU 78646); Mazatlán (* KU 63391-99; JMS osteo. coll.; JRM 1096); N Mazatlán (CSCLB 2082-87, 2092; LMK 7337-41; UAZ 11277); about 2 mi. N Mazatlán (LACM 6620-24); about 4 mi. N Mazatlán (LACM 6626-27); 5 mi. N Mazatlán (CSCLB 2074-76); 10 mi. N Mazatlán (LACM 8636); 11.4 mi. N Mazatlán (CSCLB 2075); 8.4 mi. NE Mazatlán (UAZ 14357-62); 1.5 km. SE Mazatlán, 3 m. (* KU 29580-81, 29585); 5.4 mi. SE Mazatlán (UAZ 2373); NW Mazatlán (LACM 6644); 1 mi. NW Mazatlán (LACM 6642-43; 8625-35); 5 km. NNW Mazatlán, 8 m. (* KU 29574-75, 29582-84, 29586); 4 km. SW Navolato, 6 m. (* KU 73694-95); 1 mi. E Pánuco (CSCLB 2077); 1.5 km. S Pericos (* KU 37627-31); Rancho de los Pocitos, 14.2 mi. WNW Pericos junc. (UAZ 4374); Rancho Huanacastle (LACM 6631-36; JMS osteo. coll.); Rosario (UCLA 14820); 8 km. SSE Rosario, 30 m. (* KU 29573, 29577); San Ignacio (LACM 6628-30, 6641); E of San Blas (UAZ 9388, 9392); 5 km. SW San Ignacio, 200 m. (* KU 78644-45); 1.5 km. ENE San Lorenzo (* KU 48705); San Miguel (* KU 40399, 40403-04); 5 km. NE San Miguel, 92 m. (* KU 63693-96); Santa Lucía, 1100 m. (* KU 75566-67); near Santa Lucía (CSCLB 2093); 1.5 km. E Santa Lucía, 1700 m. (* KU 44757); 44 km. ENE Sinaloa, 180 m. (* KU 69928); Teacapán (LACM 6645-54); 11 mi. NE Teacapán (LACM 6655); 2 mi. E Teacapán (LACM 6656-57); Terreros (LACM 6637-40); Urique [Chihuahua] (* KU 56215-17); 13 km. NNE Vaca, 400 m. (* KU 80724-30); 1 km. SE Vaca, 200 m. (* KU 80719-23); Yecorato (UCLA 13924).

Literature records.—Ahome (Bogert and Oliver, 1945:348, 402); Bacubirito (Smith, 1939c:132); Costa Rica (Smith and Van Gelder, 1955:145); El Carrizo (Lewis and Johnson, 1956:278); El Dorado (Fugler and Dixon, 1961:11); Escuinapa; Los Mochis (Smith, 1939c:132); Mazatlán (Burt, 1935:171; Lewis and Johnson, 1956:278; Smith, 1939c:132; Van Denburgh, 1898:463); 1 mi. E Mazatlán (Smith, 1939c:132); 2 mi. E Mazatlán (Taylor, 1938:520); 9 mi. S Mazatlán; Mocorito; Presidio (Smith, 1939c:132); 10 mi. S Presidio (Taylor, 1938:520); Rincón de Urías; Rosario; San Francisquito; Sierra de Choix (Smith, 1939c:132); Yecorato (Bogert and Oliver, 1945:402).

Additional records.—Carrizo, 100 ft. (UMMZ 114882); Chele, about 300 ft. (UMMZ 110912); 2 mi. N Choix (FMNH 71496); 25 mi. NE Choix (UIMNH 20548); Costa Rica (UIMNH 34947-48); 7.6 mi. N Culiacán (UMMZ 120239); 9.9 mi. N Culiacán (AMNH 86819); 11 mi. N Culiacán, 150 ft. (TCWC 12554-57); 14.5 mi. N Culiacán (UIMNH 41647); 15.6 mi. N Culiacán (FAS 8500); 19.5 mi. N Culiacán (FAS 15757; UIMNH 41648-50); 21 mi. N Culiacán (UIMNH 41651); 22 mi. N Culiacán (UIMNH 41652-53); 10.5 mi. NW Culiacán (AMNH 75860); El Dorado (AMNH 90774-78; SM 12210-16); 10 mi. N El Dorado (SM 12218-20); 9 mi. SW El Dorado (SM 12221); 1 mi. NNE El Fuerte (FMNH 71495); 4 mi. NNE El Fuerte (FMNH 71493); 8 mi. NNE El Fuerte (FMNH 71494); Escuinapa, ca. 15 ft. (AMNH 1366-71, 1553-54); 31 mi. S Escuinapa (UF 12839); 5 mi. NW Escuinapa (UIMNH 6411-12); 12.3 mi. S Guamúchil (FAS 15905); 23 mi. S Guamúchil (UIMNH 41654-55); 1.5 mi. N Guasave turnoff, on hwy. 15 (FAS 16888-89); 30 mi. N Los Mochis (UIMNH 40468); 22.5 mi. NNE Los Mochis (UIMNH 40465-67); 13 mi. NE Los Mochis (UIMNH 40464); 1 mi. WNW Los Mochis (FAS 12909); Mazatlán, 25 ft. (AMNH 86817; SM 12199-200, 12207-09; UMMZ 114880); near Mazatlán (USNM 47269-70); N Mazatlán (AMNH 15499-509, 20680-90, 20714-15; USNM 51382-83); 1 mi. N Mazatlán (SM 12204-06, 12217); 3 mi. N Mazatlán (UNSM 151802); 22 mi. N Mazatlán (SM 12203); 36 mi. N Mazatlán (UIMNH 40173-74); 11 mi. N, 1.5 mi. E Mazatlán (UMMZ 112595); 1.5 mi. NW, 2.3 mi. E Mazatlán (FAS

7719-20, 7723); 1 mi. E Mazatlán (UIMNH 20552); 9 mi. S Mazatlán (FMNH 33332-35); 37.4 mi. S Mazatlán (FAS 7748); 73 mi. S Mazatlán (FAS 8707-08); 1 mi. NW Mazatlán (SM 12201-02); 6 mi. NNW Mazatlán, 50 ft. (UMMZ 114881); 40 mi. NNW Mazatlán (UMMZ 118810); Mocorito (USNM 33573); 12.1 mi. N Pericos (UIMNH 40172); 9 mi. NW Piaxtla (SM 12222-29); Presidio (FMNH 33328-31, 33336-37, 105380-81, 105576-77; UIMNH 20549-50); 2 mi. N Presidio (EHT-HMS 667-83); 8-10 km. S Presidio (UIMNH 20551); Rincón de Urías (AMNH 20716-17); S Rincón de Urías (AMNH 20691-92); Rosario (UIMNH 62757-63); 8 mi. NNW Rosario (UMMZ 112596); Villa Unión (AMNH 94756).

Sceloporus horridus albiventris Smith

Sceloporus horridus albiventris Smith, Field Mus. Nat. Hist., Zool. ser., 26:108, July 27, 1939 (type locality, Tepic, Nayarit).

Remarks.—Eight specimens of *Sceloporus horridus albiventris* have the following measurements: total femoral pores, 4-6 (5.8); dorsal scales, 30-35 (32.5); snout-vent length 64-91 (77.8). The venter is white in four and exhibits a pale blue tint laterally in four. The chin is white in five, has a pale blue tint in two, and is barred laterally with gray in one. These characters are in agreement with those presented by Smith (1939c:108). Specimens from near Culiacán represent the northernmost locality for the species in Sinaloa. The lizard is to be expected in the foothills to the northeast of Culiacán as suggested by its occurrence in Chihuahua (Tanner and Robison, 1959:79). Individuals were collected from fence posts, logs, and on rock piles. This species apparently is more terrestrial than *Sceloporus clarkii boulengeri*.

Distribution in Sinaloa.—In the foothills and on the coastal plain of Sinaloa south of Culiacán. See Fig. 49.

Specimens examined.—1.5 km. SE Camino Real, 120 m. (* KU 63703); 1 km. S Concepción, 76 m. (* KU 63701-02); 6 km. E Cosalá, 460 m. (* KU 73725); 14 mi. N Culiacán (CSCLB 2067-68); 5 km. NW Escuinapa, 155 m. (* KU 73727); 5.4 mi. NW Escuinapa (LACM 6663); La Cruz (LACM 6659-62); 7.3 km. SW Matatán, 155 m. (* KU 78647-48); San Ignacio, 210 m. (* KU 73726).

Literature records.—Mármol (Lewis and Johnson, 1956:279); Rosario (Smith, 1939c:110).

Additional records.—12 mi. N Escuinapa (FAS 16891); 41.3 mi. S Escuinapa (FAS 11420); near Mazatlán (FMNH 62416); Rosario (MCZ 46925; UIMNH 62757-63).

Sceloporus jarrovii jarrovii Cope

Sceloporus jarrovii Cope, U. S. Geog. Geol. Surv. W. 100th Mr., 5:569, 1875 (type locality, Southern Arizona).

Sceloporus jarrovii jarrovii: Smith, Univ. Kansas Sci. Bull., 24:624, February 16, 1938.

Remarks.—One specimen of *Sceloporus jarrovii jarrovii* agrees with the descriptions given by Smith (1938:624-28, 1939c:226-27).

The specimen, a male, has the following characters: snout-vent 90; tail incomplete; dorsal scales 43; supraoculars complete; 30 femoral pores separated medially by eight scales; lateral scales as large as dorsals; two white lines on head, upper one continuous on neck to shoulder; nuchal collar three scales wide with light border broken posteriorly, anterior light border indistinct; dorsal scales not with conspicuous white centers; lateral belly patches blue; groin black.

Smith (1938:628) commented that specimens from western Chihuahua have a peculiar variation in collar pattern. The black nuchal collar is continuous with black of the back and neck, obscuring the light borders of the collar. Also, the dorsal scales of Mexican specimens lack white spots characteristic of specimens in Arizona. Both of these color variations are present in the specimen at hand.

Distribution in Sinaloa.—Known only from the eastern mountains. See Fig. 50.

Specimens examined.—1 km. NE Santa Lucía (CSCLB 2065-66); 15 km. N, 65 km. E Sinaloa, 1400 m. (° KU 69931).

Literature record.—10 mi. and 17 mi. (by road) NE El Batel, 6400 ft. (Zweifel, 1954b:145).

Sceloporus magister magister Hallowell

Sceloporus magister Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 7:93, 1854 (type locality, Fort Yuma, Yuma county, Arizona).

Sceloporus magister magister: Linsdale, Univ. California Publ. Zool., 38:365, 1932.

Remarks.—Two males of this species are 60 and 111 in snout-vent length, with 30, 32 dorsal scales; 29, 27 femoral pores; and 2-1, 2 rows of lorilabials beneath suboculars. Four females are 119, 106, 90, 74 in snout-vent length with 29, 29, 31, 32 dorsal scales; 29, 25, 28, 26 femoral pores; and 2 rows of lorilabials beneath suboculars; a fifth female has 25 femoral pores (CSCLB 2071). The frontoparietals are separated medially in all specimens (excluding CSCLB 2071).

These records are the first reports of *Sceloporus magister* from Sinaloa. Specimens were collected in dense portions of the arid thorn woodland from Guamúchil northward.

Distribution in Sinaloa.—Known only from the northern coastal lowlands and Isla Tachetizte. See Fig. 47.

Specimens examined.—22 km. N Guamúchil (° CSCLB 2071); 19 km. NE Guasave (° JLC 1128); Isla Tachetizte, 6 km. E Isla Altamura (° KU 69929-30); 4 mi. N Los Mochis turnoff (° LACM 25797); 16 km. SE Topolobampo, 7 m. (° KU 69926-27).

Sceloporus nelsoni Cochran

Sceloporus nelsoni Cochran, Jour. Washington Acad. Sci., 13:185, 1923 (type locality, Plomosas, Sinaloa).

Remarks.—Specimens of *Sceloporus nelsoni* from the region near Mazatlán are lighter in color than those elsewhere (Cochran, 1923:186). Smith (1939c:367) commented that females from this area “have much less ventral maculation on the throat, breast, and sides of abdomen, than females from elsewhere, and males have less maculation on the chest.” However, Smith did not consider these differences sufficient to warrant subspecific recognition.

Tanner and Robison (1959:79) using ten specimens from Urique, Chihuahua, described the subspecies *Sceloporus nelsoni coeruleus* (= *S. n. barrancorum*, Tanner and Robison, 1960:114). They diagnosed *barrancorum*, in part, as being smaller than *nelsoni*, as having more dorsals and fewer postrostrals (three), and the males as having extensive deep blue from throat to hind legs.

Analysis of five characters for 16 specimens from Chihuahua and 56 specimens from Sinaloa (Table 4) fails to support the conclusions reached by Tanner and Robison, except that the maximum snout-vent length is slightly smaller in Chihuahua and northern Sinaloa than in southern Sinaloa. Additional material and localities may reveal clinal variation with respect to certain of these characters. The color pattern of the chest and belly of males is the most conspicuous variable. In specimens from Chihuahua and Choix, Sinaloa, (KU 73728) the chest and belly are solid black or very deep blue. The chest and belly are deep blue in male lizards from El Fuerte (KU 78669-75). A male (LACM 6682) from Terreros has the belly nearly all blue, darker midventrally; the chest is spotted with blue scales on white. A male from near Badiraguato (KU 83400) has black-edged, blue belly patches separated by a white median line that is continuous with a white chest. In the two specimens from south of Culiacán (KU 37773, 44850) the belly is blue laterally, darker blue medially, and the chest is white with large irregular blue blotches, similar to the Terreros specimen. Lizards from San Ignacio and vicinity (KU 73730-31, 78678-79; LACM 6675-77, 6679, 6681) have blue belly patches edged with black medially and posteriorly. The belly patches are in contact medially about two-thirds of their length, with white indentations anterior and posterior. The chests of these males are either all white, speckled blue and white, or blue-black with three or four white blotches. Males from vicinity of Mazatlán

TABLE 4.—Analysis of Five Characters for *Sceloporus nelsoni* from Various Localities in Chihuahua and Sinaloa.

LOCALITIES	Number of specimens	Dorsal scales from post. edge hind legs to parietal	Total femoral pores	Snout-vent length	Postrostrals between lorilabials	Lamellae beneath fourth toe
Chihuahua						
Urique-type series ¹	10	38-43 (40.2)	17-19 ² (18.3)	51.5-57.5	3-4	
1.5 mi. SW Tocuina (14) 23 mi. S, 1.5 mi. E Creal (1) 3 mi. NE Temores (1)	16	38-45 (41.0)	29-37 (32.8)	51-59 (54.9)	3-5 (3.4)	16-21 (18.4)
El Fuerte Choix	8	40-46 (43.9)	31-38 (33.8)	41-59 (50.1)	(4.0)	17-19 (18.3)
Sinaloa						
Carrizalejo	3	37-42 (40.0)	33-35 (33.7)	47-53 (49.0)	3-4 (3.7)	(17.0)
Sinaloa						
Radiragnato Terreros Culiacán (12 mi. N)	7	38-42 (40.1)	35-39 (36.7)	51-61 (54.5)	3-4 (3.6)	16-18 (17.1)
Sinaloa						
Cosalá Culiacán (32 mi. SSE)	2	36, 43 (39.5)	36, 38 (37.0)	54, 61 (57.5)	3, 4 (3.5)	17, 18 (17.5)
Sinaloa						
Camino Real, San Ignacio	17	37-42 (39.6)	31-40 (34.6)	48-64 (56.1)	2-4 (3.4)	16-21 (18.5)
Sinaloa						
Villa Unión, El Palmito, Santa Lucía	19	37-44 (40.1)	27-38 (33.0)	42-65 (58.0)	2-4 (3.2)	16-19 (17.7)

1. Tanner and Robison, 1959:81.

2. One side only.

have less maculation on the chest than those previously discussed. These color patterns indicate a clinal loss of black or blue ventral pigmentation in *S. nelsoni* from north to south.

Based on the evidence that the geographic variation involving ventral coloration is continuous, and that there are no consistent differences in numbers of dorsal scales and postrostrals, we conclude that *S. nelsoni barrancorum* should be allocated to the synonymy of *S. nelsoni*.

Sceloporus nelsoni is found at moderate to high elevations in the foothills and on the western slope of the Sierra Madre Occidental in western México. Lizards also have been taken in suitable habitat at a few isolated localities on the coastal plain. Specimens were collected on rocky outcroppings, along arroyos and rocky streams, usually in heavily shaded areas. All adult females collected in July and August were gravid.

Distribution in Sinaloa.—Most of the state except in the north-western lowlands. See Fig. 51.

Specimens examined.—21 km. ESE Badiraguato, 210 m. (* KU 83400); 1.5 km. SE Camino Real, Río Piaxtla, 120 m. (* KU 63706-08); 8 km. N Carrizalejo, 460 m. (* KU 78676-77); 16 km. NNE Choix, 520 m. (* KU 73728); 8.3 mi. ENE Concordia (UAZ 14252-54); 6 km. E Cosalá, 460 m. (* KU 73729); 23 mi. S, 1.5 mi. E Creel (Chihuahua) (* KU 44293); 19 km. N Culiacán (* KU 44850); 58 mi. N Culiacán (CSCLB 2099); 51 km. SSE Culiacán (* KU 37773); 74 km. S Culiacán (CSCLB 2070); 6 km. NE El Fuerte, 150 m. (* KU 78669-75); 5 km. SW El Palmito, 1859 m. (* KU 75582); 8.4 mi. NE Mazatlán (UAZ 14395); 1 mi. E Pánuco (CSCLB 2069); San Ignacio, 210 m. (* KU 73730-32; * LACM 6673-81; JMS osteo. coll.); 5 km. SW San Ignacio, 200 m. (* KU 78678-79); 1.5 km. E Santa Lucía (* KU 44840-49); 2.5 km. E Santa Lucía (* KU 44833-39); 44 km. ENE Sinaloa, 185 m. (* KU 69932); 3 mi. NE Temores (Chihuahua) (* KU 51795); 3-4 mi. W Terreros (* LACM 6682-86); 1.5 mi. SW Tocuina, 1500 ft. (Chihuahua) (* KU 47426-28, 51060-70); 8 km. N Villa Unión, 135 m. (* KU 80731); 1 mi. S, 26 mi. E Villa Unión, hwy. 40 (CSCLB 2097-98).

Literature records.—Culiacán (Cochran, 1923:186; Smith, 1939c:367); Mármol (Lewis and Johnson, 1956:278); near Mazatlán (Cochran, 1923:186; Smith, 1939c:367); 2 mi. E Mazatlán; 4 mi. SE Mazatlán (Taylor, 1938:518); S Rincón de Urías (Smith, 1939c:367); Rosario (Cochran, 1923:186; Smith, 1939c:367).

Additional records.—Culiacán (USNM 46629); 11 mi. N Culiacán, 150 ft. (TCWC 12448-54); 4 mi. NNE El Fuerte (FMNH 71490-92); Mazatlán (UMMZ 81958); near Mazatlán (FMNH 33480-82; USNM 47271, 47273-75); 9 mi. N Mazatlán (MVZ 59129-30); 36 mi. N Mazatlán (UIMNH 40155); 11 mi. N, 1.5 mi. E Mazatlán (UMMZ 115166); 3 mi. SE Mazatlán (UIMNH 21399); Rosario (USNM 47690-91); Santa Lucía (UMMZ 102585).

Sceloporus shannonorum Langebartel

Sceloporus shannonorum Langebartel, *Herpetologica*, 15:25, February 25, 1959 (type locality, 37 miles by road from Concordia, Sinaloa, near the Durango-Sinaloa border, state not determined).

Remarks.—Two females have 34, 32 femoral pores; 47, 50 dorsal

scales; 52, 52 scales around midbody, and snout-vent lengths of 59 and 70, respectively. Two males have 33, 32 femoral pores; 48, 47 dorsal scales; 52, 53 scales around midbody, and snout-vent lengths of 74 and 36, respectively. One female has a grayish white belly and the other has a faint bluish white belly without lateral patches of color. The smaller of the two males has pale blue lateral belly patches that are edged with gray medially and slightly separated by a creamy white area about one and one half to two scales wide. The larger male has pale blue belly patches edged with black and in contact medially. Three of the lizards have brown or tan sides but the larger male has pale blue mottling on the otherwise brown sides. The scales on the posterior surface of the thighs of the large male are definitely keeled, but those of the females are less strongly keeled. The other male (smallest specimen) lacks keels on the posterior surface of the thigh.

Two of these specimens were collected in pine-oak forest in August.

Distribution in Sinaloa.—Southern pine-oak forest between 1800 and 2000 m. See Fig. 49.

Specimens examined.—5 km. SW El Palmito, 1850 m. (° KU 75583); 13 km. W El Palmito, 1850 m. (° KU 63705); 19.2 km. NE Santa Lucía, 1940 m. (° KU 78692-93).

Sceloporus utiformis Cope

Sceloporus utiformis Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 177, 1864 (type locality, Colima, Colima).

Remarks.—Three females and one male have the following characteristics, respectively: rows of lorilabials below center of eye 1-1, 2-2, 1-2, —; dorsals 43, 45, 50, 47; snout-vent 49, 33, 63, 41; tail length 116 (KU 44866 only); femoral pores 31, 32, 30 (excluding KU 44866). In all specimens the frontoparietals are separated by an azygous scale, which also separates the frontal and interparietal. Another azygous scale separates the prefrontals; the posterior frontal is divided longitudinally on all specimens. One female (KU 44868) has the frontal and interparietal in contact on the right but separated on the left by an azygous scale. The preanal scales of the two larger females are keeled, but those of the smallest female and the male are smooth. Other characters are in general agreement with those given by Smith (1939c:325-29). One female has a tail length of 116 and snout-vent/tail ratio of 0.42.

One female (KU 80732) taken on October 25, 1963, contains six eggs which measure 7×10 to 8×12 mm. Another specimen (KU

44866), taken June 23, 1955, contains 19 or more ovarian eggs 0.5-1.0 mm. in diameter. The testes of the male, taken on June 23, 1955, are 3 mm. long. These data do not support the contention of Smith (1939c:329) that the species is ovoviviparous.

Scattered records from southern Sinaloa suggest that this lizard has a wide range from sea level to near 1750 meters. Specimens have been reported to be abundant near the oyster shell middens near Teacapán (Scott, 1962:23).

Distribution in Sinaloa.—Probably inhabits most of Sinaloa south of Mazatlán. See Fig. 51.

Specimens examined.—1.5 km. E Santa Lucía, 1750 m. (° KU 44867-68); 2.5 km. E Santa Lucía, 1700 m. (° KU 44866); 2 mi. SE Teacapán (LACM 6687); 8 km. N Villa Unión, 135 m. (° KU 80732).

Literature records.—12 mi. S Presidio (Taylor, 1938:519); 15 mi. S Presidio; Rosario (Smith, 1939c:330).

Additional records.—Chele, about 300 ft. (UMMZ 110911); 59 mi. S Mazatlán (FMNH 116621, 116646); near Presidio (UIMNH 21932-34); Rosario (USNM 47687-88, 47692).

Urosaurus bicarinatus tuberculatus (Schmidt)

Uta tuberculata Schmidt, Amer. Mus. Novitates, 22:4, December 1, 1921 (type locality, Colima, Colima).

Uta bicarinata tuberculata: Mittleman, Jour. Washington Acad. Sci., 31:73-74, 1941.

Urosaurus bicarinatus tuberculatus: Mittleman, Bull. Mus. Comp. Zool., 91:169-70, September 1942.

Remarks.—Seven females and six males have ten rows of dorsal tubercles (KU 40467 excluded). The series of enlarged dorsal scales begins just posterior to the anterior edge of the insertion of the forelimbs; the postfemoral dermal pocket is absent, and the imbricate ventral scales are either rounded, rounded and mucronate, or all mucronate. The frontal is divided in two males (KU 40466-67) and one female (KU 44099). The total femoral pores in seven males are 20-27 (22.4), and in the females are 21-23 (22.0). Mittleman (1942:169) reported the frontal as "variable, usually divided" and the postfemoral dermal pocket as "variable, occasionally present."

We have examined specimens identified as *Urosaurus unicus* from near El Fuerte and are unable to distinguish between "*unicus*" and *bicarinatus*. We agree with Oliver (1943:106) and Tanner and Robison (1959:82) that *Urosaurus unicus* is synonymous with *Urosaurus bicarinatus tuberculatus*.

Most specimens were collected on tree trunks or branches. The

decrease in number and size of trees in northwest Sinaloa may account for the apparent absence of this species in that region.

Distribution in Sinaloa.—Generally known throughout the state below 1200 meters. See Fig. 52.

Specimens examined.—Cerro Pocitos, 17.5 mi. W Pericos juc. (UAZ 4348); 16 km. NNE Choix, 520 m. (° KU 73738-39); 53.2 mi. NW, 3.1 mi. E Culiacán (UAZ 3405); 19 km. N Culiacán (° KU 40466-67); 17.5 km. NW Culiacán, 30 m. (° KU 67622); 29 km. SSE Guamúchil (° KU 44097-99); Palmillas (LACM 6692-93); Plomosas, 760 m. (° KU 73740); San Ignacio (LACM 6688-90); Santa Lucía, 1100 m. (° KU 75584); Terreros (LACM 6691); 13 km. NNE Vaca, 400 m. (° KU 80733-36); 1 mi. S, 26 mi. NE Villa Union (CSCLB 2017).

Literature records.—35 mi. S Culiacán; Mármol (Lewis and Johnson, 1956; 280); Presidio (Boulenger, 1885b:215; Mittleman, 1942:169; Smith and Taylor, 1950b:147); 15 mi. S Presidio (Smith, 1935a:171; Taylor, 1938:518).

Additional records.—Culiacán (AMNH 62343); 11 mi. N Culiacán, 150 ft. (TCWC 12782); 6 km. NE El Fuerte (KU 77878); 8 km. N El Fuerte (KU 77879-80); Elota (AMNH 62344); 10 mi. S Presidio (FMNH 106516); S Rincón de Urías, near Mazatlán (AMNH 19694).

Urosaurus ornatus lateralis (Boulenger)

Uta lateralis Boulenger, Ann. Mag. Nat. Hist., (ser. 5) 11:342, 1883 (based on specimens from Tres Marias Islands and Presidio, Sinaloa; type locality restricted to Presidio, Sinaloa by Oliver, Copeia, no. 2:97, June 30, 1943).

Uta ornata lateralis: Van Denburgh, Occ. Pap. California Acad. Sci., 10:199, November 23, 1922.

Urosaurus ornatus lateralis: Langebartel and Smith, Herpetologica, 10:133, August 1, 1954.

Remarks.—Boulenger (1883:342) described *Uta lateralis* (= *Urosaurus ornatus lateralis*) based on specimens collected by Alphonso Forrer from the Tres Marias Islands and Presidio. Oliver (1943:97) restricted the type locality to Presidio, Sinaloa. Subsequent collections from the vicinity of Presidio and throughout southern Sinaloa have failed to reveal additional specimens. It is possible that specimens of *ornatus* were included by mistake with *Urosaurus bicarinatus* from Presidio, which Boulenger (1883:342; 1885b:215) also reported at the same locality. Zweifel (1960:119) also questioned the presence of *Urosaurus ornatus* at Presidio, Sinaloa.

Sixteen females and 27 males have 18-24 (20.3) (KU 77859, 80738 excluded) and 17-24 (19.9) (KU 44644, 44650, 77850, 77871, 77873 excluded) femoral pores, respectively. All specimens examined (18 females and 32 males) have two rows of dorsal tubercles (plus a few variously scattered tubercles not in rows); the enlarged dorsals are present cranial to a line joining the anterior edges of the forelimbs; the postfemoral pocket is present, but reduced in some (KU 77864 excluded); the frontal is divided and in a few the

anterior part is partially or completely divided longitudinally; the ventrals are rounded and smooth. No geographic variation is evident among these specimens.

Urosaurus ornatus lateralis and *U. bicarinatus tuberculatus* occur sympatrically in Sinaloa. The two species have been collected together near Vaca, El Fuerte, and Culiacán, but nothing was observed regarding their ecological distribution at these localities. Field observations at other localities suggest a possible ecologic separation of the two species. *Urosaurus ornatus* is primarily a terrestrial lizard that seeks shelter in dense vegetation or beneath surface objects, whereas *U. bicarinatus* primarily inhabits tree trunks.

Distribution in Sinaloa.—Northern lowland thorn forest. See Fig. 53.

Specimens examined.—Ahome (LACM 5810); 16 km. NNE Choix, 370 m. (° KU 73741-42); 15.8 mi. N Culiacán (CSCLB 2004); 37 mi. N Culiacán (CSCLB 2003); 8 km. N El Fuerte, 150 m. (° KU 77863-68); 6 km. NE El Fuerte, 150 m. (° KU 77850-62, 77869-76); Estero la Ballena (UAZ 9585-87); 8 mi. N Guamúchil (SU 18250, 22300); 89.5 mi. N Guamúchil (LACM 6694); 3 mi. NW Guamúchil (UAZ 14387-94); 8.3 mi. NW Guamúchil (CSCLB 2011-12); Isla San Ignacio, 3 m. (° KU 6933-34); Los Mochis (CSCLB 2005-09); 36 mi. N Mazatlán (UIMNH 40154); Playa Visnaga (UAZ 9584); 2.7 mi. SE Playa Visnaga (UAZ 9579-83, 9588-90); San Miguel, 110 m. (° KU 44642-53); 1.5 mi. N Topolobampo (CSCLB 2013-15); 3.9 mi. NE Topolobampo (UAZ 4067-69); 0.5 mi. E Topolobampo (CSCLB 2010); 1.5 km. NW Topolobampo (° KU 73743); 13 km. NNE Vaca, 400 m. (° KU 80737-42).

Literature records.—Ahome; Culiacán (Oliver, 1943:99); El Carrizo (Lewis and Johnson, 1956:279); Presidio [needs verification] (Boulenger, 1883:343; Boulenger, 1885b:214; Van Denburgh, 1922:201).

Additional records.—Culiacán (AMNH 62346; USNM 46628); El Dorado (SM 11740); 1 mi. NNE El Fuerte (FMNH 71519-27); 4 mi. NNE El Fuerte (FMNH 71503-11); 8 mi. NNE El Fuerte (FMNH 71512-18); 7 mi. W Guamúchil (MVZ 59011-12); 43 mi. SE Guasave (SM 11737-39); 35 mi. N Los Mochis (UIMNH 62267-68); 2 mi. S Los Mochis (AMNH 96607); 1 mi. N Topolobampo (SM 11732-34); 6 mi. W Topolobampo (SM 11735-36).

Family Scincidae

Eumeces callicephalus Bocourt

Eumeces callicephalus Bocourt, Miss. Sci. Méxique et Cent. Amer., livr. 6:431, 1879 (type locality, Guanajuato [state]).

Remarks.—All specimens of *Eumeces* from the coastal lowlands are assigned to *E. callicephalus*, based on the findings of Richard B. Loomis and Robert C. Stephens (MS). *Eumeces bocourti* Boulenger, 1883:342 (= *E. humilis* Boulenger, 1887:377) is included with *E. callicephalus*.

One male (KU 73745) has a primary temporal; frontal and interparietal separated; postnasal present; two postmentals; prefrontals

in contact; superciliaries 7-8; supralabials ?-7; infralabials 7-7; 28 scale rows at midbody; snout-vent 49; adpressed limbs overlap lengths of digits. The dorsolateral light stripes, visible only on the head and neck, are less than one scale wide and are separated by four complete scale rows on the neck.

A single specimen was obtained beneath banana leaves at La Cruz on July 4. The leaves were piled beneath the trees and were in an advanced state of decay. Four skinks were uncovered but only one was collected. Two lizards had bright blue tails in life. Two clutches of eggs (six eggs in each) were found in separate depressions in moist soil beneath the leaves. In both instances the lizards were coiled around the eggs and only when attempts were made at capture did the lizards leave. Two other specimens, both juveniles, were collected in dry palm leaves near Teacapán. Zweifel (1962:64) reported a specimen found during bulldozing operations near Mazatlán in January.

Distribution in Sinaloa.—Throughout the lowlands below about 600 meters. See Fig. 54.

Specimens examined.—16 km. NNE Choix, 520 m. (° KU 73745); La Cruz (LACM 6768); Teacapán (LACM 6769-70).

Literature records.—5 mi. N Mazatlán (Zweifel, 1962:64); Presidio (Bou-lenger, 1883:342; Taylor, 1936c:363).

Eumeces colimensis Taylor

Eumeces colimensis Taylor, Field Mus. Nat. Hist., Zool. Ser., 20:77, May 15, 1935 (type locality, Colima, Colima).

Remarks.—Taylor (1935a:77-80) described *Eumeces colimensis* from one specimen having no primary temporal and the frontal and interparietal in contact. Taylor (p. 80) remarked that only additional collecting would determine if the temporal and frontal-interparietal conditions are normal. Since Taylor's description three additional specimens have become available. Two specimens from Michoacán were reported by Peters (1954:16-17); one specimen from Sinaloa was reported by Webb (1959:42).

Data from all known specimens reveal that the type is unique in the characters of the frontal-interparietal contact, absence of the primary temporal, and in that the adpressed limbs overlap the length of the foot. The prefrontals are in contact in two specimens and separated in two (KU 44733 and holotype). The type has 6 superciliaries (Taylor, 1935a:78), but as pointed out by Peters (1954:16-17) the illustration of the type (fig. 7) shows seven. Taylor (1936c:71, fig. 4, A, D) defined the superciliaries of the

genus *Eumeces*; according to these figures, the figure of the type shows seven superciliaries. Taylor (1935a:78) stated that the type has "six superciliaries, anterior largest, last next in size." According to Taylor's figure seven, the only count resulting in "anterior largest, last next in size" is seven. Accordingly, superciliaries are usually seven to nine. Infralabials six to seven, supralabials seven, scale rows at midbody 26 or 28.

Distribution in Sinaloa.—Known only from the southern highlands. See Fig. 54.

Specimens examined.—1.5 km. E Santa Lucía, 1700 m. (* KU 44733).

Eumeces parvulus Taylor

Eumeces parvulus Taylor, Proc. Biol. Soc. Washington, 46:175, October 26, 1933 (type locality, Tepic, Nayarit).

Remarks.—A small specimen of *Eumeces* was discovered in Sinaloa by Nelson and Goldman during their biological investigations of México, and was referred to the species *parvulus* by Taylor (1933:175). Taylor later (1936c:364) suggested that their specimen might represent a new species because of certain supposed anomalies including the presence of a distinct light lateral stripe. However, Smith (1943b:250), in a short summary of the known specimens of this species, suggested that the small (8.5 mm.) specimen from Plomosas is a juvenile, and that the distinct lateral stripe is a juvenile character.

An adult male from near Plomosas is 47 mm. in snout-vent length and has the following characters: 24 scale rows around body; 58 dorsal scales from parietal to above anus; frontal contracts frontonasal and third supraocular; interparietal longer than wide; parietals enclose interparietal; broad faint lateral stripes present enclosing six complete and two half scale rows; brown above changing to gray below; very faint pale brown stripes extend from rostral along supraoculars to shoulders; sides of head and neck darker brown than top of head and neck; lower parts of supralabials, chin, and throat cream-colored; tail brown at base, becoming black distally, but with ash-gray tip.

The single available specimen conforms to the scale characters and color pattern described by Taylor (1933:175-78), but the stripes may be less distinct than those possessed by the type (Taylor, 1936c:603, plate 31, fig. 4). This specimen differs from the description of the apparently closely related Sonoran species, *E. parviauriculatus*, by having the interparietal enclosed by parietals, relatively

larger ear openings than one illustrated (Taylor, 1933:179, fig. 2), postlabial scales not overlapping anterior edge of ear opening, and 24 scales around body rather than 20.

The specimen examined was found in a pocket gopher burrow in pine-oak forest.

Distribution in Sinaloa.—Known only from the southern highlands. See Fig. 54.

Specimens examined.—5 km. SE Plomosas, 1200 m. (° KU 91415).

Literature record.—Plomosas (Taylor, 1933:177).

Family Teiidae

Cnemidophorus costatus griseocephalus Zweifel

Cnemidophorus sacki griseocephalus Zweifel, Bull. Amer. Mus. Nat. Hist., 117:96, April 27, 1959 (type locality, 11.4 miles east of Navojoa, Sonora).

Cnemidophorus costatus griseocephalus: Duellman and Zweifel, Bull. Amer. Mus. Nat. Hist., 123:180, February 26, 1962.

Remarks.—See Zweifel (1959a:96-102) for a discussion of variation and distribution of this subspecies.

Twenty-five specimens have 31-43 (35.6) femoral pores; 201-254 (225.6) granules from occiput to rump (excluding KU 69935, 78769); 87-113 (101.1) granules around body at ventral 15 from axilla (GAB) (excluding KU 78769); 9-20 (15.5) granules between paravertebral stripes (PV) (excluding KU 73746, 73749, 78762-63); and snout-vent lengths of 46-120 (73.5) mm. (excluding KU 78769). The PV/GAB ratio is 0.091-0.192 (0.151). Two lizards (snout-vent lengths of 46, 57 mm.) have pattern type I (Zweifel, 1959a:66-67), 12 (46-76 mm.) have pattern II, four (74-101 mm.) have pattern III, three (90-93 mm.) have pattern IV, and four (80-120 mm.) have pattern V. The circumorbital scales contact the frontal in three and do not reach the frontal in 22.

Five large individuals from El Fuerte have white to gray chins and two have almost totally black chins. Three of these lizards have almost totally black bellies. Two lizards, not from El Fuerte, have black bellies.

Distribution in Sinaloa.—Throughout the northern lowlands and foothills, south to Badiraguato and Guamúchil and on adjacent coastal islands. See Fig. 55.

Specimens examined.—6 km. E Altamura, Isla Tachetizte (° KU 69937); Badiraguato, 210 m. (° KU 86606); 58 mi. N Culiacán (CSCLB 2055-59); 6 km. NE El Fuerte, 150 m. (° KU 78762-77); 14 mi. N Guamúchil (CSCLB 2050-51); 8.3 mi. NW, 5 mi. W Guamúchil (CSCLB 2052-53); Los Mochis (CSCLB 2054); 4 mi. N Los Mochis turnoff (LACM 25860-61); 6 km. SW

San Blas, 9 m. (° KU 73746-49); San Ignacio, Isla (° KU 69935); San Miguel (° KU 44698); 44 km. ENE Sinaloa, 180 m. (° KU 69936).

Literature records.—Ahome (Bogert and Oliver, 1945:402); 1 mi. NE El Fuerte; 7 mi. W Guamúchil; 10.1 mi. SE Los Mochis; 29.2 mi. SE Los Mochis; 37 mi. SE Los Mochis (Zweifel, 1959a:102).

Additional records.—Ahome (AMNH 85635-44); 1 mi. E Guasave (FAS 11425); 20.2 mi. S Los Mochis (FAS 10427-28, 10435, 10439); 22 mi. NNE Los Mochis (UIMNH 40498-510).

Cnemidophorus costatus huico Zweifel

Cnemidophorus sacki huico Zweifel, Bull. Amer. Mus. Nat. Hist., 117:85, April 27, 1959 (type locality, Peñitas, approximately 12 miles south-southeast of Rosamorada, Nayarit).

Cnemidophorus costatus huico: Duellman and Zweifel, Bull. Amer. Mus. Nat. Hist., 123:180, February 26, 1962.

Remarks.—Zweifel (1959a:85-89) described *Cnemidophorus sacki huico* (= *C. costatus huico*) and discussed its distribution and intergradation. The specimens reported herein mainly support Zweifel's conclusions, but present some new information regarding distribution.

Twenty-seven specimens examined have 32-43 (37.7) femoral pores (excluding KU 63720); 199-245 (225.6) granules from occiput to rump (excluding KU 63718-20, 63725); 93-122 (103.8) granules around body (GAB) at 15th ventral from axilla (excluding KU 63719-20, 63725, 73754); 11-19 (15.7) granules between the paravertebral stripes (PV) (excluding KU 73754, 73760); and are 37-111 (76.5) mm. in snout-vent length. The PV/GAB ratio is 0.116-0.178 (0.152) in 22 specimens. Two lizards (snout-vent lengths of 37, 47 mm.) have pattern I (Zweifel, 1959a:66-67), ten (45-75 mm.) have pattern II, six (71-95 mm.) have pattern III, six (92-111 mm.) have pattern IV, and three (97-101 mm.) have pattern V. The circumorbital scales contact the frontal in five lizards and do not reach the frontals in 21 (KU 63723 excluded). Three lizards (KU 78788, 78790, 78792) from 7.3 kilometers southwest of Mazatlán show evidence of intergradation with *C. c. mazatlanensis* by retaining distinct stripes (pattern III) at snout-vent lengths of 80-95 mm.; two of these lack any trace of gray on the chin. A single male (KU 75607) from Santa Lucía (1100 m.) is a typical *C. c. huico*, but has 23 granules between the paravertebral stripes. Several lizards from 5 kilometers southwest of El Palmito (Durango) are apparently more closely related to *C. c. mazatlanensis* than to *huico*.

This lizard is common along roads, in open areas, and along river beds. In December near Teacapán a large proportion of the active

individuals were juveniles, but adults predominated in July (Scott, 1962:27).

Distribution in Sinaloa.—Southern part of state, intergrading with *C. c. mazatlanensis* in an area a few kilometers south of Mazatlán. See Fig. 55.

Specimens examined.—1 km. S Concepción, 76 m. (° KU 63715-25); 7 mi. SW Concordia (° KU 33810); 5 km. NW Escuinapa, 150 m. (° KU 73755-59); 5.4 mi. NW Escuinapa (JMS osteo. coll.; LACM 6733-41); Isla Palmito del Verde, middle (° KU 73760); Isla Palmito de la Virgen, 5 m. (° KU 73750-51); 7.3 km. SW Matatán, 155 m. (° KU 78788-92); Palmillas (LACM 6761); Rancho Huanacastle (LACM 6742-56); Rosario, 150 m. (° KU 73752-54); Santa Lucía, 1100 m. (° KU 75607); Teacapán (LACM 6763-64); 2 mi. SE Teacapán (LACM 6762); 1 mi. S, 26 mi. E Villa Unión (CSCLB 2045-49, 2062-64).

Literature records.—Chele, about 300 ft.; Concordia (Zweifel, 1959a:89); 7 mi. SW Concordia (Chrapliwy and Fugler, 1955:126); 10 mi. W Concordia; Escuinapa; 16 mi. SE Escuinapa; 7 mi. NNW Escuinapa; 1.5 mi. W La Concha; Plomosas; 7 mi. WNW Rosario (Zweifel, 1959a:89).

Additional records.—19.4 mi. SE Escuinapa (UIMNH 6828-29); 17.5 mi. S Escuinapa (FAS 16894-98); 11 mi. N, 1.5 mi. E Mazatlán (UMMZ 119471); Presidio (UIMNH 19962; EHT-HMS 684-88); 10 mi. S Presidio (EHT-HMS 535-51); Rosario, 250 ft. (UIMNH 62754; USNM 47670); 3 mi. SE Rosario (UIMNH 6830-32).

Cnemidophorus costatus mazatlanensis Zweifel

Cnemidophorus sacki mazatlanensis Zweifel, Bull. Amer. Mus. Nat. Hist., 117:89, April 27, 1959 (type locality, two miles north of Coyotitán, Sinaloa).

Cnemidophorus costatus mazatlanensis: Duellman and Zweifel, Bull. Amer. Mus. Nat. Hist., 123:181, February 26, 1962.

Remarks.—This subspecies is discussed by Zweifel (1959a:89-93). Thirty specimens have 34-50 (38.5) femoral pores (excluding KU 29749); 190-240 (216.5) granules from occiput to rump (excluding KU 29736); 85-117 (98.5) granules around the body (GAB) at ventral 15 from axilla; 8-17 (13.3) granules between paravertebral stripes (PV) (excluding KU 78794); and are 43-103 (71.2) mm. in snout-vent length. The PV/GAB ratio is 0.90-0.179 (0.135) for 29 specimens. Seven lizards (snout-vent lengths of 59-91 mm.) have pattern I (Zweifel, 1959a:66-67), 14 (43-82 mm.) have pattern II, seven (58-91 mm.) have pattern III, one (90 mm.) has pattern IV, and one (89 mm.) has pattern V. The circumorbital scales contact the frontal in three specimens and do not reach the frontal in 27.

Five specimens (KU 75608-12) from five kilometers southwest of El Palmito, Durango (in Sinaloa) are unquestionably of pattern I; the belly is without black markings in three and with moderate black markings like *huico* and *mazatlanensis* in two; one has a

white chin, three have a white chin with a few black scales and one has a black spotted chin like *mazatlanensis*. Another specimen (KU 78808) from 19.2 kilometers northeast of Santa Lucía, between the population represented by the above five lizards and a population of *huico* represented by one specimen (KU 75607) from Santa Lucía, shows no noticeable trend toward *huico*.

Another series of nine lizards (KU 73761; LACM 6697-704) from La Cruz on the Río Elota is intermediate between *nigrigularis* and *mazatlanensis*.

These lizards are common in the coconut palm groves along the beach north of Mazatlán. Near San Ignacio, individuals were observed along the dry river bed, in denser vegetation along the river, and in arroyos surrounded by dense forest. No specimens were seen in heavily shaded portions of the forest. Nearly all adult females collected in July were gravid.

Distribution in Sinaloa.—From near Mazatlán northward to near La Cruz in the lowlands and near El Palmito (Durango) in the highlands. See Fig. 55.

Specimens examined.—1.5 km. SE Camino Real, Río Piaxtla, 120 m. (* KU 63726-29); 8.3 mi. ENE Concordia (UAZ 14230-39); 10 mi. S Elota (UAZ 11275, 11281-82, 11284-86); 5 km. SW El Palmito, 1900 m. (* KU 75608-12); La Cruz, 9 m. (* KU 73761; LACM 6697-704); N Mazatlán (LACM 6715-16; CSCLB 2060-61); 2 mi. N Mazatlán (LACM 6711-14); 7 mi. N Mazatlán (LACM 25856-58); 1.5 km. SE Mazatlán (* KU 29749); 5.4 mi. SE Mazatlán (UAZ 6262, 6271); 8 km. NW Mazatlán (* KU 63409-10); 5 km. NNW Mazatlán (* KU 29736, 29741); 1 mi. W Mexican hwy. 15, Río Piaxtla (CSCLB 2043); 21.2 mi. S Río San Lorenzo (UAZ 14220-29); 5 km. SW San Ignacio, 200 m. (* KU 78793-807); San Ignacio (LACM 6722-32); 19.2 km. NE Santa Lucía, 1940 m. (* KU 78808); 54 mi. N Tropic of Cancer [on hwy. 15] (LACM 6717-21).

Literature records.—2 mi. N Coyotitán; 9 mi. S Coyotitán (Zweifel, 1959a:93); Isla de los Chivos (Martín del Campo, 1941:761); Mazatlán (Burt, 1935:176; Taylor, 1938:522; Van Denburgh, 1898:463; Zweifel, 1959a:93); N Mazatlán; 9 mi. N Mazatlán; 20 mi. N Mazatlán; 11 mi. N, 1.5 mi. E Mazatlán; 1 mi. SE Mazatlán; 2.3 mi. E, 1.5 mi. S Mazatlán; 5.4 mi. SE Mazatlán; 2.6 mi. N, 1.4 mi. W Mazatlán; 2.6 mi. NNW Mazatlán, 25 ft.; Rincón de Urías, E Mazatlán (Zweifel, 1959a:93).

Additional records.—Mazatlán (EHT-HMS 581, 588-90, 750-54; AMNH 86830; UIMNH 19954-61, 19963-64).

Cnemidophorus costatus nigrigularis Zweifel

Cnemidophorus sacki nigrigularis Zweifel, Bull. Amer. Mus. Nat. Hist., 117:93, April 17, 1959 (type locality, 10.5 miles northwest of Culiacán, Sinaloa).

Cnemidophorus costatus nigrigularis: Duellman and Zweifel, Bull. Amer. Mus. Nat. Hist., 123:181, February 26, 1962.

Remarks.—See Zweifel (1959a:93-96) for a discussion of variation and distribution of this subspecies.

Twenty-six specimens have 33-42 (36.6) femoral pores (excluding KU 44683, 44687, 44690); 214-252 (235.0) granules from occiput to rump (excluding KU 44687, 44690, 44694-95); 89-113 (105.1) granules around body at ventral 15 from axilla (GAB) (excluding KU 44683, 44685, 44687, 44690, 44694, 44696); 11-20 (15.8) granules between paravertebral stripes (PV) (excluding KU 44694, 62819, 73764); and snout-vent lengths of 44-105 (65.0) mm. (excluding KU 44694). The PV/GAB ratio is 0.108-0.190 (0.151). Dorsal pattern types I and III (Zweifel, 1959a:66-67) are not represented in the specimens at hand. Twenty-three specimens (snout-vent lengths of 97-103 mm.) have pattern V. The circumorbital scales contact the frontal in two and do not reach the frontal in 24.

All of the large individuals examined have black on the chin; the bellies of three specimens are almost totally black, and one male (KU 73764, snout-vent length 103 mm.) is completely black ventrally with the exception of some white spots on the hind legs and tail.

Distribution in Sinaloa.—Coastal lowlands approximately between Terreros and Abuya. See Fig. 55.

Specimens examined.—6 km. E Cosalá, 460 m. (° KU 73765); N. Culiacán (CSCLB 2041-42); 19 km. N Culiacán, 120 m. (° KU 44677-97); 14 mi. N Culiacán (CSCLB 2044); 1.5 km. NW Culiacán (KU 48207, 48508-09); 17.5 km. NW Culiacán (° KU 62819-20); 9 mi. S Guamúchil (LACM 25859); 4 km. SW Navolato, 6 m. (° KU 73763-64); 1.5 km. ENE San Lorenzo (KU 48491-507); Terreros (LACM 6705-06, 6710).

Literature records.—23.3 mi. S Caitime; 4 mi. S Culiacán; 10.5 mi. NW, 15.6 mi. NW, 16.5 mi. NW, 20 mi. NW Culiacán; 25-26 mi. NW Elota; 36.8 mi. NW Elota (Zweifel, 1959a:96).

Additional records.—Costa Rica (UIMNH 34934-35); 9.9 mi. N Culiacán (AMNH 86831); 12.1 mi. N Pericos (UIMNH 39242-46).

***Cnemidophorus tigris* Baird and Girard**

Cnemidophorus tigris Baird and Girard, Proc. Acad. Nat. Sci., Philadelphia, 6:69, 1852 (type locality, Valley of the Great Salt Lake, Utah).

Remarks.—There are two populations of *Cnemidophorus tigris* in Sinaloa. One occurs in the northern lowlands and the other inhabits the foothills of the Río Fuerte drainage. The lowland population is represented by nine specimens from Topolobampo (CSCLB 1507-1515) and two specimens from San Miguel (KU 44724-25). These eleven lizards have the following characteristics: snout-vent length 52-69 (60.7) mm.; granules from occiput to rump, 192-217 (207.2) (except CSCLB 1513); granules around midbody, 79-95 (87.0) (except CSCLB 1510-13); femoral pores (total), 34-41 (36.7); lamellae beneath fourth toe, 29-34 (30.8); and scales be-

tween femoral pores, 3-5 (4.1). The same characteristics for one specimen (KU 48207) from Culiacán are respectively, 61, 192, 85, —, 32, and 4. The foothill population is represented by three specimens (KU 78885-87) from eight kilometers north of El Fuerte and 17 specimens (KU 78883-84, 78888-902) from six kilometers north-east of El Fuerte that have the following characteristics, respectively: 55-70 (61.3); 195-214 (204.9) (except KU 78886, 78897); 86-100 (91.7) (except KU 78883-84, 78896); 35-41 (37.9) (except KU 78893, 78896-97); 30-35 (32.2) (except KU 78897); and 2-4 (3.1) (except KU 78893).

Specimens from the lowlands have distinct stripes continuous on the back. Specimens from the foothills have distinct light stripes, but the vertebral and paravertebral stripes are broken and discontinuous from the shoulders to the rump, giving a reticulated appearance. Males of both populations have black chests and black and white mottled chins. Females have immaculate chests and bellies with small black specks on their chins. Young have orangish tails. All of the females except one contain eggs (KU 78884 was not examined for eggs). One female (KU 78891) with a snout-vent length of 60 mm. has two eggs, each 16 mm. long. Another female (KU 78898) with a snout-vent length of 57 mm. has two eggs 14 and 16 mm. long. In both cases the eggs are shelled and appear to be mature. The testes of one male (KU 78892), with a snout-vent length of 65 mm. contain sperm. Sinaloan specimens of *C. tigris* are much smaller than specimens of *Cnemidophorus tigris aethiops* from Sonora. John W. Wright and Charles H. Lowe, Jr., are currently studying these populations of *C. tigris*.

Distribution in Sinaloa.—This species inhabits the lowland thorn forest north of Culiacán and the foothills of the Río Fuerte drainage. See Fig. 50.

Specimens examined.—1.5 km. NW Culiacán (* KU 48207); 8 km. N El Fuerte (* KU 78885-87); 6 km. NE El Fuerte, 150 m. (* KU 78883-84, 78888-902); San Miguel, 110 m. (* KU 44724-25); 2.5 km. N Topolobampo (* CSCLB 1507-15).

Family Anguidae

Gerrhonotus kingii ferrugineus Webb

Gerrhonotus kingi ferrugineus Webb, *Herpetologica*, 18:73, June 22, 1962 (type locality, two miles north of Pueblo Nuevo, ca. 6000 ft., Durango).

Remarks.—One adult female with ovarian eggs has a snout-vent length of 108; tail length 268; 58 dorsals from interparietal to posterior edge of hind legs; 16 dorsal scale rows; 12 rows of scales

across nape; 12 ventral scale rows; granular scales on sides of neck; anterior internasals and postrostral absent; suboculars extending to lowest primary temporal; 15 complete brown bands across back, one scale or less in width; ventral body and tail cream colored; few dark brown spots on head posterior to eyes and on base of tail. The specimen agrees in other respects with the original description (Webb, 1962b:73).

Distribution in Sinaloa.—Known only from the tropical deciduous forest of the southern highlands. See Fig. 56.

Specimen examined.—1 km. NE Santa Lucía, 1155 m. (° KU 78903).

***Gerrhonotus liocephalus liocephalus* Wiegmann**

[*Gerrhonotus*] *liocephalus* Wiegmann, Isis von Oken, 21:381, 1828 (type locality, México).

Gerrhonotus liocephalus liocephalus: Cope, Ann. Rept. U. S. Natl. Mus., 1898:516, 1900.

Remarks.—One male has a snout-vent length of 150; tail 265 (incomplete); 48 dorsals from interparietal to posterior edge of hind legs; 18 dorsal scale rows; eight rows of scales across nape; 12 rows of ventral scales; postrostral, anterior internasal, and frontonasal present; suboculars separated from lowest primary temporal. The dorsal coloration consists of nine indistinct pale blue bands on a ground color of pale brown.

Distribution in Sinaloa.—Known only from pine-oak forest in the southern highlands. See Fig. 56.

Specimen examined.—19.2 km. NE Santa Lucía, 1940 m. (° KU 78904).

Additional records.—5.0 mi. (by road) SW El Palmito, 6800 ft. (UMMZ 123044); 7.2 mi. (by road) E Santa Lucía (JFC 63:141).

Family Helodermatidae

***Heloderma horridum exasperatum* Bogert and Martín del Campo**

Heloderma horridum exasperatum Bogert and Martín del Campo, Bull. Amer. Mus. Nat. Hist., 109:28, April 16, 1956 (type locality, near Guirocoba, Sonora).

Remarks.—One specimen, represented by a skin with head, tail and legs attached, has 81 caudals; preanals not enlarged; one pair of infralabials reaching chin shields; supranasal contacting postnasal; and eight scales present across head between posterior superciliaries. The specimen probably had a body length of about 300 mm. In pattern, the specimen resembles the holotype as illustrated by Bogert and Martín del Campo (1956, pl. 8, fig. 3), but the yellow coloration is more prominent.

Specimens from western México demonstrate wide overlap in characters of *horridum* and *exasperatum*. The supranasal contacts the postrostral in two of nine specimen of *horridum*; four of eight specimens of *horridum* have eight or more scales between superciliaries; the second supralabial contacts the nasal or prenasal in six of nine specimens of *horridum*. Although we have not seen an animal with a color pattern obviously intermediate between the two races in Sinaloa, Bogert and Martín del Campo (1956:65) suggested clinal variation in this character as well. A detailed study of *Heloderma* in northern Sinaloa probably will indicate that *exasperatum* is representative of the northern terminus of *Heloderma horridum* and that clinal variation accounts for the distinctiveness of this population, as visualized by Bogert and Martín del Campo (1956:28). However, we continue to recognize two races in Sinaloa until additional material from the foothills between the Río Culiacán and the Río Fuerte becomes available.

Distribution in Sinaloa.—Known only from the area drained by the Río Fuerte. See Fig. 57.

Specimen examined.—13 km. NNE Vaca, 400 m. (° KU 80743).

Literature record.—San Blas, 100 m. (Bogert and Martín del Campo, 1956:32).

***Heloderma horridum horridum* (Wiegmann)**

Trachyderma horridum Wiegmann, Isis von Oken, 22:421, 1829 (type locality, "México"; type locality restricted to Cuernavaca, Morelos by Bogert and Martín del Campo, Bull. Amer. Mus. Nat. Hist., 109:21, April 16, 1956).

Heloderma horridum Wiegmann, Isis von Oken, 22:628, 1829.

Heloderma horridum horridum: Bogert and Martín del Campo, Bull. Amer. Mus. Nat. Hist., 109:20, April 16, 1956.

Remarks.—Three specimens of *Heloderma h. horridum* (KU 73770, 78905-06) have the following characteristics, respectively: snout-vent lengths 246, 310, 268; tail lengths 192, 227, 189; tail/snout-vent length ratios 0.78, 0.73, 0.72; ventrals from gular fold to anus 62, 64, 62; subcaudals 84, 78, 78; scales across head between posterior superciliaries 9, 7, 7; pairs of infralabials reaching chin shields 2, 1, 1; supranasal contacts postnasal no, yes, no; preanal scales not enlarged. Two specimens are essentially similar in pattern, having a brown ground color with yellow scales appearing just anterior to midbody; the yellow scales become more numerous from anterior to posterior, and there are five pairs of yellow bands on the tail. The yellow spots begin on the nape of the other lizard (KU 78906).

Most specimens were collected on the road in late evening or at night. A few individuals were active in the morning, suggesting a crepuscular activity period.

Distribution in Sinaloa.—Probably occurs throughout the state south of the Río Mocorito. See Fig. 57.

Specimens examined.—7.3 mi. S Elota, Río (LACM 6596); 41 mi. S Elota (JMS osteo. coll.); 25.2 mi. S Escuinapa (CSCLB 2106); Matatán, 170 m. (° KU 73770); 17.8 mi. N Mazatlán (CSCLB 2105); 24.9 mi. N Mazatlán (UAZ 7176); 26.8 mi. N Mazatlán (LACM 6594); 82 mi. N Mazatlán (CSCLB 2109); Palmillas (LACM 6597); San Ignacio (LACM 6595); 5 km. (by road) SW San Ignacio, 200 m. (° KU 78905-06); Terreros (JMS osteo. coll.).

Literature records.—Escuinapa, 100 m. (Bogert and Martín del Campo, 1956:27); Piaxtla, 75 m. [80 km. N Mazatlán] Bogert and Martín del Campo, 1956:27; Smith and Van Gelder, 1955:145; Palmillas (Scott, 1962:28); Presidio; 12 mi. NW Rosario, 100 m. (Bogert and Martín del Campo, 1956:27; Boulenger, 1885b:302).

Additional records.—Between Acaponeta [Nayarit] and Escuinapa (MVZ 66199); 2 mi. ENE Copala, 1400 ft. (TCWC 12430); Costa Rica (UIMNH 34932); Crucero de Piaxtla (UF 12836); 41.3 mi. N Culicán (MVZ 70256); 90 mi. N Culiacán (FAS 9077); 40 mi. S. Culiacán (MVZ 71318); 7 mi. SE Escuinapa (MVZ 68970); 28.4 mi. S Espinal (FAS 17002); 63 mi. N Mazatlán (FAS 16909); 15 mi. S Mazatlán (MVZ 66200); 1.3 mi. W, 2.5 mi. N Mazatlán (FAS 9054).

Heloderma suspectum suspectum Cope

Heloderma suspectum Cope, Proc. Acad. Nat. Sci. Philadelphia, 21:5, 1869 (type locality, Sierra de Moreno on the boundary between the United States and México).

Heloderma suspectum suspectum: Bogert and Martín del Campo, Bull. Amer. Mus. Nat. Hist., 109:35, April 16, 1956.

Remarks.—One specimen from El Dorado (Bogert, personal communication) is the first record for Sinaloa and the southernmost record for the species. There is an apparent overlap of about 310 kilometers in the range of the two species of *Heloderma* in northern Sinaloa.

Distribution in Sinaloa.—Known only from the central coastal lowlands. See Fig. 57.

Specimens examined.—None.

Additional record.—El Dorado (AMNH 90786).

Suborder SERPENTES

Family Typhlopidae

Typhlops braminus (Daudin)

Eryx braminus Daudin, Hist. Nat. . . . des reptiles, 7:279-280, 1803 (type locality, Vizagapatam, India).

Typhlops braminus: Cuvier, Regne Animal, Ed. 2, 2:73, 1829.

Remarks.—Four specimens agree with the description given by

Boulenger (1893:16), and the illustration of the head plates by Taylor (1940b:444). These specimens have been compared with others of the same species from Ceylon, the Philippine Islands, and Guerrero. The five snakes (KU 63416-18, 73487 and 82980) have, respectively, 334, 307, 292, 309, 320, middorsal scales from the prefrontal to the tail spine, snout-vent lengths of 103, 99, 69, 160, 94 mm., and tail lengths of 3, 3, 2.5, 4, 3 mm. All have 20 scales around the midbody. The ratio of snout-vent length to total length is 0.97 in all specimens. All are brown dorsally with a lighter brown venter; the snout, chin, anus, and tip of tail are white. Each dorsal scale has a pale gray base which may be overlapped by the preceding scale.

This small burrowing reptile has been introduced into Mazatlán and Rosario and become well established. Three specimens (KU 63416-18) were unearthed by laborers digging near a trailer park in Mazatlán. Two other individuals (CSCLB 1147-48) were collected at night on the grounds of the trailer park in July. Another specimen (KU 734787) was found during the excavation of a flower bed. Campbell and Simmons (1962:202) reported a specimen (UCLA 14693) found under a rock at the Mazatlán airport.

Distribution in Sinaloa.—Known only from the vicinity of Mazatlán and Rosario. See Fig. 58.

Specimens examined.—Mazatlán (* KU 63416-18, 73487, 82980; CSCLB 1147-48).

Literature record.—Mazatlán (Campbell and Simmons, 1962:202).

Additional records.—Mazatlán (USNM 152455); 5 mi. N Mazatlán (AMNH 85777); Rosario (AMNH 91604).

Family Leptotyphlopidae

Leptotyphlops humilis dugesii (Bocourt)

Catodon dugesii Bocourt, Bull. Soc. Philom. (7), 6:81, 1881 (type locality, Colima).

Leptotyphlops humilis dugesii: Klauber, Trans. San Diego Soc. Nat. Hist., 9:129, April 30, 1940.

Remarks.—Klauber (1940:131) suggested that *Leptotyphlops humilis dugesii* was most closely related to *L. h. slevini*, but that intergradation of *dugesii* with *L. h. humilis* or *L. h. tenuiculus* might eventually be disclosed. The dorsal counts for his specimens are 235-257 (242) with the northernmost locality represented being Mazatlán. Bogert and Oliver (1945:349) referred one specimen from Alamos, Sonora, to *dugesii* on the basis of pigmentation and a dorsal scale count of 257. Langebartel and Smith (1954:134)

reported a specimen of *L. h. dugesii* from 45.1 miles south of Santa Ana, Sonora; it has 5 pigmented dorsal rows, suggestive of intergradation with *L. h. caluila* rather than *L. h. humilis*. They further point out that the central Sonoran population possibly is distinct from both *humilis* and *dugesii*. Fugler and Dixon (1961:12) obtained one specimen of *L. h. dugesii* from El Dorado, Sinaloa.

Three specimens examined have 14 rows of scales around body; 12 rows of scales around tail; 255, 255, 248 middorsal scales from rostral to tail spine. The seven median dorsal scale rows and half of each adjacent lateral scale row are brown; the remaining rows lack pigmentation. One specimen, a male, (KU 95951), has a snout-vent length of 307 and a tail length of 14. Our specimens confirm Klauber's contention (1940:131) that dorsal scales increase from south to north along the Pacific coast of México. Two individuals (LACM 6772, 6773) were found at night on the road following a heavy rain.

Distribution in Sinaloa.—Probably occurs throughout the lowlands of the state. See Fig. 58.

Specimens examined.—11 mi. N Culiacán (° LACM 6772); El Salado, 300 ft. (° KU 95951); 0.5 mi. N Terreros (° LACM 6773).

Literature records.—El Dorado (Fugler and Dixon, 1961:12); Mazatlán; Presidio (Klauber, 1940:131; Smith and Taylor, 1945:21).

Additional records.—11.4 mi. S Agua Caliente (UF 12790); 5.6 mi. N Culiacán (UMMZ 120228); El Dorado (AMNH 90760-64).

Family Boidae

Boa constrictor imperator Daudin

Boa imperator Daudin, Hist. Nat., . . . des reptiles, 5:150, 1803 (type locality, México).

Boa constrictor imperator: Forcart, Herpetologica, 7:199, December 31, 1951.

Remarks.—Four specimens have 66, 71, 70, 74 dorsal scales at midbody, 245, 233, 239, 242 ventrals, and 53, 61, 57, 60 subcaudals.

During the summer of 1962 more than 150 specimens of this ubiquitous species were collected but, because of the abundance and size of the species, only a few were preserved. Boas are more abundant in the southern part of the state. The snake is primarily nocturnal and most individuals were encountered on the road at night between 1930 and 2400 hours, when air temperatures ranged from 22° to 29°C. A few were taken in the dry season, but the snakes are most common during the rainy season.

Two boas approximately 1200 mm. in length were reported mating near Teacapán on April 6 (Scott, 1962:31). A female about 1200

mm. in length gave birth to 17 young on July 23 near San Ignacio. The largest boa collected, a female measuring 2250 mm., gave birth to 36 young on August 11 (Scott, 1962:32). The first young of the year were collected on July 30, and young individuals were collected almost every night thereafter through September 15.

Distribution in Sinaloa.—Low to moderate elevations throughout the state. See Fig. 59.

Specimens examined.—7.8 mi. [by hwy. 15] N Acaponeta [Nayarit] (LACM 6783); 7.7 mi. S Cerro Prieto (UAZ 9372); 16 km. NNE Choix, 519 m. (° KU 73484); 10 mi. NE Concordia (UAZ 16280); 7.1 mi. S Coyotitán (JFC 63:142); Culiacán (LACM 6774); 10.5 mi. S Culiacán (CSCLB 1967); 25.6 mi. S Culiacán (LACM 6780); 31.7 mi. S Culiacán (LACM 6781); 37.6 mi. S Culiacán (LACM 6782); 34 mi. NW Culiacán (JRM 1103); 24 mi. SSE Escuinapa (CSCLB 1958, 1966); Equinal [?Espinal] (UCLA 14839); 7.2 mi. S Guamúchil (LACM 6784); 6.7 mi. N La Cruz rd. on hwy. 15 (LACM 6777); 14.6 mi. NE Los Mochis junc. (UAZ 16284); Mazatlán (LACM 6778); N Mazatlán (UCLA 5875); 0-13 mi. N Mazatlán (UAZ 16281-83); 1.6 mi. N Mazatlán (CSCLB 1963); 5 km. N Mazatlán (° KU 73486); 4 mi. N Mazatlán (JFC 62:36); 5.2 mi. N Mazatlán (UAZ 16285); 6 mi. N Mazatlán (CSCLB 1965); 10.2 mi. N Mazatlán (CSCLB 1962); 29 km. N Mazatlán (° KU 61348); 38.5 mi. N Mazatlán (CSCLB 1960); 42.5 mi. N Mazatlán (CSCLB 1961); 50.6 mi. N Mazatlán (UAZ 16286); 58 mi. N Mazatlán (JFC 62:37); 15 mi. NNW Mazatlán (KU 69110); 15.7 mi. SE Mazatlán (UAZ 16287); 4.1 mi. N Piaxtla, Río (CSCLB 1964); Teacapán (LACM 6785-95); 14.4 mi. S Terreros (LACM 6779); 21 km. SE Villa Unión (° KU 73485).

Literature records.—Near Mazatlán (Lewis and Johnson, 1956:280); Sierra de Choix (Smith, 1943a:409).

Additional records.—Camino Real de Piaxtla (AMNH 69684); Choix (USNM 46503); 2 mi. N Culiacán (AMNH 76872); 4.2 mi. N Culiacán (FAS 7724); 20-24 mi. N. Culiacán (FAS 11357); 15 mi. NW Culiacán (AMNH 62988); 8.8 mi. N El Dorado (SU 23792); 5.7 mi. N Escuinapa (FAS 14840); Higuera de Zaragoza (SDSNH 18285, 38871-85, 38891-93, 40350-51); 19 mi. N Los Mochis (AMNH 77590); 4 mi. N Mazatlán (UF 12791); 12 mi. N. Mazatlán, 200 ft. (TCWC 12604); 25 mi. N Mazatlán (UF 12792); 30.3 mi. N Mazatlán (SU 23791); 2 mi. NE Mazatlán (MCZ 80908); 2 mi. E Mazatlán (EHT-HMS 711); 3 mi. NNW Mazatlán, 25 ft. (UMMZ 114651); 28.5 mi. NNW Mazatlán, 300 ft. (UMMZ 114647); 29.5 mi. NNW Mazatlán, 300 ft. (UMMZ 114662); 23.6 mi. SE Río Piaxtla (SU 23789); Presidio (EHT-HMS 691).

Family Colubridae

Arizona elegans noctivaga Klauber

Arizona elegans noctivaga Klauber, Trans. San Diego Soc. Nat. Hist., 10:343, March 29, 1946 (type locality, eight miles northwest of Owlshead, Pima County, Arizona).

Remarks.—A single specimen was reported from the lowland thorn forest by Greer (1964:215).

Distribution in Sinaloa.—Known only from the lowlands in the vicinity of Mazatlán. See Fig. 60.

Specimens examined.—None.

Literature record.—1.1 mi. N. Mazatlán (Greer, 1964:215).

Coniophanes lateritius lateritius Cope

Coniophanes lateritius Cope, Proc. Acad. Nat. Sci. Philadelphia, 13:524, 1862 (type locality, Guadalajara, Jalisco).

Coniophanes lateritius lateritius: Smith and Grant, Herpetologica, 14:20, April 25, 1958.

Remarks.—One male (KU 83401) and one female (LACM 28717) represent the first records in Sinaloa—a 270 kilometer northward extension of the known range. The two specimens, collected on the road, have 145, 146 ventrals; ?, 84 subcaudals; 20-19-17, 19-19-17 dorsal scale rows; snout-vent lengths of 270, 521; and tail lengths of ?, 163. The general coloration and pattern agree with the description by Smith and Grant (1958:20-22). The female is darker than other known specimens, in that the posterior two-thirds of the body and entire dorsal surface of the tail are nearly black.

Distribution in Sinaloa.—Known only from the southern lowlands in the vicinity of Villa Unión. See Fig. 60.

Specimens examined.—8 km. N Villa Unión (° KU 83401); about 30 mi. NE Villa Unión (° LACM 28717).

Conopsis nasus nasus Günther

Conopsis nasus Günther, Catalogue Collection Snakes British Mus., London, p. 6, 1858 (type locality, "California" [in error according to Taylor and Smith, Univ. Kansas Sci. Bull., 28(II):329, November 12, 1942]).

Conopsis nasus nasus: Tanner, Herpetologica, 17:15, April 15, 1961.

Remarks.—One male with an incomplete tail has 132 ventrals; smooth scales in 17 rows; supralabials, 7-7 (3 and 4 enter the eye); infralabials, 7-7; preoculars, 1-1; postoculars, 2-2; temporals, 1-2/1-2; anal divided; nasal divided below nare; no loreal or internasals (rostral contacts prefrontal); snout-vent length 112; dorsal dark brown spots, 46. The cream-colored venter is heavily checked with black and the subcaudal surface is immaculate with a mid-ventral zig-zag black stripe (black borders of adjacent subcaudal scutes). The posterior maxillary teeth are faintly grooved, suggestive of *Toluca*, but the dorsal pattern, other scale characters, and geographic position are more in accord with *Conopsis nasus*. There are no characters that agree with those diagnostic for *C. nasus labialis* as given by Tanner (1961:15).

This specimen was taken on August 8, 1963, in pine-oak forest.

Distribution in Sinaloa.—Tropical deciduous and pine-oak forest of the southern highlands. See Fig. 60.

Specimen examined.—19.2 km. NE Santa Lucía, 1935 m. (° KU 80872).

Literature record.—37 mi. E Concordia (Tanner, 1961:17).

Dryadophis cliftoni Hardy

Dryadophis cliftoni Hardy, Copeia, no. 4:714, December 31, 1964 (type locality, Plomosas, 22 kilometers east of Matatán, 762.5 meters, Sinaloa).

Remarks.—Seven specimens have 17-17-15 scale rows and a single preocular on each side. One specimen has three postoculars on the left and two on the right; the rest have two on each side. The number of temporals on the left and right sides respectively for the seven Sinaloan specimens are: 6-5, 6-6, 7-8, 5-6, 7-7, 6-6, and 7-7. Supralabials are eight on each side in all except one (KU 73491), which has eight on the right and nine on the left. The numbers of infralabials are 9-9, 9-9, 10-10, 10-10, 11-11, 11-11, 10-10; ventrals and subcaudals are respectively: 183, ?; 185, ?; 184, ?; 191, ?; 188, 139; 185, 145; 188, ?. Freshly killed specimens (KU 78932, 78934-35) had bright orange-red on the head, neck, and throat, followed by a salmon to pale pink belly at midbody. The dorsal blotches were dark brown, and the interspaces were tan. One juvenile (KU 78933) agrees with the adults in pattern, but differs in color by having chocolate brown dorsal blotches and tan interspaces. In all specimens the venter is immaculate creamy white.

The specimens from Plomosas (KU 73489-91) were taken in humid tropical deciduous forest. In the mountains above Santa Lucía one specimen (KU 78935) was taken in a boulder-strewn streambed bordered by dense tropical deciduous forest (Plate 7, Fig 2). Three other specimens (KU 78932-34) were taken at 1930 meters elevation in pine-oak forest. All were collected in July and August. Nickerson and Heringhi (1966:136) obtained this species in southern Sonora (near the Chihuahua border) during August.

Distribution in Sinaloa.—Known only from the vicinities of Plomosas and Santa Lucía in the highlands of southern Sinaloa, but might occur throughout the highlands. See Fig. 61.

Specimens examined.—Plomosas, 22 km. E Matatán, 762.5 m. (* KU 73489-91); 19.2 km. (via hwy. 40) NE Santa Lucía, 1937.5 m. (* KU 78932-34; 1 km. NE Santa Lucía, 1156.2 m. (* KU 78935); 1.1 mi. W Santa Rita on hwy. 40 (LACM 6888; this locality is 10.3 km. [via hwy. 40] NE Santa Lucía, 1586 m.).

Dryadophis melanolomus stuarti Smith

Dryadophis melanolomus stuarti Smith, Proc. U. S. Nat. Mus., 93:418, 1943 (type locality, near Acapulco, Guerrero).

Remarks.—One male has 178 ventrals, 9-9 supralabials, 10-10 infralabials, 19-17-15 scale rows, a snout-vent length of 660, and an incomplete tail.

Anterior ventral spotting is present but indistinct; the dorsal scales

are distinctly black edged, more pronounced laterally than mid-dorsally. On the anterior and posterior part of the body the black edging of the dorsal scales can be made visible by spreading the scales. The supralabials are lightly mottled with gray and there is no distinct ocular stripe. In other characters, this specimen agrees with the original description (Smith, 1943a:418).

This is the first record of the species in Sinaloa. The specimen was taken in tropical dry forest (Plate 7, Fig. 1).

Distribution in Sinaloa.—Known only from the southern lowlands, in the vicinity of Villa Unión. See Fig. 61.

Specimen examined.—8 km. N Villa Unión, 140 m. (° KU 80746).

Additional record.—15 mi. SE Escuinapa (UMMZ 118784).

Drymarchon corais rubidus Smith

Drymarchon corais rubidus Smith, Jour. Washington Acad. Sci., 31:474, November 11, 1941 (type locality, Rosario, Sinaloa).

Remarks.—Duellman (1961:93-94) reported specimens of *Drymarchon corais rubidus* from Michoacán that deviate from the uniform black dorsal coloration reported by Smith (1941d:475) by being either pale brown anteriorly with black flecks arranged as narrow transverse bands, or black above with reddish or "rust-colored" cross-bands on the anterior half of the body. Eight of the 19 specimens at hand have a pale brown dorsal coloration anteriorly that is either mottled or flecked with black; the amount of black increases progressively to the tail, which is uniformly black above. One specimen (LACM 6801) is reddish brown dorsally with black flecks on the anterior half of body; the flecks form bars near midbody; the posterior quarter of the snake is black. Another specimen (LACM 6802) is black with reddish, chevron-shaped cross bands on the anterior half of body. Scott (1962:46) reported snakes of glossy, jet black; dull grayish black, often with a red tint; and one or two dull, brick-red specimens. The ventral coloration varies from coral-red to white to gray anteriorly; the caudal coloration is dark gray or black. The geographical variation in coloration of *Drymarchon*, as pointed out by Duellman (1961:94) and supported by our data, points to a need for re-evaluation of the subspecific status of certain populations of *Drymarchon* and for a re-examination of the alleged intergrades (Smith, 1941d:476-77).

Smith (1941d:475) reported the range of ventrals for this subspecies as 190-203, and the range of subcaudals as 69-78. Seventeen specimens examined have 187-197 (190.1) ventrals (excluding KU 73492-93), and nine specimens have 59-73 (66.6) subcaudals. The

ventral counts reported here are generally lower than those reported by Bogert and Oliver (1945:360) for eight specimens from southern Sonora and by Fugler and Dixon (1961:12) for one specimen from central Sinaloa.

All specimens examined have 8-8 supralabials and 8-8 infralabials; the temporal formula $1/2 + 2$ occurs nine times, $2 + 1/2$ twice, $2 + 2$ occurs 17 times, $2 + 1$ once, $2 + 3$ seven times; the dorsal scale rows are 17-17-15 in five specimens, 17-17-16 in one, 18-17-15 in three, 18-17-16 in two, 19-17-15 in five, and 19-17-16 in one (excluding KU 73492-93).

This large terrestrial species is active in the morning or late afternoon. Perhaps it is associated mainly with aquatic situations. Scott (1962:45) observed an adult specimen floating on a mat of aquatic vegetation in a large pond near Teacapán, apparently searching for frogs. Zweifel and Norris (1955:238) reported that specimens were more common near streams than elsewhere at Guirocoba, Sonora. Food items taken from stomachs included *Sigmodon*, *Cnemidophorus costatus*, *Ctenosaura pectinata*, *Masticophis striolatus*, and a 250 mm. fish. A large specimen, found at about 2200 hours on the road in northern Nayarit, was in the process of eating a *Masticophis bilineatus*. Both of these snakes normally are considered to be diurnal. Two recently hatched young were found on August 16 near Teacapán and August 17 near Mazatlán. The smallest specimen measured 455 mm. total length. The longest specimen measured 2390 mm. total length.

Distribution in Sinaloa.—Probably occurs throughout the state. See Fig. 62.

Specimens examined.—2.5 km. N Badiraguato, 230 m. (° KU 83402); 2.5 km. S Concepción, 75 m. (° KU 63734; KU 63732-33); Isla Palmito del Verde, S end (° KU 73495-96); La Cruz (° LACM 6796-97); Mazatlán (KU 63419); 1.3 mi. N Mazatlán (° LACM 6799); 10.8 mi. N Mazatlán (CSCLB 1364); Plomosas, 760 m. (° KU 73494); Rosario, 150 m. (° KU 73492-93); 1 mi. S Rosario (° LACM 6800); San Ignacio (° LACM 6798); San Ignacio turnoff on highway 15 (° LACM 25900); 2.2 km. NE Santa Lucía, 1155 m. (° KU 78936); Teacapán (° LACM 6801-03); 8 km. N Villa Unión, 140 m. (° KU 80747-48).

Literature records.—Ahome (Bogert and Oliver, 1945:404); El Dorado (Fugler and Dixon, 1961:12).

Additional records.—El Dorado (AMNH 90692-95); 15 mi. SE Escuinapa, 300 ft. (UMMZ 118784); 19.8 mi. S Escuinapa (CAS 95828); 24 mi. SE Piaxtla (SM 11131); Rosario (UIMNH 62810); 13.4 mi. N San Lorenzo, Río (SU 23805).

Drymobius margaritiferus fistulosus Smith

Drymobius margaritiferus fistulosus Smith, Proc. U. S. Nat. Mus., 92:382, November 5, 1942 (type locality, Miramar, Nayarit).

Remarks.—Five specimens (three females and two males) have 1-1 preoculars, 2-2 postoculars, and 2+2/2+2 temporals. One female has 17-15-15 scale rows; the others have 17-17-15 rows. The three females and two males have, respectively: 143, 143, 145, 147, 144 ventrals; 8-9, 8-8, 8-9, 10-9, 9-9 supralabials; 9-9, 10-10, 10-9, 10-10, 10-10 infralabials; and 4-5/4-6, 4-5/4-5, 4-5/4-6, 5-7/4-6, 4-6/4-6 labials entering eye. One female has 127 subcaudals; all other specimens have incomplete tails. Eighteen specimens from near Teacapán have 142-151 (145) ventrals and 122-136 (129) subcaudals (Scott, 1962:48-50). The color and pattern of all specimens agree with the description by Smith (1942c:384).

Drymobius margaritiferus is a diurnal species that is abundant in the vicinity of Teacapán. Individuals commonly were collected in the ecotone between pastureland and forest. This snake is primarily terrestrial, invariably retreating on the ground. A specimen from San Ignacio was shot about 1.5 meters above the ground in a bush. Two snakes were found copulating in the forest on March 30. Two females each contained six well developed ova without shells on June 12 and in early August (Scott, 1962).

Distribution in Sinaloa.—Throughout the southern half of the state below 500 meters, and northward along the foothills into southern Sonora. See Fig. 63.

Specimens examined.—6 km. E Cosalá, 460 m. (* KU 73498); 17.9 mi. S Escuinapa (CSCLB 1365); 30.3 mi. S Escuinapa (CSCLB 1366); Isla Palmito del Verde, middle (* KU 73499-501); Isla Palmito del Verde, S end (* KU 73502); Mazatlán (JRM 1099); San Ignacio (LACM 6804); Teacapán (LACM 6805-15, 7237-39); 3 mi. NE Teacapán (LACM 6816-17); 1 mi. E Teacapán (LACM 6818); 2.5 mi. E Teacapán (LACM 6819).

Literature record.—Presidio (Boulenger, 1894:17).

Additional records.—El Dorado (AMNH 90696-98); Escuinapa AMNH 3477-79); 2.7 mi. N. Escuinapa (FAS 14469); 5 mi. N Mazatlán (AMNH 19596).

Elaphe triaspis intermedia (Boettger)

Pityophis intermedius Boettger, Ber. Offenb. Ver. Nat., 22:148, 1883 (type locality, "México"; restricted to Hacienda El Sabino, about 20 miles south of Uruapan, Michoacán by Dowling, Zoologica, 45:74, August 15, 1960).

Elaphe triaspis intermedia: Mertens and Dowling, Senckenbergiana, 33:201, November 15, 1952.

Remarks.—Two males have 8-9, 8-8 supralabials; 10-10, 10-10 infralabials; 248, 244 ventrals; 110, 101 subcaudals; 80, 84 dorsals (totals of three counts—neck, midbody, anterior to anus). Four females have 8-8, 8-8, 8-9, 9-9 supralabials; 9-9, 10-10, 10-9, 10-10 infralabials; 261, 268, 269, 275 ventrals; 86, 97 subcaudals (excluding

KU 73503, 83403); and 82, 90, 86, 89 dorsals. One juvenile of unknown sex has 8-8 supralabials, 9-9 infralabials, 249 ventrals, 106 subcaudals, and 88 dorsals.

The six larger specimens are gray dorsally in preservative. The smallest individual has 61 blotches on the body and 42 on the tail. All specimens agree with the description by Dowling (1960:74-75).

Elaphe triaspis is a nocturnal species in Sinaloa, and apparently is active later in the rainy season than many other snakes. Less than 20 per cent of the specimens were taken earlier than July 20.

Distribution in Sinaloa.—Probably occurs throughout the state with the possible exception of the arid northwestern lowlands. See Fig. 64.

Specimens examined.—20 km. N, 5 km. E Badiraguato, 550 m. (* KU 83403-04); 3 mi. S Coyotitán (LACM 2564); 7.5 mi. S Coyotitán (LACM 6823); 31.6 mi. N Culiacán (LACM 6832); 42.5 mi. N Culiacán (LACM 6827); 55 mi. N Culiacán (LACM 6820); 42 km. S Culiacán (* KU 73504); 70 mi. S Culiacán (LACM 6833); 75.7 mi. S Culiacán (UAZ 16288); 11 mi SE Escuinapa (LACM 6824); 12.4 mi. N La Cruz road on hwy. 15 (LACM 6821); 15.2 mi. S La Cruz road on hwy. 15 (LACM 6828); 9.5 mi. N Mazatlán (LACM 6822); 48 km. N Mazatlán (* KU 73503); 33.3 mi. N. Mazatlán (LACM 6831); 40.7 mi. N Mazatlán (LACM 6825); 73 mi. N Mazatlán (CSCLB 1438); 95.2 mi. N Mazatlán (LACM 6826); Santa Lucía (CSCLB 1442); 4 mi. S Terreros (LACM 6829); 3 mi. S Tropic of Cancer [hwy. 15] (JFC 63:154); 6 mi. E Villa Unión (JFC 63:155); 6.1 mi. E Villa Unión (JFC 63:156); 22.8 mi. E hwy. 15 [Villa Unión] on Durango rd. [hwy. 40] (LACM 6830).

Literature records.—11 mi. S Coyotitán (Duellman, 1957b:238); 13.8 mi. NNW Mazatlán, ca. 150 ft. (Dowling, 1960:77; Duellman, 1957b:238).

Additional records.—7.6 mi. W Concordia (SU 23831); 7.9 mi. W Concordia (SU 23830); 41.4 mi. N Culiacán (SU 23827); 4.9 mi. S Elota, Río (SU 23829); 21.7 mi. S El Salado (FAS 16798); 13.9 mi. S Escuinapa (SU 23832); 47.4 mi. N Mazatlán (CAS 95798); 55.7 mi. N Mazatlán (FAS 14465); 78.3 mi. N Mazatlán (FAS 13575); 16.4 mi. S. San Lorenzo, Río (SU 23828).

Geagras redimitus Cope

Geagras redimitus Cope, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 8:141, 1876 (type locality, Tehuantepec, Oaxaca).

Remarks.—Inclusion of this species is based on the original description of *Sphenocalamus lineolatus* by Fischer (1883:5), who gave the locality as Mazatlán but did not designate the state. *Sphenocalamus lineolatus* was later referred to the synonymy of *Geagras redimitus* by Cope (1885-177). Duellman's report (1961: 96) of two specimens from the lowlands of Michoacán supports the possibility that *Geagras redimitus* occurs along the coast from Oaxaca to Sinaloa.

Distribution in Sinaloa.—Known only from Mazatlán. See Fig. 65.

Specimens examined.—None.

Additional record.—Mazatlán (Cope, 1887:82; Fischer, 1883:5).

***Geophis dugesii* Bocourt**

Geophis dugesii Bocourt, Mission scientifique au Mexique et dans l'Amérique centrale, Rept., livr. 9:573, 1883 (type locality, Tangancícuaro, Michoacán).

Remarks.—A female and a male have 154, 173 ventrals, and 38, 61 subcaudals. Both specimens have smooth scales in 15 rows, lacking apical pits; supralabials, 6; infralabials, 6; temporals 0+1+2; preoculars absent; postoculars, one; loreal, one; nasals divided; rostral visible from above; anal plate entire; supralabials three and four enter eye; mental does not contact chin shields; pupil round.

Both specimens are black with a white or pale yellow center in each third or fourth dorsal scale, imparting a faintly speckled appearance. Anteriorly, the speckles give the appearance of narrow bands three to four scales apart. The chin, ventrals, and subcaudals are white with the lateral edges of the ventrals black.

According to Floyd Downs (personal communication), who examined these specimens, their allocation to *Geophis dugesii* should be considered tentative.

Distribution in Sinaloa.—Southern highlands in lower montane dry forest. See Fig. 65.

Specimens examined.—5 km. SW Palmito, 1880 m. (° KU 75622); 19.2 km. NE Santa Lucía, 1935 m. (° KU 78939).

***Gyalopion quadrangularis* (Günther)**

Ficimia quadrangularis Günther, Biologia Centrali-Americana, Rept., p. 99, pl. 35, fig. A., 1893 (type locality, Presidio, Sinaloa).

Gyalopion quadrangularis: Smith and Taylor, Jour. Washington Acad. Sci., 31:359, August 15, 1941.

Remarks.—Taylor (1936a:51) described *Ficimia desertorum* from a single specimen and compared it to *F. quadrangularis*, then known from a single specimen. When Smith and Taylor (1941:359) transferred *F. desertorum* and *F. quadrangularis* to the genus *Gyalopion*, the only specimens of each were the types. Bogert and Oliver (1945:404) reported three specimens of *G. desertorum* from Sinaloa that indicated individual variation in the size of the dark cross bands. Duellman (1957b:238) confirmed differences in coloration of the two nominal species, but suggested that they might be conspecific. A total of 13 specimens (six were examined) from nine localities in Sonora and Sinaloa, including a specimen of "intermediate" coloration and pattern from El Dorado, led Dixon and Fugler (1959:164) to regard *desertorum* as a subspecies of *G. quadrangularis*. They separated the populations on the basis of differ-

ences in color, pattern, and the presence or absence of the loreal. They found no populational differences in the numbers of ventrals, subcaudals, body or tail blotches, or the condition of the anal plate. Fugler and Dixon later (1961:13) reported on a second "intermediate" specimen from El Dorado. They based their interpretation on the presence of a loreal on one side of the head only, whereas *G. q. quadrangularis* lacks loreals and *G. q. desertorum* possesses them. Campbell and Simmons (1962:196) suggested that the dorsal bands are reduced in size in the southern part of the range, reaching the extreme condition in the vicinity of Mazatlán. They reported two specimens from south of Culiacán that have "characters intermediate between the two subspecies." Greer (1965a:69) noted that the width of the black dorsal body blotches varies clinally throughout the known range of the species, extending to the tips of the ventrals or first dorsal row in specimens from southern Arizona, to the second dorsal row at El Dorado (Sinaloa), to the fourth or fifth dorsal row near Mazatlán and to the seventh dorsal row in southern Sinaloa and Nayarit.

Since the above observations were made, many more specimens have been obtained at localities from Arizona to Nayarit. We have examined 67 specimens and have an additional 20 locality records from Sinaloa.

Geographic variation in the following 11 characteristics does not demonstrate the existence of two distinct or intergrading populations, nor does it clearly indicate clinal trends. The infralabials are 5-8 (6.3, N = 67) with variations occurring throughout the range. The sum of ventrals and subcaudals is 141-166 (153.5, N = 61; except KU 93492, LACM 6856, MCZ 61414, MVZ 50741-42, UMMZ 118946), and the number of dorsal caudal blotches is 3-10 (6.7, N = 66; except UMMZ 118946). Dorsal body-blotches are 16-41 (26.4, N = 66; except MVZ 50741), with many low counts due to fusion of spots in pairs and many high counts due to splitting of spots; however, neither change suggests a geographic trend. The lengths (in numbers of scales) of the first dorsal body blotches posterior to the nuchal collar are 1.5-7.5 (4.6, N = 66; except FAS 11653); middle dorsal body-blotches 1.5-6.5 (2.6, N = 66; except FAS 11653); last dorsal body-blotches 1.5-4.5 (2.6, N = 65; except FAS 11653, 14757). The nuchal collar extends beyond the posterior edge of the parietals 4-8 (5.7, N = 67) scale lengths; the collar is separated from the black head-cap in six (9.0%) specimens (ASDM 2234; KU 73513; LACM 6834-35, 6854, 6856), and contacts the

head-cap in the rest. In 39 specimens (58.2%) the pale scales of the ground color have black tips giving a dark appearance to the snakes, but 28 others (41.8%) lack black-tipped scales. The anal is entire on all specimens where the condition is known, including the holotype.

Eight of the characteristics examined demonstrate clinal trends. The number of dorsal scale rows around the neck is 17 in all specimens north of 24 degrees north latitude, but 20 per cent of the specimens examined from south of 25 degrees north latitude show reduction to 15 or 16 scale rows at the neck. At midbody, five per cent of the specimens from south of 25 degrees north latitude show reduction to 16 rows, but all other specimens have 17 rows. Anterior to the cloaca the scale rows are 18 in specimens from north of 24 degrees north latitude (six %) and are 15, 16 or 18 in specimens from south of 25 degrees north latitude (15%). The number of supralabials is 5-8 with a distinct gradation from a mode of 7 in the north to a mode of 6 in the south (Table 5 and Fig. 10). The presence or absence of the loreal scale was used by Dixon and Fugler (1959:163) to separate two populations. The loreal scale is present on both sides of the head in all specimens from Culiacán southward, but is absent in all specimens from Guaymas, Sonora, northward. Between Culiacán and Guaymas 17 specimens have loreals and seven lack loreals. One specimen (KU 73515) from

TABLE 5.—Three Characters that Show Clinal Variation from North to South in *Gyalopion quadrangularis*. (Each sample consists of all specimens available from the areas included in each degree latitude throughout the geographic range of the species.)

DEGREES NORTH LATITUDE	Number of supralabials			Black subcaudal spots		Black spots on ventrals	
	Number of specimens	Mean	Mode	Specimens with spots	Specimens without spots	Specimens with spots	Specimens without spots
31.....	4	7.0	7	5	0	3	2
30.....	0	0	0	0	0
29.....	2	7.0	7	2	0	2	0
28.....	1	6.0	6	1	0	1	0
27.....	2	5.8	6	2	0	0	2
26.....	2	6.5	2	0	1	1
25.....	19	6.6	7	18	1	16	3
24.....	8	6.1	6	7	1	4	4
23.....	27	6.0	6	18	9	10	17
22.....	1	6.0	6	0	1	1	0

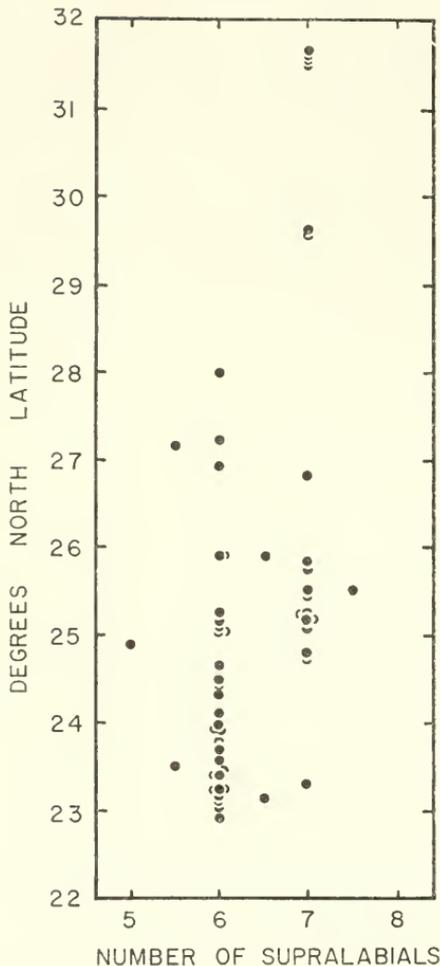


FIG. 10. Geographic variation in the number of supralabials in *Gyalopion quadrangularis*, using the mean of counts from both sides of the head.

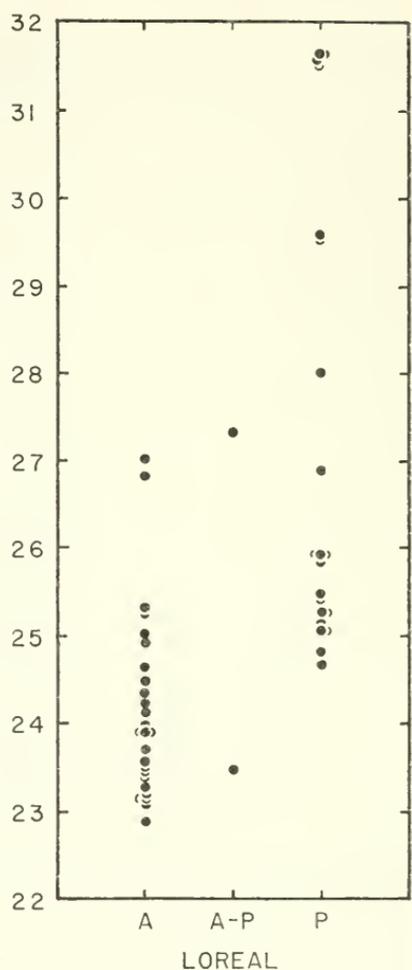


FIG. 11. Geographic variation in the presence or absence of the loreal in *Gyalopion quadrangularis*. A = loreal absent on both sides of head; A-P = loreal absent on one side but present on the other; P = loreal present on both sides of head.

20 miles north of Mazatlán has a single loreal (on the left) and another specimen from 6.1 miles northwest of Navojoa, Sonora, (MVZ 50741) has one loreal (on the left). We do not regard these two specimens as intergrades because of their geographic separation and the large areas of sympatry of specimens with and without loreals (Fig. 11). The variation is of a clinal nature with loreals present in the north and absent in the south. The loss of the loreals

may be due to a single gene as suggested by Dixon and Fugler (1959:163).

The ratio of tail length/total length shows a clinal trend. The longest tails are those of males in the north (15.2, 15.3% for two specimens from southern Arizona). In males, the shortest tails are from southern Sinaloa (12.9%, south of Rosario); however, the shortest tails in females are from northern Sinaloa (12.4, 13.2, 13.3 and 13.5%).

In general, the lateral interblotches are absent in the south and present in the north. With one exception (LACM 6838 from 36.1 miles south of Coyotitán) all specimens south of El Dorado lack lateral interblotches. With one exception (ASDM 1925 from five miles north of Navojoa, Sonora) all specimens north of Terreros have lateral interblotches. The southernmost specimen with lateral interblotches has only a few blotches (LACM 6838); the next southernmost specimen with lateral interblotches is AMNH 79916 from El Dorado. A specimen from 0.8 miles south of Guamúchil (LACM 6857) has lateral interblotches that include the tips of the ventrals. To the south, at 46.4 miles north of Culiacán (LACM 6848), the lateral interblotches do not include the ventrals; the lateral interblotches decrease in number at 43 miles north of Culiacán (LACM 6847) and are absent at 9 miles north of Culiacán (LACM 6844). At least some lateral interblotch pigment is indicated in specimens from southern Sinaloa, but is infrequent in occurrence. In general, there is a gradual decrease in lateral interblotch pigment from the north to the south.

The amount of black pigment on the ventrals increases from south to north (Table 5). The subcaudal black spots also vary clinally; the number of specimens with black subcaudal spots increases from south to north (Table 5).

The lateral extent of the black dorsal body blotches can be measured by counting the scales separating the lateral margins of the dorsal blotches and the lateral margins of the ventrals. This separation varies from zero (dorsal blotch in contact with ventrals) at the northern limit of the distribution of the species (ASDM 1681 in southern Arizona) to eight in southern Sinaloa (KU 87449). The dorsal blotch contacts the ventrals in four specimens from Arizona, two specimens from Sonora and in several specimens in Sinaloa southward to Mazatlán. The dorsal blotches become smaller from north to south, being separated by a maximum of two scale rows in Arizona, three scale rows in Sonora, four scale rows in

northern Sinaloa and eight scale rows in southern Sinaloa. Although snakes with complete blotches occur almost throughout the range of the species, there are none with four or more rows separating blotches and ventrals north of Guamúchil.

Sinaloan specimens of this species are red or red-orange in dorsal ground color, with black blotches and a white venter. The color of a living specimen from Sonora (LACM 6834 from 15 miles south of Santa Ana) is as follows: black blotches have light centers laterally and are separated from each other by pale cream interspaces middorsally, to give the appearance of an interrupted mid-dorsal stripe; ground color laterally and between black blotches orange; first two scale rows above ventrals white; lateral interspaces with one or two black-tipped scales; head with orange border around black interorbital spot and anterior part of nuchal collar; snout white; ventrals and subcaudals white, some subcaudals with black spots.

The geographic irregularity of variation in some characteristics and the clinal nature of the variation in other characteristics does not justify the recognition of subspecies. Therefore, we place *Gyalopion quadrangularis desertorum* in the synonymy of *G. quadrangularis*.

Most specimens of this small nocturnal snake were taken on the road at night. None were collected when the air temperature was below 27°C, and the majority were active at night at an air temperature between 28° and 29°C. A specimen from near Terreros was found beneath a rock. Another was found after a morning rain on a floating stick in a water-filled irrigation ditch at Villa Unión. Greer (1966:372) reported the species to be oviparous.

Distribution in Sinaloa.—Throughout the state from sea level to 1220 meters elevation. See Fig. 66.

Specimens examined.—Ahome (° LACM 8651-53); 13 mi. ESE Badiraguato, 800 ft. (° KU 83405); 36.1 mi. S Coyotitán [San Ignacio turnoff] (° LACM 6838); 8.7 mi. N Culiacán (° LACM 6844); 17.3 mi. N Culiacán (CSCLB 1402); 31.2 mi. N Culiacán (° LACM 6845); 32.5 mi. N Culiacán (° LACM 6846); 43 mi. N Culiacán (° LACM 6847); 46.4 mi. N Culiacán (° LACM 6848); 63 mi. N Culiacán (° KU 73505); 19 km. SSE Culiacán (° KU 73517); 18 mi. S. Culiacán (° LACM 6853); 50.5 mi. S Culiacán (FAS 13776); 30 mi. W Culiacán (° ASDM 1791); El Cajon, 1700 ft. (° KU 93492); El Dorado (° AMNH 79916); 17.3 mi. S Escuinapa (CSCLB 1410); 34 mi. S Escuinapa (CSCLB 1404); 0.8 mi. S Guamúchil (° LACM 6857); 6.5 mi. S Guamúchil (° LACM 6855); 3.1 mi. E La Cruz (° LACM 6835); 1.5 mi. N Los Mochis (° FAS 11653); 8 mi. NE Los Mochis (° KU 73506); 2.9 mi. N Mazatlán (° LACM 6836); 3 mi. N Mazatlán (° MCZ 61415); 5-10 mi. N Mazatlán (° LACM 8654); 9.3 mi. N Mazatlán (CSCLB 1403); 9.6 mi. N Mazatlán (CSCLB 1412); 10.6 mi. N Mazatlán (CSCLB 1409); 11.5 mi. N Mazatlán (° LACM 6839); 12 mi. N Mazatlán (JFC 62:46); 13.3 mi. N Mazatlán

(° LACM 6840-41); 14.9 mi. N Mazatlán (CSCLB 1407); 26 km. N Mazatlán (° KU 73512); 32 km. N Mazatlán (° KU 73515); 22.9 mi. N Mazatlán (° LACM 6842); 66 km. N Mazatlán (° KU 73511); 74 km. N Mazatlán (° KU 73513-14); 50 mi. N Mazatlán (° LACM 6837); 54.6 mi. N Mazatlán (CSCLB 1408); 93 km. N Mazatlán (° KU 73516); 59.7 mi. N Mazatlán (CSCLB 1411); 70.4 mi. N Mazatlán (° LACM 6843); 18 km. E Mazatlán (° KU 73510); 4.2 mi. S Mazatlán (° LACM 8655); 5 km. S Mazatlán (° FAS 14757); 2.1 mi. SE Mazatlán (° MCZ 61416); 10 mi. SE Mazatlán (° MCZ 61414); 11 km. NW Mazatlán (° KU 73508-09); 4.2 mi. NNW Mazatlán, 50 ft. (° UMMZ 114481); 24 mi. NNW Mazatlán, 150 ft. (° UMMZ 114480); 44.1 mi. N Río Elota (° LACM 6849); 8.4 mi. N Río Fuerte (UAZ 16294); 1.8 mi. N Rosario (CSCLB 1406); 11 km. S Rosario, 15 m. (° KU 87449); halfway between Rosario and Villa Unión (JFC 62:45); 3.2 km. (by rd.) SW Santa Lucía, 4000 ft. (° KU 95953); 6.1 mi. N Sinaloa-Nayarit border (CSCLB 1405); Tecorito (° UMMZ 118946-47); 1.5 mi. N Terreros (° LACM 6854); 0.2 mi. S Terreros (° LACM 6852); 0.7 mi. S Terreros (° LACM 6856); 1.2 mi. S Terreros (° LACM 6851); 41 mi. S Terreros (° LACM 6850); 4.3 mi. N Tropic of Cancer (JFC 65:141); 25 mi. N Tropic of Cancer (CSCLB 1414); Villa Unión (° KU 73507).

Arizona: 5 mi. N Arizona hwy. 289 on U. S. hwy. 89 (° ASDM 1680); 1.2 mi. W U. S. hwy. 89 on Arizona hwy. 289 (° ASDM 1681); Nogales, Santa Cruz co. (° ASDM 2234); 2 mi. S Patagonia, Alum Canyon (° ASDM 1682); 3 mi. W Patagonia (° ASDM 1679).

Sonora: ca. 12 km. NW Guaymas (° UIMNH 25065); Guirocoba (° MVZ 50742); 38.4 mi. N Hermosillo (° MVZ 71366); 5 mi. N Navojoa (° ASDM 1925); 6.1 mi. NW Navojoa (° MVZ 50741); 15 mi. S Santa Ana (° LACM 6834).

Literature records.—47.5 mi. S Culiacán; 55.2 mi. S Culiacán (Campbell and Simmons, 1962:196; Fouquette and Rossman, 1963:191); El Dorado (Dixon and Fugler, 1959:163; Fugler and Dixon, 1961:13); 4 mi. N Mazatlán; 24 mi. N Mazatlán (Dixon and Fugler, 1959:164); 20-40 mi. S Mazatlán (Campbell and Simmons, 1962:196); 4.2 mi. NNW Mazatlán, 150 ft.; 24 mi. NNW Mazatlán, 50 ft. (Duellman, 1957b:238); Presidio (Boulenger, 1894:272; Günther, 1893:99; Dixon and Fugler, 1959:164).

Additional records.—28.5 mi. N Culiacán, Río (SU 23807); 6.7 mi. N Escuinapa (SU 23811); 16.8 mi. N jct. La Cruz rd. and hwy. 15, on hwy. 15 (SU 23808); Los Mochis, proximity of (SU 23806); 9.3 mi. N Los Mochis (UF 16787); Mazatlán (SDSNH 52911); 28.8 mi. N Mazatlán (SU 23810); 30.6 mi. S Presidio, Río (SU 23812); 0.4 mi. N San Lorenzo, Río (SU 23809); Tecorito (UMMZ 118946-47).

Hypsigena torquata (Günther)

Leptodeira torquata Günther, Ann. Mag. Nat. Hist., ser. 3, 5:170, pl. 10, fig. A, April, 1860 (type locality, Laguna Island, Nicaragua).

Hypsigena torquata: Cope, Bull. U. S. Nat. Mus., 32:78, 1887.

Remarks.—The status of *Hypsigena* in western México has been in question for many years. *Hypsigena torquata* and *H. ochrorhyncha* have been treated as species by Taylor (1939b:368-75), Tanner (1944:45), Davis and Dixon (1957a:24-25), and Dixon (1965:125). *Hypsigena ochrorhyncha* was considered a subspecies of *H. torquata* by Bogert and Oliver (1945:378-81), Zweifel and Norris (1955:245), Smith and Van Gelder (1955:146), Duellman (1957b:238-39), Fugler and Dixon (1961:13-14), Duellman (1961:99-100), and Fouquette and Rossman (1963:192-93).

Much of the confusion has involved the apparent occurrence of intergradation between the two forms in Sinaloa (Smith and Van Gelder, 1955:146). The population representing the name *torquata* is composed of individuals that have the dark nuchal blotch preceded by a creamy white band about as wide as the nuchal blotch, whereas individuals having the dark nuchal blotch preceded by the normal brown or pale brown dorsal coloration are referred to *ochrorhyncha*. Specimens having each pattern have been taken from several localities in Sinaloa. On September 28, two specimens, representing both patterns, were taken on Mexican highway 15, 74 kilometers north-northwest of Mazatlán, at 2210 and 2212 hours. Two other specimens, representing both patterns, were taken eight miles northeast of La Cruz at 2020 hours, on July 2, 1962. Snakes with the *ochrorhyncha* nuchal pattern have been taken throughout the lowlands of Sinaloa, at localities that completely overlap the range of snakes with the *torquata* nuchal pattern in southern Sonora and Sinaloa.

Examination of specimens from western México indicates that, with the exception of nuchal patterns, there is no way to distinguish the two taxa. Contrary to what Dixon (1965:126) stated, we find a decrease in the total number of ventral and subcaudal scales of *ochrorhyncha*-patterned snakes from Arizona and Sonora into Sinaloa and of *torquata*-patterned snakes from southern Sonora through Sinaloa and western México to Guerrero. In the area where snakes with both nuchal patterns occur the ventral-subcaudal scale counts fall within the same range. The cline in the number of ventral-subcaudal scales is independent of nuchal pattern. In addition, snakes with different nuchal patterns from the same area are virtually identical in other details of coloration and pattern. Our findings suggest that the presence of two nuchal conditions in *Hypsiglena* is a case of pattern dimorphism in a single, otherwise uniform, species. Therefore, we refer all Sinaloan specimens to *Hypsiglena torquata* pending results of a detailed study now in progress.

Distribution in Sinaloa.—Throughout the lowlands of the state. See Fig. 67.

Specimens examined.—Ahome (LACM 8650); 2.7 km. NE Chupaderos, 400 m. (KU 78940); 5.7 mi. S Coyotitán (JFC 65:142); 13.1 mi. S Coyotitán (LACM 7267); 41.2 mi. S Coyotitán (LACM 7258); 11.7 mi. N Culiacán (LACM 7274); 15.5 mi. N Culiacán (LACM 7284); 16.3 mi. N Culiacán (CSCLB 1933); 26.3 mi. N Culiacán (LACM 7277); 19.8 mi. S Culiacán (LACM 7278); 43 km. S Culiacán (CSCLB 1930); 73.7 mi. S Culiacán (LACM 7279); 97.2 mi. S Culiacán (LACM 7280); 29 km. NW Culiacán (by hwy.

15) (KU 73526); 3.1 mi. W El Guaybo (UAZ 9378); 13.4 mi. N Elota, Río (LACM 7257); 23.2 mi. S Elota, Río (LACM 7266); 28.9 mi. S Elota, Río (LACM 7265); 32.5 mi. S Escuinapa (CSCLB 1935); 34.2 mi. S. Escuinapa (CSCLB 1934); 4.8 mi. N Fuerte, Río (CSCLB 1932); 5.9 mi. S Guamúchil (LACM 7286); Isla Palmito del Verde, middle (KU 73527); 7 mi. NE La Cruz turnoff [on hwy. 15] (LACM 7262); 8.1 mi. NE La Cruz turnoff [on hwy. 15] (LACM 7260-61); 11.4 mi. S La Cruz turnoff [on hwy. 15] (LACM 7275); Mazatlán (KU 63421, 73518-19); 1.5 km. N Mazatlán (KU 40336); 5 mi. N Mazatlán (LACM 2374; CSCLB 1943); 10 km. N Mazatlán (KU 73520); 18.9 mi. N Mazatlán (LACM 7264); 19 mi. N Mazatlán (JFC 62:54); 39 km. N Mazatlán (KU 73521); 47 km. N Mazatlán (KU 73522); 74 km. N Mazatlán (KU 73523-24, 86607); 92 km. N Mazatlán (KU 73525); 112.2 mi. N Mazatlán (LACM 7271-72); 116.5 mi. N Mazatlán (LACM 7273); 2.8 mi. SE Mazatlán (LACM 7268); 5 mi. SE Mazatlán (CSCLB 1937); Piaxtla, Río (CSCLB 1938); 2 mi. NW Rancho Huanacastle (LACM 7327); San Ignacio (LACM 7259, 7288); 6 mi. S Sonora-Sinaloa border (CSCLB 1931); Teacapán (LACM 7282); 4.8 mi. N Terreros (LACM 7287); 90.4 mi. N Terreros (LACM 7256); 17.2 mi. S Terreros (LACM 7283); 3 mi. W Terreros (LACM 7285); 13.3 mi. S Tropic of Cancer (CSCLB 1936); 6.5 mi. SE Villa Unión (LACM 7263).

Literature records.—Costa Rica (Smith and Van Gelder, 1955:146); El Dorado (Fugler and Dixon, 1961:13); 39 mi. N Los Mochis, 100 ft. (Davis and Dixon, 1957a:24); Mazatlán (Van Denburgh, 1898:464); 6-38 mi. NNW Mazatlán (Duellman, 1957b:238); Presidio (Boulenger, 1894:210; Taylor, 1939b:373); Villa Unión, 100 ft. (Davis and Dixon, 1957a:24).

Additional records.—6.9 N Cañas, Río (SU 23841); 9.9 mi. N Culiacán, Río (SU 23836); 36.6 mi. N Culiacán, Río (SU 23835); 13.0 mi. S Culiacán, Río (SU 23837); 58.3 mi. S Culiacán (UF 12801); El Dorado (AMNH 90699-702); 1 mi. NNE El Fuerte (FMNH 71529); 15.5 mi. S El Salado (FAS 16815); 19.2 mi. S El Salado (FAS 16816); 27.9 mi. S El Salado (FAS 16804); Escuinapa (AMNH 4312); Mazatlán (SDSNH 52903; USNM 147982, 151781); 2 mi. N Mazatlán (UIMNH 53057); 3 mi. N Mazatlán (AMNH 19785-86); 5 mi. N Mazatlán (AMNH 86939-40); 7 mi. N Mazatlán (AMNH 75893); 16 mi. N Mazatlán (MCZ 61417); 36 mi. N Mazatlán (FAS 10040); 70 mi. N Mazatlán (FAS 16803); 15.4 mi. N Mocerito, Río (SU 23833); 10.6 mi. S Mocerito, Río (SU 23834); 13.3 mi. S San Lorenzo, Río (SU 23838); 14.7 mi. S San Lorenzo, Río (SU 23839); 17.4 mi. S San Lorenzo, Río (SU 23840); 2 mi. SE Urías (AMNH 94804); 3 mi. SE Villa Unión, 100 ft. (TCWC 12601).

Imantodes gemmistratus latistratus (Cope)

Dipsas gemmistrata latistrata Cope, Bull. U. S. Nat. Mus., 32:68, 1887 (type locality, Valley of Toluca and Guadalajara, Jalisco; type locality restricted to southern Jalisco by Zweifel, Amer. Mus. Novitates, 1961:4, September 16, 1959).

Imantodes gemmistratus latistratus: Zweifel, Amer. Mus. Novitates, 1961:3, September 16, 1959.

Remarks.—Zweifel (1959d) assigned all *Imantodes* from western México to one species, *I. gemmistratus*, with the subspecies *latistratus* occurring in Sinaloa.

Six males have 224-236 (230.4) ventrals, 114-126 (120.8) subcaudals (except KU 67673, 78947). Seven females have 226-237 (231.0) ventrals, 115-129 (121.6) subcaudals. Coloration and pattern generally are typical of the race (Zweifel, 1959d:4-7). Twenty-one males have 36-63 (48.3) body blotches, 15-25 (19.3) middorsal

scales in the anterior three body blotches; and faint posterior coloration (except LACM 6867). Head pattern "A" (Zweifel, 1959d:5, fig. 2) occurred 17 times, "B" twice and "C" twice. Fourteen females have 38-63 (48.2) body blotches; 14-24 (18.9) middorsal scales in the anterior three body blotches; fainter posterior coloration (except LACM 6881); head pattern "A." One male has 114 subcaudal scales, slightly fewer than the range of 117-130 that Zweifel (1959d:7) reported for northern males. All other characteristics are within the ranges observed by Zweifel (1959d).

More than 30 specimens of this supposedly arboreal snake were collected on the road at night. Individuals were especially abundant during or following rains. A specimen was collected in daytime beneath palm leaves on the ground near Teacapán.

Distribution in Sinaloa.—Throughout the lowlands south of Guamúchil and at higher elevations along the foothills into southern Sonora. See Fig. 68.

Specimens examined.—16 km. NNE Choix, 520 m. (° KU 68752); 9.7 S Coyotitán (JFC 65:143); Culiacán (CSCLB 1446-47); 22 km. N Culiacán (° KU 73532); 43 mi. N Culiacán (° LACM 6867); 5 mi. S Culiacán (JFC 62:52); 8.4 mi. S Culiacán (° LACM 6874); 36.8 mi. S Culiacán (° LACM 6875); 42.4 mi. S Culiacán (CSCLB 1451); 74 km. S Culiacán (° KU 73531); 50.9 mi. S Culiacán (° LACM 6881); 57.8 mi. S Culiacán (UAZ 16296); 61.5 mi. S Culiacán (° LACM 6876); 18 km. NE Elota, 30 m. (° KU 67673); 32.4 mi. N Elota, Río (° LACM 6871); 24.7 mi. S Elota, Río (LACM 6863); 31 mi. S Elota, Río (° LACM 6864); hwy. 15 between Escuinapa and Palmillas (° LACM 6884-87, 7244); 27.3 mi. S Escuinapa (CSCLB 1448); 31.6 mi. S Escuinapa (CSCLB 1449); 32.2 mi. S Escuinapa (CSCLB 1450); 5 mi. S Espinal (CSCLB 1456); 14 mi. N La Cruz turnoff [hwy 15] (° LACM 6861); 66.4 mi. S La Cruz turnoff [hwy. 15] (JMS osteo. coll.); 1 km. N Mazatlán (CSCLB 1444); 1.4 mi. N Mazatlán (° LACM 6868); 3.2 mi. N Mazatlán (UAZ 16297); 8 km. N Mazatlán (° KU 73530); 5.9 mi. N Mazatlán (° LACM 6880); 9.5 km. N Mazatlán (° KU 73528); 11.9 mi. N Mazatlán (° LACM 6858); 12.1 mi. N Mazatlán (° LACM 6860); 13.7 mi. N Mazatlán (° LACM 6859); 16.8 mi. N Mazatlán (° LACM 6865); 17.8 mi. N Mazatlán (° LACM 6862); 18.8 mi. N Mazatlán (° LACM 6879); 50 km. N Mazatlán (° KU 73529); 65.4 mi. N Mazatlán (° LACM 6870); 95.1 mi. N Mazatlán (° LACM 6866); 16.5 mi. SE Mazatlán (° LACM 6869); 1 mi. N Palmillas (° LACM 6877); 2 mi. S Palmillas (° LACM 25912); 11 mi. N Rosario (CSCLB 1452); 2.4 mi. NW Rosario (° LACM 6873); 2.2 km. NE Santa Lucia, 1155 m. (° KU 78941); Teacapán (° LACM 6878); 7 mi. S Terreros (° LACM 6882); 17 mi. S Terreros (° LACM 6872); 32 km. (by hwy. 15) N Tropic of Cancer (° KU 80752); S Tropic of Cancer (CSCLB 1445).

Literature records.—3 mi. S Coyotitán, 450 ft. (Zweifel, 1959d:12); 18 mi. NW Culiacán (Conant, 1965:17); Escuinapa (Zweifel, 1959d:12); 6-31 mi. NNW Mazatlán (Duellman, 1957b:239); 6.6 mi. NNW Mazatlán, 100 ft.; 8.3 mi. NNW Mazatlán; 10.3 mi. NNW Mazatlán, 200 ft.; 31.8 mi. NNW Mazatlán, 400 ft. (Zweifel, 1959d:12).

Additional records.—39.8 mi. N Culiacán, Río (SU 23820); 8 mi. S Culiacán, (CAS 95759); 10.2 mi. S El Salado (FAS 16805); 16.2 mi. S El Salado (FAS 16808); 19.2 mi. S El Salado (FAS 16800); 5.2 mi. S Escuinapa (SU 23823); 9.7 mi. N Espinal (UF 16538); 3.8 mi. E La Cruz (SU 23822); 1 mi. N Mazatlán (UF 12803); 1.9 mi. N Mazatlán (ASDM 1753); 3 mi. N Mazatlán (UF 12802); 6.8 mi. N Mazatlán (UF 16539); 11.2 mi. N Mazatlán (FAS

14833); 12 mi. N Mazatlán (MCZ 61418); 16 mi. N Mazatlán (MCZ 61419); 18 mi. N Mazatlán (MCZ 61420); 18.8 mi. N Mazatlán (MCZ 61421); 26.4 mi. N Mazatlán (UF 12804); 31 mi. N Mazatlán (FAS 14776); 45 mi. N Mazatlán (FAS 16819); 46.6 mi. N Mazatlán (FAS 14505); 15.3 mi. S San Lorenzo, Río (SU 23821).

Lampropeltis getulus nigrilus Zweifel and Norris

Lampropeltis getulus nigrilus Zweifel and Norris, Amer. Midland Nat., 54:238, August 27, 1955 (type locality, 30.6 miles [by road] south of Hermosillo, Sonora).

Remarks.—One specimen has been reported from Sinaloa (Campbell and Simmons, 1962:196). Two additional specimens (CSCLB 1417, LACM 28715) are males and have 216, 221 ventrals; 46, 55 subcaudals in two rows; 23-23-19 dorsal scale rows; 8-8, 7-7 supralabials; 9-9 infralabials; 1-1 preoculars; 2-2, 1-2 postoculars; and 1 + 2, 2 + 3 temporals. The dorsum is black with a very small light spot on many scales; the ventrals are black with one or two white marks on each ventral, decreasing in area posteriorly; the subcaudals are black with a few small light spots on the lateral edges. The head, labials, neck, and gular area are black, and chin shields are nearly all white. In coloration these specimens are similar to a specimen from Arizona reported by Zweifel and Norris (1955:239-40) as an intergrade between *L. getulus nigrilus*, *L. g. splendida*, and *L. g. yumensis*. The presence of an "intermediate" color pattern in Sinaloa suggests that the race *nigrilus* is much more variable than previously understood and probably is nothing more than the intermediate population or color phase between *splendida* and *yumensis*. All specimens were collected at night on Mexican highway 15.

Distribution in Sinaloa.—Known only from the extreme northern lowlands. See Fig. 60.

Specimens examined.—6 km. SE Los Mochis turnoff (LACM 28715); 25.6 mi. S Los Mochis (CSCLB 1417).

Literature records.—5.6 mi. S Sonora-Sinaloa state line (Campbell and Simmons, 1962:196).

Lampropeltis triangulum nelsoni Blanchard

Lampropeltis triangulum nelsoni Blanchard, Occ. Pap., Mus. Zool., Univ. Michigan, 81:6, fig. 1, April 28, 1920 (type locality Acámbaro, Guanajuato).

Remarks.—The 13 specimens examined include eight males, three females, and two specimens of unknown sex. The eight males have 217-230 (220.6) ventrals; 49-56 (53.7) subcaudals (excluding KU 73537); 10-13 (12.0) white bands on the body; and 3-4 (3.9) white

bands on the tail (excluding KU 73537). Seven to 13 (10.6) of the white bands on the body are complete ventrally. The dorsal scale rows are 21 behind the head, 21 at midbody and 17-19 just anterior to the vent. The three females and two specimens of unknown sex (KU 63422, 40355) have the following characteristics respectively: 216, 207, 217, ?, ? ventrals; 16, 11, 12, 15, 13 white bands on the body; 16, 10, 12, ?, 13 of the white bands are complete ventrally; 21 scale rows behind the head and at midbody and 19, 19, 19, 18, 19 scale rows anterior to the anus. All females have incomplete tails. One specimen (KU 73541) from Isla Palmito del Verde has black tips on the red scales and the snout is black with white mottling. All of the other specimens lack black tips on the red scales. Six specimens have white snouts that are mottled with black, and four specimens have black snouts that are mottled with white (excluding KU 40355, 63422). Two specimens (KU 73533-34) have one incomplete white band on the posterior part of the body. Another specimen (KU 73539) has two white bands that are incomplete dorsally by four and 12 scales. A fourth specimen (KU 73536) is even more unusually marked by having three lateral black-bordered white blotches alternating between the second and third complete white bands. The white blotches (two on the right and one on the left side) are 4, 14, and 7 scales long from anterior to posterior, and are bordered by black pigment which is confluent ventrally; dorsally the black pigment of any blotch does not contact the vertebral scale row.

Blanchard (1921:157) suggested that *nelsoni* probably intergrades with *annulata* somewhere on the Mexican plateau. Fugler and Dixon (1961:14) regarded one specimen that has only eight of the 15 white bands continuous ventrally as an indication of intergradation with *L. t. arcifera*. Five specimens with one to five white bands discontinuous ventrally are from the southern part of the state, and may indicate intergradation. We suspect that this color variant is inherent in the population here referred to *nelsoni*. Zweifel (1960: 104-07) pointed out that the coastal population of *Lampropeltis triangulum* may be distinct from *nelsoni*. Zweifel outlined the problem in some detail and discussed the variation in coloration in this species. Based on the color variation of material from Sinaloa and the lack of knowledge of the variation and distribution of different populations, as pointed out by Duellman (1961:102), we refer the Sinaloan specimens to *nelsoni*. Only a detailed study of all specimens of *Lampropeltis triangulum* from México will clarify the status

of the recognized subspecies and adequately demonstrate the relationship of the Sinaloan population.

This snake is nocturnal and apparently is a mimic of *Micrurus distans*. The local people generally are unable to differentiate between the two snakes and equally fear both species.

Distribution in Sinaloa.—Known from throughout the southern part of the state below an altitude of 1000 meters. *Lampropeltis triangulum* probably ranges northward in Sonora along the foothills of the northern part of the state. See Fig. 69.

Specimens examined.—Sinaloa (no specific locality) (CSCLB 1907); 6 km. SW Concordia (° KU 73538); 15.1 mi. S Coyotitán (LACM 6894); 44 mi. N Culiacán (LACM 6904); 9 mi. S Culiacán (LACM 6907); 31 mi. S Culiacán (JFC 62:38); 47 mi. S Culiacán (LACM 6901); 50 mi. S Culiacán (LACM 6908); 54.9 mi. S Culiacán (CSCLB 1906); 58 mi. S Culiacán (CSCLB 1908); 60.6 mi. S Culiacán (LACM 6902); 66 mi. S Culiacán (CSCLB 1909); 7 mi. NW Culiacán (JRM 1102); 47.7 mi. S Elota, Río (LACM 6895); 13.7 mi. S Guamúchil (LACM 6906); 54.5 mi. SE Culiacán (UAZ 16298); Isla Palmito del Verde, S end (° KU 73541); 1.6 mi. E La Cruz (LACM 6892); Matatlán, 170 m. (° KU 73537); Mazatlán (° KU 63422); 5 mi. N Mazatlán (LACM 25913); 10 km. N Mazatlán (° KU 73535); 9 mi. N Mazatlán (LACM 6889); 14 mi. N Mazatlán (LACM 6891); 16.9 mi. N Mazatlán (LACM 6890); 18.5 mi. N Mazatlán (UAZ 16299); 22.1 mi. N Mazatlán (LACM 6898); 22.4 mi. N Mazatlán (LACM 6896); 32.4 mi. N Mazatlán (CSCLB 1913); 58 km. N Mazatlán (° KU 73534); 69 km. N Mazatlán (° KU 73536); 52 mi. N Mazatlán (CSCLB 1912); 57 mi. N Mazatlán (JFC 62:39); 63 mi. N Mazatlán (JFC 62:40); 10 km. NE Mazatlán (° KU 73533); Plomosos, 760 m. (° KU 73540); 4.8 mi. N Rancho Huanacastle (LACM 6903); 1.5 km. NW Rosario (° KU 73539); San Ignacio (LACM 6893); 3 km. E San Lorenzo, 90 m. (° KU 91421); Teacapán (LACM 6909, 7241); 1 mi. N Teacapán (LACM 6911); 2 mi. SE Teacapán (LACM 6910); 34.6 mi. N Terreros (LACM 6899); 12 mi. S Terreros (LACM 6900); 21.3 mi. S Terreros (LACM 6905); 13 km. NNE Vaca, 400 m. (° KU 80754); 8.5 mi. N Villa Unión (CSCLB 1910); 2.3 mi. E Villa Unión (CSCLB 1914); 13 km. E Villa Unión (° KU 40355); 18.4 mi. SE Villa Unión (LACM 6897); 11 mi. S Villa Unión (CSCLB 1911).

Literature records.—Costa Rica (Smith and Van Gelder, 1955:145); 22.6 mi. N Culiacán (Fouquette and Rossman, 1963:193); El Dorado (Fugler and Dixon, 1961:14); Escuinapa (Blanchard, 1920:7 and 1921:158; Tanner and Loomis, 1957:37); 1 mi. NW Guamúchil (Tanner and Loomis, 1957:37); Mazatlán; Presidio (Boulenger, 1894:204; Blanchard, 1921:157).

Additional records.—Costa Rica (UIMNH 34919); 9.6 mi. N Culiacán, Río (SU 23847); 32 mi. N Culiacán (UF 16541); El Dorado (AMNH 90703-10); 17 mi. N Espinal (UF 16542); 22.0 mi. S La Cruz road, on hwy. 15 (SU 23849); La Noria (MVZ 10353); 2 mi. N Mazatlán (UMMZ 114297); 6.6 mi. N Mazatlán (FAS 12973); 17 mi. N Mazatlán (MVZ 59295); 19 mi. N Mazatlán (MVZ 70268); 23.8 mi. N Mazatlán (MVZ 70269); 24 mi. N Mazatlán, 150 ft. (TCWC 12646); 30.5 mi. N Mazatlán (FAS 12406); 14 mi. NNW Mazatlán, 150 ft. (UMMZ 114652); 19.6 mi. S Mocorito, Río (SU 23846); 4.9 mi. S Presidio, Río (SU 23850); 0.8 mi. S San Lorenzo, Río (SU 23848).

Leptodeira maculata Hallowell

Leptodeira maculata Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1861 (for 1860):488 (type locality, "Tahiti"; type locality restricted to Manzanillo, Colima by Duellman, Bull. Amer. Mus. Nat. Hist., 114:54, February 24, 1958).

Leptodeira personata Cope, Proc. Acad. Nat. Sci. Philadelphia, 20:310, 1869 (type locality, Mazatlán, Sinaloa).

Remarks.—There are more body blotches (*ca.* 22-27) and lateral intercalary spots are more frequent in specimens of *Leptodeira maculata* in Sinaloa than in specimens from farther south (Duellman, 1958a:55-56). Two males from southern Sinaloa have 167, 165 ventrals; 69, 69 subcaudals; 23, 24 dorsal body blotches; and 10, 15 dorsal tail blotches. Both specimens have 21-23-17 scale rows; the lateral blotches are faintly evident and the upper labials are smudged with brown. Most specimens were collected at night in proximity to roadside ponds, where the snakes were attracted by the multitude of breeding amphibians. An individual (LACM 6913) was collected with a half-engulfed *Bufo mazatlanensis* in its mouth. The toad was dislodged but died shortly. An obvious discoloration was noted on the anterior portion of the toad, probably a result of the mild venom utilized by the snake in securing prey. Scott (1962:54) reported specimens feeding on the smashed remains of frogs and toads on the highway near Palmillas. A specimen taken from a hole in the buttress roots of a large fig tree regurgitated a *Bufo mazatlanensis*. During the dry season specimens have been collected beneath rocks or surface debris along rivers or near dry ponds.

Distribution in Sinaloa.—Occurs throughout the state from Mazatlán southward. See Fig. 70.

Specimens examined.—3 mi. NE Concordia (CAS 91920); 3.7 mi. NE Concordia (CSCLB 1889-90); 4.9 mi. NE Concordia (LACM 6912); between Escuinapa and Palmillas (on hwy. 15) (LACM 6919-20, 7243); 17 mi. S Escuinapa (JFC 62:55); Matatán, 170 m. (* KU 73543); 15 mi. S Mazatlán, Río Presidio (SU 18260); 5.7 mi. S Rancho Huanacastle (LACM 6917); Rosario, 150 m. (* KU 73542); 7 mi. SE Rosario (LACM 6914); 7.2 mi. NW Rosario (LACM 6915); Santa Lucía (CSCLB 1888); 5.1 mi. N Sinaloa-Nayarit border (LACM 6918); Teacapán (LACM 6921); 2.5 mi. E Teacapán (LACM 6923); 2 mi. SE Teacapán (LACM 6922); 8.4 mi. NE Villa Unión (LACM 6913).

Literature records.—Chele, 300 ft. (Duellman, 1958a:57); Mazatlán (Smith, 1943a:440; Duellman, 1958a:57); Presidio (Duellman, 1958a:57); 1 mi. N Presidio; 10 mi. S Presidio (Taylor, 1938:526); Rosario (Smith, 1943a:440; Duellman, 1958a:57).

Additional records.—Concordia (UMMZ 102484-85); 11 mi. NE Concordia (SM 10936-40); 12 mi. NE Concordia (SM 11022); 18.9 mi. SE Escuinapa (FAS 14848); 36.9 mi. S Escuinapa (FAS 14764); 4 mi. E Villa Unión (UF 16827); 24.8 mi. E hwy. 15 (Villa Unión) on hwy. 40 (SU 23853-54).

Leptodeira punctata (Peters)

Crotaphopeltis punctata Peters, Monatsber. Akad. Wiss. Berlin, for 1866:93, 1867 [type locality, South Africa (by error)].

Leptodeira pacifica Cope, Proc. Acad. Nat. Sci. Philadelphia, 20:310, 1869 (type locality, Mazatlán, Sinaloa).

Leptodeira punctata: Boulenger, Zoologist, ser. 3, 11:178, 1887.

Remarks.—Ten specimens of *Leptodeira punctata*, which include two males, seven females and one specimen of undetermined sex, have ventrals, 152-159 (156.5); dorsal scale rows, 20-19-14 (1), 19-19-15 (8), 18-19-15 (1); supralabials, 7-7 (10); infralabials, 9-9 (8), 10-10 (1), 10-9 (1); preoculars, 2-2 (9), 2-1 (1); postoculars, 2-2 (10); temporals, 1-2/1-2 (9), 1-1-2/1-1-2 (1); lower preoculars usually very small. One male has 69 subcaudals and six females have 51-64 (56.7) subcaudals (excluding KU 73546-47). The dorsal spots are separate and distinct in seven of the specimens. The dorsal pairs of spots are fused together over most of the body in one specimen, over the anterior half of the body in another specimen, and over the posterior half in the remaining snake. A specimen collected near Guasave (LACM 6939) exhibits an aberrant color pattern. The black nuchal blotches and about six anterior dorsal blotches are all that remain of the normal dorsal pattern. The remainder of the dorsum is uniform yellow brown.

Although *Leptodeira punctata* was once considered rare (Taylor, 1938:527), we found it to be the most common snake encountered during the course of field work. Most specimens were taken at night on the road, but some were found under rocks, beneath an oyster shell, and under a stove pipe. The majority were taken from late June through September but a few were collected in December, February, and April. A large female caught on July 20 laid six eggs on July 29. Another female taken on the same night laid seven eggs on August 7 (Scott, 1962:56).

A more complete treatment of the species, including sexual dimorphism and color in life, is in a monograph of the genus (Duellman, 1958a:94-95).

Distribution in Sinaloa.—Throughout the lowlands. See Fig. 71.

Specimens examined.—9.8 mi. NW Acaponeta [Nayarit] (LACM 6942); Concepción; near Concepción (JMS osteo. coll.); about 10 km. SW Concordia (* KU 73547); Coyotitán (JFC 62:4); N edge Culiacán (CSCLB 1891); 27 km. N Culiacán (* KU 73550); 26.7 mi. N Culiacán (LACM 6936); 85 mi. N Culiacán (LACM 6935); 40.3 mi. S Culiacán (LACM 6940); 41.4 mi. S Culiacán (LACM 6941); 74 km. S (on hwy. 15) Culiacán (* KU 73551); 71.3 mi. SE Culiacán (UAZ 16289); 3.6 mi. E El Guaybo (UAZ 9374); between Escuinapa and Palmillas, hwy. 15 (LACM 6962-65); 0.5 mi. S Escuinapa (CSCLB 1905); 18.3 mi. S Escuinapa (CSCLB 1896); 19 mi. S Escuinapa (CSCLB 1897); 28.4 mi. S Escuinapa (CSCLB 1898); 30.2 mi. S Escuinapa (CSCLB 1895); 31.3 mi. S Escuinapa (CSCLB 1894); 33.4 mi. S Escuinapa (CSCLB 1900); 8.6 mi. S Espinal (CSCLB 1903); 2.9 mi. S Guamúchil (LACM 6945); La Cruz (LACM 6931); 2 mi. NE La Cruz turnoff, hwy. 15 (LACM 6928); 4.7 mi. NE La Cruz turnoff, hwy. 15 (LACM 6929); 5.2 mi. NE La Cruz turnoff, hwy. 15 (LACM 6926); 8.1 mi. NE La Cruz turnoff, hwy. 15 (LACM 6927); 39 mi. S Los Mochis turnoff, hwy. 15 (LACM 6939); Mazatlán (* KU 63424; CAS 89691-93; LACM 6925, 6951-55, 6957); N Mazatlán (CSCLB 1892-93; LACM 6944); 2 mi. N Mazatlán (UAZ 16290);

3.3 mi. N Mazatlán (UAZ 16291); 3.6 mi. N Mazatlán (UAZ 16292); 4.2 mi. N Mazatlán (LACM 6932); 5 mi. N Mazatlán (CSCLB 2963); 10-20 mi. N Mazatlán (JFC 62:145); 20 mi. N Mazatlán (LACM 6943); 20.4 mi. N Mazatlán (CSCLB 1901); 21 mi. N Mazatlán (LACM 6930); 45.3 mi. N Mazatlán (JMS osteo. coll.); 74 km. N (hwy. 15) Mazatlán (* KU 73548); 98 km. N (hwy. 15) Mazatlán (* KU 73549); 111 mi. N Mazatlán (LACM 6934); 7 mi. SE Mazatlán (LACM 6924); 1 mi. NW Mazatlán (LACM 6956); 2.5 mi. N, 0.5 mi. W Mazatlán (LACM 2563); 12.6 mi. SE Mazatlán (UAZ 16293); 1 mi. N Palmillas (LACM 25917); 1 mi. W hwy. 15 along Río Piaxtla (CSCLB 2962, 2964-65); 6 mi. SE Rancho Huanacastle (LACM 7326); between Rosario and [Sinaloa]-Nayarit border (LACM 8656); 2.7 mi. S Rosario (JMS osteo. coll.); 3.8 mi. NW Rosario (LACM 6938); 9.9 mi. W San Blas (CSCLB 1899); 21.3 mi. S San Ignacio turnoff and hwy. 15 (JMS osteo. coll.); Teacapan (LACM 6958-61, 7242); 15 mi. S Terreros (LACM 6937); Villa Unión (* KU 73545-46); 2.8 mi. N Villa Unión (CSCLB 1902, 1904); 3.9 km. N (on hwy. 15) Villa Unión (* KU 78943); 22.5 mi. SE Villa Unión (LACM 6933); 6 km. NE (on hwy. 15) Villa Unión (* KU 75623).

Literature Records.—6 mi. N Caitime; 10.9 mi. S Caitime (Duellman, 1958a:95); El Dorado (Fugler and Dixon, 1961:14); Mazatlán (Smith, 1943a:441; Smith and Taylor, 1945:89; Duellman, 1958a:95; Fugler and Dixon, 1961:15); 1 mi. E Mazatlán (Taylor, 1938:527 and 1939a:319); 2 mi. E Mazatlán (Duellman, 1958a:95); 3 mi. E Mazatlán, 50 ft. (Davis and Dixon, 1957a:25; Duellman, 1958a:95); 2-4 mi. NNW Mazatlán (Duellman, 1957b:239; 1958a:95); 5 mi. NNW Mazatlán (Duellman, 1958a:95); 6 mi. NNW Mazatlán, 10 ft. (Davis and Dixon, 1957a:25; Duellman, 1958a:95); 19 mi. NNW Mazatlán (Duellman, 1957b:239; 1958a:95); Presidio (Boulenger, 1896:91; Smith and Taylor, 1945:89; Duellman, 1958a:95).

Additional records.—6.3 mi. N Caitime (FAS 8505); 0.2 mi. N Cañas, Río (SU 23933); 2.8 mi. N Cañas, Río (SU 23943); 3.5 mi. N Cañas, Río (SU 23934); 4-8 mi. N Culiacán (FAS 11360); 60-65 mi. N Culiacán (FAS 12924); 56.5 mi. S Culiacán (FAS 15014); 68.5 mi. S Culiacán (FAS 15013); 0.8 mi. N Culiacán, Río (SU 23881); 7.5 mi. N Culiacán, Río (SU 23879); 7.6 mi. N Culiacán (UMMZ 120232); 26.7 mi. N Culiacán, Río (SU 23878); 27.5 mi. N Culiacán, Río (SU 23877); 28.0 mi. N Culiacán, Río (SU 23876); 42.6 mi. S Culiacán (UF 12811); 52.3 mi. S Culiacán (UF 12810); 55.2 mi. S Culiacán (UF 12809); 0.8 mi. W hwy. 15 on Culiacánquito road (SU 23880); 1.6 mi. W hwy. 15 on Culiacánquito road (SU 23882); 3.8 mi. W hwy. 15 on Culiacánquito road (SU 23883); 9.3 mi. W hwy. 15 on Culiacánquito road (SU 23884); 10.4 mi. W hwy. 15 on Culiacánquito road (SU 23885); El Dorado (AMNH 90711-19); 30.7 mi. N El Dorado (SU 23900); 31.1 mi. N El Dorado (SU 23899); 31.7 mi. N El Dorado (SU 23897-98); 12.5 mi. N Escuinapa (SU 23927); 2.1 mi. S Escuinapa (SU 23928); 2.6-7.6 mi. S Escuinapa (FAS 13305); 5.6 mi. S Escuinapa (SU 23929); 13.4 mi. S Escuinapa (SU 23930); 18.2 mi. S Escuinapa (SU 23931-32); 1 mi. N La Cruz road on hwy. 15 (SU 23913); 2.5 mi. N La Cruz road on hwy. 15 (SU 23911); 2.7 mi. N La Cruz road on hwy. 15 (SU 23910); 9.5 mi. N La Cruz road on hwy 15 (SU 23912); 12.4 mi. N La Cruz road on hwy. 15 (SU 23909); 4.2 mi. E La Cruz (SU 23915); 4.4 mi. E La Cruz (SU 23914); 9.6 mi. E La Cruz (SU 23916); Mazatlán (USNM 6836, 151782); N Mazatlán (MCZ 61425; SDSNH 52899-902; SU 23917); 1.1 mi. N Mazatlán (FAS 14825); 3 mi. N Mazatlán (USNM 146458); 4 mi. N Mazatlán (AMNH 19853-54); 5 mi. N Mazatlán (AMNH 86554-56, 87391-93; MCZ 61424); 5.1 mi. N Mazatlán (FAS 14462); 20 mi. N Mazatlán (MCZ 61422-23); 75 mi. S Mazatlán (FAS 1446); 2-4 mi. NW Mazatlán (AMNH 19853; UMMZ 114469, 114471-76, 115383); 5 mi. NW Mazatlán (AMNH 75883); 2-4 mi. NNW Mazatlán, 25 ft. (UMMZ 114471-76, 115383); 3.8 mi. NNW Mazatlán, 50 ft. (UMMZ 114469); 9.3 mi. N Mocerito, Río (SU 23875); 1.8 mi. E Navolato (SU 23887); 3.4 mi. E Navolato (SU 23888, 23890); 6.6 mi. E Navolato (SU 23889); 8.6 mi. E Navolato (SU 23891); 9.0 mi. E Navolato (SU 23892); 9.8 mi. E Navolato (SU 23893); 9.9 mi. E Navolato (SU 23894); 10.3 mi. E Navolato (SU 23895); 10.4 mi. E Navolato (SU 23896); 12.5 mi. E Navolato (SU 23902); 16.1 mi. E Navolato (SU 23903);

1.6 mi. SE Navolato (SU 23886); 11.4 mi. SE Navolato (SU 23901); 0.9 mi. N Presidio, Río (SU 23918); 7.1 mi. N Rosario (SU 23926); 7.5 mi. N Rosario (SU 23925); 4.6 mi. S Rosario (CAS 95753); 7 mi. NW Rosario (SM 10571); 11.7 mi. N San Lorenzo, Río (SU 23904); 4.2 mi. S San Lorenzo, Río (SU 23906); 10.8 mi. S San Lorenzo, Río (SU 23905); 11.1 mi. S San Lorenzo, Río (SU 23907); 13.2 mi. S San Lorenzo, Río (SU 23908); 0.3 mi. E hwy. 15 (Villa Unión) on hwy. 40 (SU 23919); 0.5 mi. E hwy. 15 (Villa Unión) on hwy. 40 (SU 23920); 0.7 mi. E hwy. 15 (Villa Unión) on hwy. 40 (SU 23921); 3.0 mi. E hwy. 15 (Villa Unión) on hwy. 40 (SU 23922); 3.8 mi. E hwy. 15 (Villa Unión) on hwy. 40 (SU 23923); 4.3 mi. E hwy. 15 (Villa Unión) on hwy. 40 (SU 23924).

Leptodeira septentrionalis polysticta Günther

Leptodeira polysticta Günther, *Biologia Centrali-Americana*, Reptilia, p. 172, May, 1895 (type locality, Belice, British Honduras).

Leptodeira septentrionalis polysticta: Duellman, *Bull. Amer. Mus. Nat. Hist.*, 114:72, February 24, 1958.

Remarks.—Two females and one male have 202, 206, 202 ventrals; 96, 83, 109 subcaudals; 21-21-15, 21-24-16, ?-23-15 dorsal scale rows; 3-2, 2-3, 2-2 preoculars; 2-2, 2-2, 2-2 postoculars, 8-8, 8-8, 8-8 supralabials; 10-10 infralabials (LACM 6967 only); 53, 60, 64 dorsal blotches anterior to vent that extend laterally to dorsal scale rows 8, 5-7, 5-6 and are $1\frac{1}{4}$ to 2 scales long; 27, 26, 27 dorsal blotches on tail that are united distally; a single median nape stripe extends posteriorly three to four scales from the parietals.

Duellman (1958a:73) regarded typical *polysticta* as having body blotches that are one to three scales long and that extend laterally to scale rows five to seven. Duellman (1958a:74) recorded the range of this species as extending from Nayarit southward along the Pacific Coast into Middle America. Three specimens were collected at night north of Mazatlán and represent the first records from Sinaloa, extending the known range of the species about 250 kilometers. The specimens are similar in all characters to specimens from the south and seemingly continue north-south clinal variation in numbers of body blotches, ventrals, and midbody scale rows.

Distribution in Sinaloa.—Known only from the southern lowlands. See Fig. 72.

Specimens examined.—29 km. N Mazatlán (° LACM 6966); 45 km. N Mazatlán (° LACM 6967); 55 km. N Mazatlán (° LACM 6968).

Leptodeira splendida ephippiata Smith and Tanner

Leptodeira ephippiata Smith and Tanner, *Copeia*, no. 3:131, September 30, 1944 (type locality, 8.3 miles west-northwest of Alamos, Sonora).

Leptodeira splendida ephippiata: Duellman, *Bull. Amer. Mus. Nat. Hist.*, 114:82, February 24, 1958.

Remarks.—A specimen of this subspecies from Plomosas has been referred to *Leptodeira bressoni* (= *L. s. bressoni*) by Taylor (1939a:

324) and to *L. ephippiata* by Smith and Tanner (1944:131). Duellman (1958a:84) considered the same specimen to be an intergrade between *L. s. ephippiata* in the north and *L. s. bressoni* in the south.

Seven females examined by us have 21-31 (24.7) dorsal body spots that extend to scale row one (4) or two (3); 174-178 (175.7) ventrals; and 76, 80, 83 subcaudals (KU 73552-54, 78945, and CSCLB 2001 not counted). One male has 29 dorsal body spots that extend to the second scale row, 169 ventrals, and an incomplete tail. All of the specimens (8) have 3-3 preoculars; 8-8 (6), 8-9 (2) supralabials, and 10-10 (7), 9-10 (1) infralabials. The nuchal blotch is continuous with the nape stripe in two and is not continuous in the other six specimens; however, the postocular stripe is continuous with the nuchal blotch in four (only on right in one) and is not continuous in four specimens. The dorsal scale rows are 19-21-16 (1), 19-21-17 (1), 21-21-17 (5), and 23-21-17 (1).

One specimen (CSCLB 2001) has a body length of 793 mm. and a total length of 888 mm. (tail incomplete), 280 mm. longer than the longest reported by Duellman (1958a:83). This specimen probably had more dark tail bands (16 on incomplete tail); all specimens have fewer ventrals than reported by Duellman (1958a:82).

The two specimens from Cosalá have 29 and 31 dorsal blotches, which approach the lower limit for *L. s. bressoni* (Duellman, 1958a:84), but they are widely separated geographically from the range of *bressoni*. Other specimens from southern Sinaloa have lower blotch counts.

One specimen was found at night among the exposed roots of a tree overhanging a pool of a small rocky stream in the lowland thorn woodland of northern Sinaloa.

Distribution in Sinaloa.—Probably occurs at moderate to high elevations throughout the state. See Fig. 72.

Specimens examined.—8 km. N Carrizalejo, 460 m. (° KU 77976); about 10 km. SW Concordia (° KU 73554); 6 km. E Cosalá, 460 m. (° KU 73552-53); 38.5 mi. N Mazatlán (° CSCLB 2001); San Ignacio, 210 m. (° KU 73555); 2.4 km. NE (on hwy. 40) Santa Lucía, 1155 m. (° KU 78945); 12.3 km. SW (on hwy. 40) Santa Lucía (° KU 78944).

Literature records.—14 mi. SW El Batel [Durango]; Plomosas (Duellman, 1958a:84); Plomosas (Smith, 1943a:439; Smith and Tanner, 1944:131); Presidio (Boulenger, 1896:94).

Leptophis diplotropis (Günther)

Ahaetulla diplotropis Günther, Ann. Mag. Nat. Hist., ser. 4, 9:25, 1872 (type locality, Tehuantepec, Oaxaca).

Leptophis diplotropis: Günther, Biologia Centrali-Americana, Rept., p. 130, 1894.

Remarks.—Two specimens from the Tres Mariás Islands have 185, 186 ventrals and 160, 160 subcaudals (Boulenger, 1894:111). Smith (1943a:443) referred these specimens to a new subspecies on the basis of the high ventral and subcaudal counts. Specimens of *L. diplotropis* from Sonora have more ventrals than do snakes of this species from Oaxaca. Oliver (1948:210), in a monograph of the genus, believed that the variation in ventral count is clinal and did not recognize the subspecies described by Smith. However, Oliver suggested that when more material became available northern and southern subspecies might be defined.

Nineteen specimens examined by us have one preocular and two postoculars on each side. The supralabials are 8-8 in 18 specimens and 7-8 in one; infralabials are 10-10 in 14, 11-10 in one, and 10-9 in two specimens (excluding KU 29507, 78948); temporals are 1 + 2/1 + 2 in 12, 1 + 1/1 + 2 in two, 1 + 1 + 2/1 + 1 + 2 in one, 1 + 1/1 + 1 in one, 1 + 2/1 + 1 + 2 in one, and 1 + 2/1/1 + 2/1 in one specimen (excluding KU 78948). The dorsal scale rows are 15-15-11 in 14 specimens, 15-14-11 in one, 14-13-11 in one, 14-15-13 in one, 14-15-11 in one, and 15-15-12 in one. Sexual dimorphism is present in the number of ventrals, but not in the number of subcaudals. Seven females have 171-178 (175.4) ventrals and 145, 149, 154 subcaudals (excluding KU 73558, 73565, 80755-56), and 12 males have 163-177 (169.9) ventrals and 144-158 (150.2) subcaudals (excluding KU 73562-63, 73566, 73651, 78948, 91423). These counts are slightly lower than those recorded by Oliver (1948:209) for Sonora. Only three of the specimens examined are from localities north of Mazatlán: two males have 173 and 177 ventrals and one female has 178 ventrals, indicating that ventral scales of snakes from northern Sinaloa are probably more numerous than in specimens from the southern part of the state. Based on our material there is no evidence to warrant recognition of subspecies in northwestern México.

This snake is one of the most abundant species in the southern coastal lowlands, but its arboreal habit and cryptic coloration make it exceedingly inconspicuous. Most specimens were collected in the morning or late afternoon in bushes or trees well above the ground. Scott (1962:69) found a specimen at night loosely coiled in the top of an isolated, sparsely leaved shrub. The snake was sluggish from the cold and covered with dew droplets. Another specimen was taken at night in a tree along a creek in the southern lowlands. This is one of the few snakes known to be active through-

out the year; specimens were collected in every month. *Phyllo-medusa dacnicolor* and *Hyla smithi* have been found in stomachs. These snakes are extremely wary; when captured they will expand their neck vertically, thereby displaying blue skin. The mouth is held wide open and the head moved from side to side. When the snakes bite they imbed their rear fangs in a fast chewing movement. A mild sting, attributed to poison, persists for some time at the location of the bite. A specimen collected on August 1 and two taken August 10 exhibit umbilical scars and are presumably hatchlings.

Distribution in Sinaloa.—Throughout the state below about 2000 meters. See Fig. 73.

Specimens examined.—9.6 km. NE El Fuerte (* KU 77977); 9.4 mi. S Escuinapa (LACM 6977); Isla Palmito del Verde, S end (* KU 73566, 73651); Labrados (CAS 64975); La Cruz (LACM 6970-71); Mazatlán (* KU 63425; LACM 6972, 6980; UAZ 16300); 4 mi. N Mazatlán (LACM 6969); 6.8 mi. N Mazatlán (UAZ 16301); 8 mi. N Mazatlán (LACM 6974); 42 mi. NW Mazatlán (JRM 1101); Plomosas, 760 m. (* KU 73563-65); Rosario, 150 m. (* KU 73559-62; LACM 6975); Rosario, Río (JFC 62:50); 30 mi. N Rosario (JFC 61:203); 4 km. NW Rosario (* KU 29507); San Ignacio (LACM 6973); 3 km. E San Lorenzo, 90 m. (* KU 91423); 2.2 km. NE Santa Lucía, 1155 m. (* KU 78946); 19.2 km. NE Santa Lucía, 1940 m. (* KU 78947-48); 10.6 mi. E Santa Lucía (JFC 63:151); 10 km. S, 38 km. E Sinaloa, 240 m. (* KU 73558); Teacapán (LACM 6981-85, 7233-34); Terreros (LACM 6978-79); 8 km. N Villa Unión, 140 m. (* KU 80755-56).

Literature records.—Costa Rica (Smith and Van Gelder, 1955:145); El Dorado (Fugler and Dixon, 1961:15); Mazatlán (Van Denburgh, 1898:464); Presidio (Boulenger, 1894:111).

Additional records.—Costa Rica (UIMNH 34922); 62 mi. SE Culiacán (UMMZ 118785); El Dorado (AMNH 90720-27; UIMNH 46979); 11 mi. S Escuinapa (CAS 95804); 21 mi. S Escuinapa (CAS 95803); 36.3 mi. S Escuinapa (CAS 95805); N Mazatlán (SU 23945); 9 mi. N Mazatlán (MVZ 59296).

Masticophis bilineatus Jan

Masticophis bilineatus Jan, Elenco sistematico degli Ofidi . . . p. 65, 1863 (type locality, Western México [?]).

Remarks.—Eight specimens have 187-201 (193.3) ventrals; 127-134 (130.8) subcaudals (excluding KU 73569, 80757); 2-2 preoculars (excluding KU 78949); 2-2 postoculars (excluding KU 78949); and 8-8 supralabials. There are 9-9 infralabials in four specimens, 10-9 in one, 9-10 in one, and 10-11 in another (excluding KU 78949). Dorsal scale counts are 20-17-13 in three, 19-17-13 in two, 20-18-13 in one, and ?-17-13 in another (excluding KU 78949).

The dorsolateral light stripe is separated from the supralabials by 8-19 scales, the sublateral dark stripe is fused anteriorly and includes the tips of the ventrals, and the chin and throat are spotted with black in all specimens examined by us. Our specimens

are similar to the race of *bilineatus* purported to be restricted to the Ajo Mountains, Arizona (Hensley, 1950:344). The subspecies of *M. bilineatus* presently are being reviewed.

Although most specimens were collected during the day, there are indications that the species may be partially nocturnal in habit. A specimen was found alive at 2220 hours on the road south of Acaponeta, Nayarit, with a large *Drymarchon*. A second individual (LACM 6989) was found dead on the road at midnight on August 3. This snake was active between 2315 hours and midnight, for the same stretch of highway was carefully searched at about 2315 hours. Several other large colubrid snakes were seen on the highway at night, but due to their speed they eluded capture. Judging from their size the snakes might well have been *Masticophis bilineatus*. Certain ecological factors, such as competition from other large diurnal predatory snakes, may explain the apparent nocturnal activity of this species in Sinaloa.

Distribution in Sinaloa.—Lowlands and foothills below about 550 meters throughout the state. See Fig. 74.

Specimens examined.—6.5 km. S Casa Blanca, 520 m. (° KU 83406); 1.9 km. NE Chupaderos, 350 m. (° KU 78949); 0.2 mi. W Concordia (LACM 6992); 16 km. W Concordia (° UMMZ 102483); 15.8 mi. N Culiacán (CSCLB 1946); 5.9 mi. S Culiacán (UAZ 16302); 17 mi. NW Escuinapa on hwy. 15 (TNHC 25475); Isla Palmito del Verde, middle (° KU 73569-70); 4 mi. E. La Cruz (LACM 6987); 16 km. NNW Los Mochis (° KU 37599); Mazatlán (JRM 1095); 26.8 mi. N Mazatlán (CSCLB 1948); 31 mi. N Mazatlán (LACM 6988); Rosario, 150 m. (° KU 73568); 3.7 mi. NW Rosario (UAZ 16303); San Ignacio (LACM 6986); 5 mi. N Sinaloa-Nayarit border (LACM 6989); Terreros (LACM 6993); 8 km. N Villa Unión, 140 m. (° KU 80757); 34 mi. E Villa Unión (CSCLB 2231).

Literature records.—Mármol (Lewis and Johnson, 1956:280); Mazatlán (Van Denburgh, 1898:463); 2 mi. E Mazatlán (Taylor, 1938:523); Presidio (Boulenger, 1893:391; Günther, 1894:121); 3.6 mi. NW Rosario (Fouquette and Rossman, 1963:195).

Additional records.—Camino Real de Piaxtla (AMNH 69680); 15.6 mi. N Culiacán (FAS 8508); 15.9 mi. N Culiacán (FAS 11349); 37.5 mi. N Culiacán (FAS 9078); Elota (FAS 11479); 12 mi. N Escuinapa (UNIMNH 41593); 30 mi. S Escuinapa (FAS 11356); 1.1 mi. N Mazatlán (FAS 15906); 29 mi. N Mazatlán (FAS 15865); 52.4 mi. N Mazatlán (FAS 11369); 9 mi. NW Piaxtla (SM 11125); 6.2 mi. E hwy. 15 (Villa Unión) on hwy. 40 (SU 23955); 10.6 mi. E hwy. 15 (Villa Unión) on hwy. 40 (SU 23954); 5.8 mi. NW Villa Unión (SU 24114).

Masticophis flagellum piceus (Cope)

Basanium piceum Cope, Proc. U. S. Nat. Mus., 14:625, 1892 (type locality, Camp Grant, Graham county, Arizona).

Masticophis flagellum piceum: Smith, Jour. Washington Acad. Sci., 31:397, September 15, 1941.

Remarks.—Ortenburger (1928:112) reported the red color phase of *Masticophis flagellum piceus* from Sinaloa under the name *M. f.*

frenatus. The black color phase has not been reported from Sinaloa; however, several literature records do not state the color phase represented. Both color phases have been reported from Sonora by Klauber (1942:88-89). The taxonomic significance of these color phases has been clarified by Klauber (1942), who denied them separate taxonomic status.

An adult female has 198 ventrals, 9-8 supralabials, a horizontal cream colored line through the loreal; the tail is incomplete. The anterior body bands and light-edged head scales are as described by Smith (1941b:397). A male with the juvenile color pattern has 196 ventrals, 99 subcaudals, 8-8 supralabials, 10-10 infralabials, horizontal light line through the loreal, distinct anterior body bands, and light-edged head scales. A larger male (TCWC 21905) has 192 ventrals, incomplete tail, 8-8 supralabials, 10-10 infralabials, anterior one-half of loreal with a white dash, and no distinct body bands; the chin and throat are white, with brown spots forming two rows on the throat.

Although the Sinaloan specimens are not typical of *piceus* in their coloration, they are similar to specimens from southern Sonora discussed by Bogert and Oliver (1945:363) and mentioned by Zweifel and Norris (1955:242).

Masticophis flagellum occurs in sympatry with *Masticophis bilineatus* and *Masticophis striolatus* at Terreros.

Distribution in Sinaloa.—Lowland thorn woodland of the northern half of the state. See Fig. 61.

Specimens examined.—28 mi. N Culiacán (CSCLB 1974); 51.5 mi. N Culiacán (LACM 6995); 16 km. NW Guamúchil 15 m. (* KU 67688); hwy. 15, 3 mi. E Los Mochis (* TCWC 21905); 22.7 mi. SE Los Mochis (UAZ 16295); Terreros (LACM 6996); 13 km. NNE Vaca, 390 m. (* KU 80758).

Literature records.—Ahome (Bogert and Oliver, 1945:403); Altata (Ortenburger, 1928:120; Smith, 1941b:397; Smith, 1943a:447); Costa Rica (Smith and Van Gelder, 1955:146).

Additional records.—7.6 mi. N Culiacán (UMMZ 120233); 26.2 mi. N Culiacán (FAS 11359); El Dorado (AMNH 90728-33); 9.5 mi. N Guamúchil (AMNH 86838); 13.4 mi. S Guamúchil (SU 23964); 8.3 mi. S Los Mochis (FAS 10984); 12.6 mi. S Terreros (FAS 16808).

Masticophis striolatus (Mertens)

Coluber striolatus Mertens, Die Insel-Reptilien, ihre Austreibung, Variation und Artbildung 32:190, 1934 (based on a specimen from México).

Masticophis flagellum striolatus: Smith, Jour. Washington Acad. Sci., 31:393, September 15, 1941.

Masticophis striolatus striolatus: Zweifel and Norris, Amer. Midland Nat., 54:242, July, 1955.

Remarks.—The name of this species has long been problematical. According to article 59(c) (International Code Zool. Nomencl., 1964), if a junior secondary homonym was rejected before 1961 it is always a homonym and is unavailable (according to the interpretation by Curtis W. Sabrosky in personal communication to E. Raymond Hall, June 14, 1965). Mertens (1934:190) proposed *Coluber striolatus* as a replacement name for *Bascanion lineatus* (Bocourt, 1890:700) which is a secondary homonym of *Coluber lineatus* Linnaeus, 1758 (= *Lygophis lineatus*). *Coluber lineatus* Linnaeus was placed in the genus *Lygophis* Fitzinger, 1843, by Dunn (1944:489) and has remained there to the present. Some workers, apparently, did not choose to suppress secondary homonyms, for example: the name *lineatus* has been used as *Masticophis flagellum lineatus* by Smith and Taylor (1950a:343) and *M. lineatus lineatus* by Fugler and Dixon (1961:15). Although the name *striolatus* has been used as a subspecific name in several combinations—*Masticophis flagellum striolatus* by Smith (1941b:393), *M. taeniatus striolatus* by Inger and Clark (1943:143), *Coluber striolatus striolatus* by Bogert and Oliver (1945:362), and *Masticophis striolatus striolatus* by Zweifel and Norris (1955:242)—according to article 59(c) (International Code Zool. Nomencl., 1964), the correct name for this species is *Masticophis striolatus* (Mertens, 1934).

Five males have 179-184 (182.0) ventrals and 13 or 14 preanal dorsal scales, whereas seven females have 178-189 (183.7) ventrals and 13-16 (14.9) preanal dorsal scales; the sex of two skins is not known. Both sexes combined have the following characteristics: 18 (1), 19 (8), 20 (2), and 21 (1) dorsal scales around the neck (excluding KU 73574 and UNM 10193); 17 dorsal scales at midbody; 8-8 (13) and 8-9 (1) supralabials; 10-10 (3), 11-10 (3), 10-11 (2), and 11-11 (4) infralabials (excluding KU 63736 and UNM 10193); 2-2 preoculars; 2-2 postoculars; temporals varying from 8 + 9 to 11 + 13; supralabials four and five entering eye. The chin and throat are immaculate white or creamy white in nine and sparsely spotted in four; all specimens have the dorsal scales tipped with black; only one specimen (KU 75627) has the anterior half of the loreal white, the others lack a white loreal stripe; on all specimens the faint dark stripes on the posterior part of the body are absent from scale rows one and three.

Recently hatched specimens were collected on July 9 and July 24. These specimens have about 18 light neck bands that gradually fade into the uniform body color. There is little or no indication of

the black spots on the tips of the dorsal scales that are characteristic of the adults.

Morphological variation in this species has been reported by Ortenburger (1928:137) and by Smith (1943a:447-48). Zweifel and Norris demonstrated (1955:242) that the head length/head width ratios of *Masticophis flagellum* and *M. striolatus* are different. The sympatric distributions of *M. flagellum* and *M. striolatus* were reported by Bogert and Oliver (1945:364).

This large diurnal snake is common in open areas, near cultivated regions, and around heavily grazed grassland interspersed with forest. This species is primarily terrestrial but, on occasion, has been seen three to four meters above ground in dense vegetation.

Distribution in Sinaloa.—*Masticophis striolatus* has been reported from various localities throughout the lowland thorn woodland at elevations up to 600 meters in the northern part of the state, and also in tropical deciduous forest up to about 2000 meters in southern Sinaloa. See Fig. 75.

Specimens examined.—Ahome (LACM 8647-49); 16 km. NNE Choix, 520 m. (* KU 73572); 1 km. S Concepción, 75 m. (* KU 63736); 17.3 mi. N Culiacán (JFC 63:148); 30 mi. N Culiacán (CSCLB 1957); 22 mi. S Culiacán (LACM 25921); Guamúchil, 45 m. (* KU 73571); 5 mi. S Guamúchil (* UNM 10193); Isla Palmito del Verde, middle (* KU 73576-78); La Cruz (LACM 7003-04); 2.8 mi. N Los Mochis junc. (UAZ 9370); Mazatlán (LACM 7005-06); N edge Mazatlán (CSCLB 1950); N Mazatlán (JFC 62:60); 13 mi. N Mazatlán (UAZ 16304); 13.8 mi. N Mazatlán (UAZ 16305); 5 mi. NW Mazatlán (JRM 1100); Plomosas, 760 m. (* KU 73574-75); Rosario, 150 m. (* KU 73573); 23.8 mi. SE Rosario (UAZ 16306); 13.9 mi. W San Miguel (UAZ 9371); Santa Lucía, 1100 m. (* KU 75627); 19.2 km. NE Santa Lucía, 1940 m. (* KU 78961); Teacapán (LACM 7009); 2 mi. N Teacapán (LACM 7240); 2 mi. NE Teacapán (LACM 7008); 2.5 mi. E Teacapán (LACM 7010); 10 km. NNW Teacapán (* KU 91425-26); Terreros (LACM 7007).

Literature records.—El Dorado (Fugler and Dixon, 1961:15); Presidio (Boulenger, 1893:388); 1 mi. N Presidio (Taylor, 1938:524); “. . . on the highway near the Río San Lorenzo” (Lewis and Johnson, 1956:280).

Additional records.—14 km. E Concordia, by rd. (UAZ 16307); El Dorado (AMNH 90734-38); 30 mi. N El Dorado (SU 24112-13); 22.4 mi. S El Fuerte (UIMNH 39199); 7 mi. NNW Escuinapa (AMNH 75886); 5.2 mi. E La Cruz (SU 23962); 6.6 mi. N Los Mochis turnoff (SU 23961); 22.2 mi. N Mazatlán (SU 23963); 2 mi. E Mazatlán (FMNH 117847); 21 mi. N Pericos (UIMNH 39200); Presidio (FMNH 117832, 117846, 17846 [?]); Rosario (UIMNH 62815); 8 mi. NNW Rosario (UMMZ 112763).

Natrix valida valida (Kennicott)

Regina valida Kennicott, Proc. Acad. Nat. Sci. Philadelphia, 12:334, 1860
(type locality, Durango).

Natrix valida valida: Cope, Proc. U. S. Nat. Mus., 14:670, 1891.

Remarks.—The range and mean for four males and five females from southern Sinaloa are, respectively, 140-148 (143.8); 139-145 (143.0) ventrals and 77-83 (79.6) (excluding KU 63738); 67-74

(71.2) subcaudals. All have eight supralabials on each side and 10 infralabials on each side (one has 11 on the left). The dorsal scale counts are 19-17-16, 19-18-15, 19-19-15, 19-19-16, 19-19-17, 20-17-15, 20-18-17, 20-19-15, and 21-17-17. This species will be reviewed in a report on Mexican snakes of the genus *Natrix* by Roger Conant (personal communication).

Natrix valida is a nocturnal species restricted to rivers and other permanent water in the northern portion of the state, but in southern Sinaloa, because of the overall increase of available moisture, the snake is more widespread. Individuals were taken in a narrow channel of an estuary near Teacapán (Scott, 1962:77). A female gave birth to twenty young on July 13.

Distribution in Sinaloa.—Coastal lowlands from sea level to approximately 250 meters elevation. See Fig. 76.

Specimens examined.—1.5 km. SE Camino Real (° KU 63737-38); 8 mi. N Concordia (LACM 7129); 2.1 mi. E Concordia (CSCLB 2201); 11.8 mi. N Culiacán (LACM 7131); 80 mi. N Culiacán (LACM 7122); 7.8 mi. N El Dorado (SU 24010, 24099-108); 13.5 mi. N El Dorado (SU 23990-24009); 1 mi. S Escuinapa (LACM 7148-49); 31.7 mi. S Escuinapa (CSCLB 2200); 33.3 mi. S Escuinapa (CSCLB 2199); 1 mi. NW Escuinapa (LACM 7130); La Concha (LACM 7132); Mazatlán (° KU 63427); CAS 89708; CSCLB 2202, 2204-26; JMS osteo. coll.; LACM 7125, 7144-46); 2 km. N Mazatlán (LACM 8657); 5 mi. N Mazatlán (CSCLB 2961); 19.9 mi. N Mazatlán (LACM 7123); 12.3 mi. E Navolato (SU 23966-89); Rosario, 150 m. (° KU 73579-83); San Ignacio (LACM 7126-28; JMS osteo. coll.); Teacapán (LACM 7147, 7150); 1 mi. E Teacapán (LACM 7151-66); Villia Unión, 16 m. (° KU 78911; CSCLB 2203; LACM 7140-43); 1.4 mi. NW Villa Unión (LACM 7124).

Literature records.—Culiacán (Conant, 1946:259); 18.5 mi. E Culiacán (Duellman, 1957b:240); El Dorado (Fugler and Dixon, 1961:20); about 10 mi. NE Concordia, Río Pánuco (Duellman, 1957b:240); Mazatlán (Conant, 1946:259); near Mazatlán (Martín del Campo, 1941:761); N Mazatlán (Conant, 1946:259); 1 mi. NNW Mazatlán, 25 ft. (Duellman, 1957b:240); Presidio (Boulenger, 1893:238; Taylor, 1938:525); 10 mi. S Presidio (Conant, 1946:259); 0.5 mi. N Villa Unión, nr. Río Presidio (Dixon and Webb, 1965:140).

Additional records.—Baluarte, Río, 3 mi. upstream from hwy. 15 (SU 24001-02); Camino Real de Piaxtla (AMNH 69682-83); 3.4 mi. N Cañas, Río (SU 24005); 5.2 mi. N Cañas, Río (SU 24004); Chupaderos (RGW 2922); 0.4 mi. W Costa Rica (SU 23983); 2.2 mi. W Costa Rica (SU 23982); Culiacán (AMNH 75190, 80083; UIMNH 46973); 11 mi. NW Culiacán (AMNH 88885); 7.8 mi. N El Dorado (SU 24010, 24098-108); 10 mi. N El Dorado (SM 11654-55); 10.2 mi. N El Dorado (SU 23994); 11.1 mi. N El Dorado (SU 23993); 12.7 mi. N El Dorado (SU 23992); 13.0 mi. N El Dorado (SU 23991); 13.5 mi. N El Dorado (SU 23989-90); 14.9 mi. N El Dorado (SU 23988); 21.0 mi. N El Dorado (SU 23987); 21.4 mi. N El Dorado (SU 23985-86); 21.5 mi. N El Dorado (SU 23984); 21.7 mi. N El Dorado (SU 23981); 21.8 mi. N El Dorado (SU 23980); 28.3 mi. N El Dorado (SU 23979); 28.7 mi. N El Dorado (SU 23978); 29.9 mi. N El Dorado (SU 23977); 31.1 mi. N El Dorado (SU 23976); 32.5 mi. N El Dorado (SU 23975); 32.7 mi. N El Dorado (SU 23974); 32.8 mi. N El Dorado (SU 23973); 33.1 mi. N El Dorado (SU 23972); within 7 km. El Dorado (AMNH 90739-50); Escuinapa, 100 ft. (TCWC 20811); 14 mi. S Escuinapa (CAS 95801); 14.4 mi. S Escuinapa (CAS 95800); 15.5 mi. S Escuinapa (SU 24003); 21 mi. SE Escuinapa (SM 11661); Guasave, Río

Sinaloa (AMNH 84080-83); 2 mi. N Ixpalino, Río Piaxtla (AMNH 88886-92); N Los Mochis, Río Fuerte (AMNH 84078-79); 21 mi. S Los Mochis (USNM 151783); Mazatlán (AMNH 19390; SDSNH 41248); near Mazatlán (FMNH 115619; UIMNH 18658); N edge Mazatlán (AMNH 85354; UF 16545); N Mazatlán (SU 23995); 0.4 mi. N Mazatlán (AMNH 85355); 1 mi. N Mazatlán (AMNH 87578; SM 11651-53); 6.6 mi. N Mazatlán (FAS 14078); 16 mi. N Mazatlán (AMNH 85356); 22.5 mi. N Mazatlán (AMNH 85357); 15 mi. ESE Mazatlán, near Presidio (FMNH 115620); 12.3 mi. E Navolato (SU 23966); 14.2 mi. E Navolato (SU 23967); 4.8 mi. SE Navolato (SU 23968); 10.2-10.8 mi. SE Navolato (SU 23969-71); 9 mi. NW Piaxtla (SM 11656-60); near Presidio (UIMNH 18657-58); near Quelite, Río Quelite (AMNH 87573-77); Rosario (UIMNH 6391); 0.5 mi. E Rosario, Río de Baluarte (UU 3788); 7 mi. NW Rosario, 100 ft. (TCWC 12610-16); 11 mi. NW Rosario (SM 11662); 24.8 mi. E hwy. 15 (Villa Unión) on hwy. 40 (SU 23996-24000).

Oxybelis aeneus auratus (Bell)

Dryinus auratus Bell, Zool. Jour., 2:324-326, pl. 12, 1825 (type locality, "México").

Oxybelis aeneus auratus: Bogert and Oliver, Bull. Amer. Mus. Nat. Hist., 83:381, March 30, 1945.

Remarks.—Fifteen males have 17-17-13 dorsal scales; 179-189 (185.4) ventrals; 169-175 (172.3) subcaudals (only KU 73585-88); and 1 + 2/1 + 2 temporals. Labials 4-6 enter the eye on both sides in 13 males; labials 4-6/5-7 enter the eye in one and 5-6/5-7 enter the eye in another. The supralabials are 8-8 in nine males, 8-9 in two, 9-9 in two, 9-8 in one, and 9-10 in one; the infralabials are 9-9 in 11, 9-8 in one, 10-9 in one, and 10-10 in one (excluding KU 73595). Five females have 17-17-13 dorsal scales, and one has 16-15-13; five have 183-195 (190.4) ventrals (excluding KU 77978); two have 175 and 176 subcaudals (KU 73596, 77978); five have 1 + 2/1 + 2 temporals, and one has 1 + 2/1 + 1 temporals. Labials 4-6/4-6 enter the eye in two, 5-7/4-6 enter the eye in two, 4-6/4-5 in one, and 5-7/5-7 in one. The supralabials are 8-8 in two, 8-7 in one, 9-9 in one, 10-9 in one, and 10-10 in one; the infralabials are 9-9 in four, 8-7 in one, and 9-10 in one. The diameter of the eye is less than the internasal length, and preoculars are 1-1 in all specimens. The ventral counts are noticeably lower than those (195-200) reported from Sonora by Bogert and Oliver (1945:381); since nearly all of the specimens are from southern Sinaloa the differences are probably real.

In Sinaloa this species has a variable dorsal color pattern of gray or grayish brown, usually with some individual scales on the anterior part of the body that have either the lower half or the upper half of the scale black (Bogert and Oliver, 1945:382). The size and number of the anterior black spots is quite variable throughout Sinaloa. The lips and throat are white or creamy white

in color and contrast with a black suborbital stripe that is indistinct above and distinct, sharp-edged below. The suborbital stripe gradually disappears on the neck.

Field observations indicate the species is diurnal, perhaps crepuscular, in activity; it probably feeds on lizards and frogs encountered in the arboreal habitat. Two females preserved on August 16 contained four and six large oviducal eggs (Scott, 1962:64).

Distribution in Sinaloa.—Throughout the lowlands, and in the foothills to about 550 meters. See Fig. 77.

Specimens examined.—16 km. NNE Choix, 520 m. (* KU 73584); 4.4 mi. SW Concordia (CSCLB 2162); 47.4 mi. N Culiacán (LACM 7014); 6 km. NE El Fuerte, 150 m. (* KU 77978); Isla Palmito del Verde, middle (* KU 73586-600); Labrados (CAS 64981); La Cruz (LACM 7012-13); 10.2 mi. N Mazatlán (LACM 7015); 44 mi. N Mazatlán (LACM 7011); Rosario, 150 m. (* KU 73585); Teacapán (LACM 7017-20, 7235-36); 2 mi. N Teacapán (LACM 7016); 8 km. N Villa Unión, 140 m. (* KU 80759, 83409); 1.5 km. NE Villa Unión (* KU 37593); 20 mi. E Villa Unión (CSCLB 2163).

Literature records.—Costa Rica (Smith and Van Gelder, 1955:145); 10 mi. S Culiacán (Fugler and Dixon, 1961:16); Presidio (Boulenger, 1896:193).

Additional records.—26 mi. N Culiacán (FAS 11373); Escuinapa (AMNH 3887-88, 4308-09); 5 mi. N Mazatlán (MVZ 59298); 9 mi. N Mazatlán (MVZ 59297); 50-55 mi. N Mazatlán (FAS 12920); 58.5 mi. N Mazatlán (UIMNH 41575); 70 mi. N Mazatlán (FAS 16818); 77 mi. N Mazatlán (FAS 14835); 3 mi. S Mazatlán (ASDM 1751); 11.5 mi. S Río Presidio (SU 24011).

Phyllorhynchus browni Stejneger

Phyllorhynchus browni Stejneger, Proc. U. S. Nat. Mus., 13:152, 1890 (type locality, Tucson, Arizona).

Remarks.—Bogert and Oliver (1945:351) described *Phyllorhynchus browni fortitus* from Sonora based on differences in color and size of blotches, relative sizes of the blotches and interspaces, and the shape of the rostral; they suggested that in the south the body blotches are much longer than the interspaces and ventrals are fewer.

Shannon and Humphrey described *P. b. klauberi* from the central Sinaloan lowlands and separated it from *P. b. fortitus* as having "generally greater total pigmentation" (1959a:145), the interspace pigment clumped into irregular macules, a posterior extension of the interorbital black band to form dark parietal spots, dorsal blotches not bordered laterally with darker pigment, longer frontal, and a narrower and less truncate rostral.

Eight males have 148-164 (156.9) ventrals; 27-34 (30.6) subcaudals; 10-18 (12.8) body blotches; 2-4 (2.8) tail blotches; and frontal width/frontal length of 0.76-0.96 (0.84) (excluding KU 73606). These characters for two females are 175, 168; 22, 21; 14, 14; 2, 2; and 0.88, 0.75 respectively. The dorsal scale rows at

midbody are 19 in nine specimens and 20 in one; 19-22 at the neck, and 16, 17 or 19 at the vent. The supralabials are 6-6 in three, 6-5 in one, 6-7 in one, and 7-7 in three (excluding KU 73602, 73604); infralabials are 7-7 in one, 8-8 in two, 8-9 in one, 9-7 in one, 9-9 in one and 10-9 in one (excluding KU 73601-02, 73604). The preoculars are either two or three, postoculars two or three (four in KU 73603), and suboculars 2 to 4. The temporals are numerous (6-12) and highly variable.

Dark pigment in the lateral interspaces is absent, or present as indistinct clumps; all dorsal blotches, except the anterior first or second, have dark edges. The interorbital band barely touches the parietals in a snake from northern Sinaloa (KU 73601); a specimen from near Guamúchil (KU 73607) has a distinct extension of the band to include part of the parietals. Six specimens from south of Guamúchil to about 24 kilometers north of Mazatlán have above one half or more of the parietals included in the interorbital band. One specimen (KU 73602) from 10 kilometers north of Mazatlán has the band barely including the parietals. A specimen from near Piaxtla has a second black band that crosses the parietals posterior to the interorbital band; the interorbital band and parietal band are connected laterally.

The ventral counts of the males, arranged in sequence from south to north, are 160, 163, 164, 158, 148, 156, 155, and 151. The numbers of body blotches for both sexes from south to north are 10, 13, 14, 12, 12, 14, 18, 15, 11, and 11. Four specimens, from localities in northern and southern Sinaloa, have dorsal bands that are more than twice the length of the interspaces and in five specimens the dorsal bands are distinctly less than twice the width of the interspaces.

None of the characteristics used by Shannon and Humphrey to distinguish *P. b. klauberi* (1959a:145) from *P. b. fortitus* is consistent in the Sinaloan specimens at hand. The variation in the number of ventrals, extent of the interorbital band, frontal width/frontal length, and the number of body blotches appear to be clinal for *P. browni* from Sinaloa and therefore casts doubt on the validity of *P. b. klauberi*. We use the binomial rather than attempting to allocate specimens from Sinaloa to either of the subspecies *fortitus* or *klauberi*. *Phyllorhynchus browni* is presently being studied by H. W. Campbell and the second author.

Nearly all specimens were collected at night on the road.

Distribution in Sinaloa.—*Phyllorhynchus browni* has been re-

corded from many localities throughout the Sinaloan lowlands. See Fig. 78.

Specimens examined.—15.4 mi. N Culiacán (CSCLB 1975); 40.2 mi. N Culiacán (LACM 7317); 40.8 mi. N Culiacán (LACM 7318); 44.9 mi. N Culiacán (LACM 7319); 37.2 mi. S Elota, Río (LACM 7310); 24 km. S Guamúchil (° KU 73607); 37 km. S Guamúchil (° KU 73608); 7 mi. S La Cruz turnoff (LACM 7320); 13.3 mi. N Los Mochis (CSCLB 1422); 51 km. N Los Mochis (° KU 73601); 10 km. N Mazatlán (° KU 73602); 12.3 mi. N Mazatlán (LACM 7322); 13.8 mi. N Mazatlán (LACM 7314); 14.2 mi. N Mazatlán (LACM 7316); 15.7 mi. N Mazatlán (LACM 7308); 16 mi. N Mazatlán (UCLA 14499); 17.3 mi. N Mazatlán (UCLA 14500); 17.6 mi. N Mazatlán (LACM 7315); 34 km. N Mazatlán (° KU 73604); 21.9 mi. N Mazatlán (LACM 7311); 22.4 mi. N Mazatlán (CSCLB 1426); 22.9 mi. N Mazatlán (LACM 7312); 40 km. N Mazatlán (° KU 73603); 51 km. N Mazatlán (° KU 86608); 42.5 mi. N Mazatlán (LACM 7309); 53.2 mi. N Mazatlán (CSCLB 1425); 85 km. NNW Mazatlán (° KU 73605); 93 km. NNW Mazatlán (° KU 73606); 1.3 mi. N Piaxtla, Río (CSCLB 1424); 4.3 mi. N Piaxtla, Río (CSCLB 1423); 1 km. E Piaxtla (° KU 37597); 3 mi. S San Ignacio turnoff (LACM 7313); 1.7 mi. N Terreros (LACM 7321); 2.6 mi. N Terreros (LACM 7325); 10.9 mi. N Terreros (LACM 7323); 11.3 mi. N Terreros (LACM 7324).

Literature records.—45.7 mi. S Culiacán; 55-60 mi. N Mazatlán (Shannon and Humphrey, 1959a:145).

Additional records.—El Dorado (AMNH 90792); 4.8 mi. S Elota, Río (SU 24016); 55.6 mi. N Mazatlán (FAS 14707); 12.3 mi. S Mocorito, Río (SU 24015).

Phyllorhynchus decurtatus Cope

Phyllorhynchus decurtatus Cope, Proc. Acad. Nat. Sci. Philadelphia, 20:310, 1869 (type locality, "the upper part of Lower California").

Remarks.—One female from southern Sinaloa has 35 body blotches that are wider than the interspaces, 171 ventrals, and 20 subcaudals. This specimen appears to be closely related to *P. d. norrisi*; however, because of the hiatus between the range of *norrisi* and this specimen, and the large amount of variation in snakes of this species (Smith and Langebartel, 1951:183), a subspecific designation is withheld pending the discovery of more specimens from western México.

Distribution in Sinaloa.—Known only from the southern lowland tropical semiarid forest near Mazatlán. See Fig 78.

Specimen examined.—42 km. N Mazatlán (° KU 73609).

Pituophis melanoleucus affinis Hallowell

Pityophis affinis Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 6:181, 1852 (type locality, Zuni, McKinley county, New Mexico).

Pituophis melanoleucas affinis: Smith and Kennedy, Herpetologica, 7:96, September 13, 1951.

Remarks.—Seven specimens (two females and five males) of *Pituophis melanoleucus affinis* have 217-230 (226.3) ventrals; 52-58

(56.7) subcaudals (excluding KU 73611); 37-50 (42.9) body blotches; 9-15 (11.7) tail blotches (excluding KU 73611); 25-31 dorsal scale rows at the neck (excluding KU 73611); 30-33 scale rows at midbody; and 21-24 scale rows at the vent. The supralabials are 8-8 in five, 9-8 in one, and 9-9 in one; infralabials are 11-11 in one, 11-12 in one, 11-13 in one, 12-11 in one, 12-12 in two, and 13-13 in one; preoculars are 1-1 in four and 2-2 in three; postoculars are 2-2 in four, 3-2 in one, and 3-3 in two; suboculars are 1-0 in one, 1-1 in four, and 2-2 in two; labials 4/4 enter the eye in four, 5/4 in one, and 5/5 in one (excluding KU 73615).

The color pattern is essentially like that described by Stull (1940: 126) and Davis and Dixon (1957a:21). A black stripe along the subcaudal surface, as reported by Zweifel (1954b:147) and Fugler and Dixon (1961:16), is present in three snakes (KU 73613-15). This nocturnal species apparently has not been affected, except perhaps to increase its abundance, by the agricultural development in northern Sinaloa, for several specimens were collected in areas of extensive cultivation.

Distribution in Sinaloa.—Throughout Sinaloa below about 500 meters elevation. See Fig. 79.

Specimens examined.—5 km. SW Concordia (* KU 73611); 32 mi. N Culiacán (CSCLB 1969); 22 mi. S Culiacán (LACM 25929); 34.6 mi. S Culiacán (LACM 7035); 10.4 mi. SW El Fuerte (CSCLB 1968); 10 km. ESE Guasave (* KU 43563); 21 km. N Mazatlán (* KU 73614); 26 km. N Mazatlán (* KU 73613); 17.6 mi. N Mazatlán (LACM 7031); 23.9 mi. N Mazatlán (LACM 7036); 39 km. N Mazatlán (* KU 73612); 27 mi. N Mazatlán (LACM 7033); 45 km. N Mazatlán (* KU 73615); San Ignacio (LACM 7030); 4 mi. S Terreros (LACM 7034); 21.7 mi. S Terreros (LACM 7037); 13 km. NNE Vaca, 400 m. (* KU 83410); 12.1 mi. SE Villa Unión (LACM 7032).

Literature records.—Ahome (Bogert and Oliver, 1945:403); El Dorado (Fugler and Dixon, 1961:16); 10 mi. NW Escuinapa, 150 ft. (Davis and Dixon, 1957a:20); 9 mi. SE Guamúchil (Duellman, 1957b:239); 13 mi. N Mazatlán; 17 mi. N Mazatlán (Zweifel, 1954b:147).

Additional records.—21.5 mi. N Culiacán, Río (SU 24018); 4 mi. NNE El Fuerte (FMNH 71530); 13 mi. N Escuinapa (FAS 15909); 16.1 mi. S Escuinapa (SU 24021); 34.7 mi. N Mazatlán (FAS 15910); 29.6 mi. NNW Mazatlán (SU 24019); 20.7 mi. N Rosario (CAS 95824); 7 mi. N San Blas (AMNH 75890); 15 mi. N Santo, Río, nr. Los Mochis (FAS 12923); 3.3 mi. E hwy. 15 (Villa Unión) on hwy. 40 (SU 24020).

Pseudoficima frontalis (Cope)

Toluca frontalis Cope, Proc. Acad. Nat. Sci. Philadelphia, 16:167, 1864 (type locality, Colima).

Pseudoficimia frontalis: Günther, Biologia Centrali-Americana, Rept. Batr., p. 96, 1893.

Remarks.—Bogert and Oliver (1945:375) described *P. hiltoni*

TABLE 6.—Comparison of Ten Characteristics of 17 Specimens of *Pseudoficimia frontalis*, Arranged in the Order of Their Localities from North (Top of Table) to South. (AMNH 63717 is the holotype of *P. hiltoni* Bogert and Oliver, 1945; USNM 31424-25 are the paralectotype and lectotype, respectively, of *P. frontalis*. C = complete; I = incomplete.)

SPECIMEN NUMBER	Sex	Total length	Ventrals	Sub-caudals	Supra-labials	Infra-labials	Total tail length (per cent)	Width of light dorsal spots at mid-body	Frontal lines		Dorsal blotches	Caudal blotches
									Ant.	Post.		
AMNH 63717.....	♂	700	153	50	7-7	8-8	18.8	3	C	C	44	20
FAS 9168.....	♀	705	152	51	7-7	8-8	18.4	2	C	I	38	17
LACM 7046.....	♂	510	148	45	7-7	7-7	18.8	3	C	I	26	11
CSCLB 1384.....	♂	568	153	44	7-7	8-7	17.8	3	C	I	38	17
AMNH 75753.....	♂	437	46	7-7	7-7	18.8	3	C	C	33	13
LACM 7043.....	♂	566	159	45	7-7	8-8	18.5	2	C	I	33	13
UCLA 14644.....	♂	402	155	49	7-7	8-7	19.9	2	C	I	34	16
KU 73618.....	♂	7-7	8-7	2	C	I	40
KU 73617.....	♀	374	150	45	7-7	8-8	18.2	4	C	C	37	15
LACM 7041.....	♀	343	156	50	7-7	7-7	19.5	3	I	C	44	20
LACM 7045.....	♂	410	156	46	7-7	8-8	18.0	2	C	C	37	13
LACM 7044.....	♂	566	158	50	7-7	8-8	19.4	2	C	C	43	21
LACM 7042.....	♂	366	160	43	7-7	7-7	17.5	4	C	I	38	11
UAZ 16308.....	♂	392	155	47	7-7	7-7	18.6	2	C	C	36	16
LACM 7040.....	♂	354	157	56	7-7	8-8	20.9	2	C	C	35	17
USNM 31424.....	♂	393	154	39	7-7	7-7	16.3	1	C	I	45	18
USNM 31425.....	♂	503	139	43	7-7	6-?	19.3	1	C	I	35	15

from southern Sonora as different from other species of *Pseudoficimia* by having light dorsal spots two or more scales wide, eight infra-labials, and a double line across the frontal region. Campbell and Simmons (1962:196) reduced *hiltoni* to subspecific rank based on one specimen from near Espinal that was apparently intermediate between *frontalis* and *hiltoni*.

Additional specimens from Sinaloa clarify the relationships between the nominal populations. Analyses of ten characters (Table 6) show a complete overlap in all characters throughout the range of the species. These data do not support the subspecific arrangement suggested by Campbell and Simmons (1962:197). We suggest that *Pseudoficimia frontalis hiltoni* be placed in the synonymy of *P. frontalis*, which is monotypic as now understood. The first author currently is evaluating the validity of *P. pulcherrima* and reviewing the generic relationship of *Pseudoficimia*. All specimens were found at night on the highway.

Distribution in Sinaloa.—Occurs throughout the lowland thorn forest and tropical deciduous forest of the state. See Fig. 80.

Specimens examined.—30 mi. SSE Alamos [Sonora] (° FAS 9168); 4 mi. NE Concordia (° LACM 7040); 26 mi. N Culiacán (° CSCLB 1384); 4 mi. S Culiacán (° AMNH 75753); 34.4 mi. N Elota, Río (° LACM 7043); 11.5 mi. N Espinal (° UCLA 14644); 0.8 mi. S Guamúchil (° LACM 7046); Guirocoba [Sonora] (° AMNH 63717, holotype of *P. hiltoni*); 12.8 mi. N Mazatlán (° UAZ 16308); 16 mi. N Mazatlán (° LACM 7042); 17.9 mi. N Mazatlán (° LACM 7044); 18 mi. N Mazatlán (° LACM 7045); 18.3 mi. N Mazatlán (° LACM 7041); 61 km. N Mazatlán (° KU 73617); 125 km. NNW Mazatlán (° KU 73618); Colima [state] (° USNM 31424, paralectotype and 31425, lectotype).

Literature record.—Presidio (Boulenger, 1894:270; Taylor and Smith, 1942:243).

Additional record.—6.8 mi. N Elota, Río (SU 24022).

Rhadinaea hesperia hesperioides Smith

Rhadinaea hesperia hesperioides Smith, Proc. Biol. Soc. Washington, 55:186, December 31, 1942 (type locality, Magdalena, Jalisco).

Remarks.—Three specimens (a male, female, and one of unidentified sex) have 154, 149, 153 ventrals; 110, 122 subcaudals (excluding KU 80870); ?-17-17, 17-17-17, 18-17-17 dorsal scale rows; 9-8, 8-8, 8-8 supralabials; and 10-10, 10-9 infralabials (excluding KU 80870). The preoculars are 2-2, postoculars 2-2, temporals 1 + 2; labials 4-5 enter the eye on all specimens except the male (KU 80870), which was damaged.

Distribution in Sinaloa.—Tropical deciduous forest of the southern highlands and foothills. See Fig. 81.

Specimens examined.—Santa Lucía (° KU 75629); 19.2 km. (via hwy. 40)

NE Santa Lucía, 1890 m. (° KU 80871); 12.3 km. (via hwy. 40) SW Santa Lucía, 1200 m. (° KU 80870).

Literature record.—Plomosas (Smith, 1942b:186 and 1943a:464; Smith and Taylor, 1945:118).

Rhinocheilus lecontei antonii Dugés

Rhinocheilus antonii Dugés, Proc. Amer. Philos. Soc., 23:290, 1886 (based on a specimen from San Blas, Nayarit).

Rhinocheilus lecontei antonii: Klauber, San Diego Soc. Nat. Hist., 9:314, September 26, 1941.

Remarks.—Six females and seven males have the following characteristics, respectively: 188-199 (194.5), 194-202 (197.1) ventrals; 41-48 (44.7), 46-52 (48.5) subcaudals (KU 91420 excluded). For all specimens: dorsal scale rows, 23-25 at the neck, 23-25 at mid-body, 19-21 at vent (KU 61100, 73624 excluded); supralabials, 8-8 (excluding the right side of KU 73621); infralabials, 9-9 in nine, 9-8 in one, 8-8 in two and one (KU 73621) has 9 on left (right excluded); preoculars, 1-1 in ten, 2-1 in one, 1-2 in one, 2-2 in one; postoculars, 2-2; temporals, 2 + 3 in all except one that has 3 + 3 on left and one that is injured on the right (KU 73621); labials 4-5 enter eye. The coloration agrees with the description of Sonoran specimens by Bogert and Oliver (1945:370).

Rhinocheilus lecontei antonii is a moderate-sized nocturnal species and one of the most common snakes encountered in the state. More than 80 specimens were taken on the roads at night from mid-June through August. This species is one of the first to become active with the onset of the rainy season. Their activity drops off markedly in August in contrast to some species which apparently reach peak activity during late July and August. Individuals were most abundant on nights when the air temperature ranged from 26.4° to about 28.2°C.

Distribution in Sinaloa.—Throughout the lowlands below about 200 meters, but most abundant from the vicinity of Culiacán southward. See Fig. 82.

Specimens examined.—1 mi. N Cerro Prieto (UAZ 9611); 5.6 mi. SW Charay (CSCLB 1928); 1.4 mi. E Concordia (CSCLB 1927); 7.3 mi. S Concordia (CSCLB 1920); 6 km. SW Concordia (° KU 73622); 2.4 mi. W Concordia (JFC 63:161); 4.8 mi. N Coyotitán (LACM 7061); 0.1 mi. S Coyotitán (LACM 7062); 1908 mi. S Coyotitán (LACM 7076); 29 mi. S Coyotitán (LACM 7075); 2.9 mi. N Culiacán (JFC 63:160); 18.4 mi. N Culiacán (JFC 63:159); 66.3 mi. N Culiacán (LACM 7082); 11.7 mi. S Culiacán (LACM 7055); 21.1 mi. S Culiacán (LACM 7056); 22 mi. S Culiacán (CSCLB 1916); 30 mi. S Culiacán (LACM 7083); 35.2 mi. S Culiacán (LACM 7057); 89.6 mi. S Culiacán (LACM 7058); El Dorado (° KU 61100); 6.9 mi. N Escuinapa (CSCLB 1929); 0.2 mi. SE Escuinapa (LACM 7079); 8 km. SE Escuinapa (° KU 73625); 18.5 mi. SE Escuinapa (LACM 7080); 20 mi. S Escuinapa (CSCLB 1919); 5.5 mi. S Espinal (CSCLB 1918); 10 km. W La Concha, 3

m. (° KU 91420); 3.4 mi. N La Cruz road (on hwy. 15) (LACM 7071); 10 mi. E La Cruz (LACM 7072); 10.3 mi. N La Cruz road (on hwy. 15) (LACM 7070); Matatán, 170 m. (° KU 73620-21); 7.3 km. SW Matatán, 155 m. (° KU 78916); 5 mi. N Mazatlán (CSCLB 2960); 5-10 mi. N Mazatlán (LACM 8658-59); 13.2 mi. N Mazatlán (UAZ 4555); 15 mi. N Mazatlán (CSCLB 1915); 15.7 mi. N Mazatlán (LACM 7066); 16.1 mi. N Mazatlán (UAZ 13651); 16.5 mi. N Mazatlán (LACM 7077); 16.6 mi. N Mazatlán (LACM 7081); 19.2 mi. N Mazatlán (CSCLB 1923); 23.1 mi. N Mazatlán (LACM 7078); 32.6 mi. N Mazatlán (LACM 7073); 33 mi. N Mazatlán (LACM 7065); 58 km. N Mazatlán (° KU 73623); 45.2 mi. N Mazatlán (CSCLB 1924); 52.7 mi. N Mazatlán (CSCLB 1926); 72.5 mi. N Mazatlán (CSCLB 1917); 26 km. NW Mazatlán (° KU 86609); 62.3 mi. NW Mazatlán (UAZ 4554); 2.9 mi. S Rancho Huanacastle (LACM 7059); 5.8 mi. S Rancho Huanacastle (LACM 7060); 3.2 mi. N Rosario (CSCLB 1922); San Ignacio (LACM 7074); Teacapan (LACM 7084); 10 km. NW Teacapan (° KU 93498-99); 10 km. NNW Teacapan (° KU 91427); 10.9 mi. S Terreros (LACM 7063); 17.3 mi. S Terreros (LACM 7064); 0.7 mi. N Villa Unión (CSCLB 1925); 10.6 mi. NE Villa Unión (LACM 7067); 19 km. NE Villa Unión (° KU 73624); 1 mi. SE, 2 mi. NE Villa Unión (on hwy. 40) (CSCLB 1921); 0.2 mi. NW Villa Unión (LACM 7069); 2.2 mi. NW Villa Unión (LACM 7068).

Literature records.—Culiacán (Klauber 1941:318; Smith, 1943a:466); El Dorado (Fugler and Dixon, 1961:16); Escuinapa (Klauber, 1941:318); 4 mi. SE Escuinapa, 50 ft. (Davis and Dixon, 1957a:19); Mazatlán (Cope, 1887:82); 15-28 mi. NNW Mazatlán (Duellman, 1957b:240).

Additional records.—1 mi. SE Aguacaliente, 300 ft. (TCWC 12619); 12.0 mi. NW Baluarte, Río (SU 24036); 1.9 mi. S Caitime (FAS 15011); 4.5 mi. S Caitime (FAS 8506); 4.6 mi. S Caitime (FAS 14808); Culiacán (USNM 46370); 3 mi. N Culiacán (UMMZ 118945); 35.7 mi. N Culiacán (FAS 16991); 55-60 mi. N Culiacán (FAS 12781); 62.6 mi. N Culiacán (FAS 14685); 7 mi. S Culiacán, hwy. 15 (AMNH 77524); 47-52 mi. S Culiacán (FAS 14086); 61.8 mi. S Culiacán (FAS 12402); El Dorado (AMNH 90751-52); Escuinapa (AMNH 3764-72); 6.9 mi. N Escuinapa (FAS 14793); 10-15 mi. N Escuinapa (FAS 13287); 3.2 mi. SE Escuinapa (SU 24039); 5.9 mi. SE Escuinapa (SU 24040); 6 mi. SE Escuinapa (SM 10591); 7.4 mi. SE Escuinapa (SU 24041); 22.6 mi. SE Escuinapa (SU 24042); 25.3 mi. SE Escuinapa (SU 24043); 29 mi. SE Escuinapa (SM 10590); 29.7 mi. S Escuinapa (FAS 14464); 22.7 mi. NNW Escuinapa (SU 24037); 34.3 mi. S Espinal (ASDM 1752); 8 mi. N Guamúchil (FAS 16993); 2.9 mi. E La Cruz (SU 24030); 16 mi. N Mazatlán (AMNH 75891); 19 mi. N Mazatlán (MCZ 61426); 28 mi. N Mazatlán (UMMZ 117367); 47.1 mi. N Mazatlán (CAS 95807); 7.9 mi. S Mazatlán (FAS 15010); 23.6 mi. S Mazatlán (FAS 15025); 24 mi. S Mazatlán (FAS 13576); 35-40 mi. S Mazatlán (FAS 13298, 15024); 41.6 mi. S Mazatlán (FAS 14702); 65 mi. S Mazatlán (FAS 16813); 75.5 mi. S Mazatlán (FAS 12407); 90 mi. S Mazatlán (FAS 13283); 17.5 mi. NNW Mazatlán (SU 24033); 30.6 mi. NNW Mazatlán (SU 24032); 6.9 mi. S Mocerito, Río (SU 24027); 11.7 mi. S Mocerito, Río (SU 24028); 16.0 mi. SE Piaxtla, Río (SU 24031); 2.8 mi. ESE Presidio, Río (SU 24034); 7.8 mi. ESE Presidio, Río (SU 24035); 37.8 mi. SE Presidio, Río (SU 24038); 4.4 mi. N San Lorenzo, Río (SU 24029); 10.4 mi. NE Villa Unión (UF 16536); 6.5 mi. SE Villa Unión (AMNH 94806).

Salvadora bairdi Jan

Salvadora bairdi Jan, Iconographie générale des ophiidiens, livr. 2, pl. 2, fig. 2, 1860 (type locality, México).

Remarks.—Four males have 190, 185, 184, 174 ventrals; 100, 103, 96, 97 subcaudals; 18-15-13, 17-17-13, 17-17-13, 17-15-13 dorsal scale rows; and 2 + 2/2 + 2, 2 + 3/2 + 3, 2 + 2/2 + 2, 2 + 3/2 + 2

temporals respectively (in order as listed in specimens examined). Each specimen has 8-8 supralabials, 9-9 infralabials, 2-2 preoculars, 2-2 postoculars, supralabials four and five entering the eye, and the posterior pair of chin shields separated medially by a series of small scales.

Smith (1943a:467) reported that the anterior nasal is separated from the second supralabial in all (10) of the specimens (from Guanajuato, Michoacán, Puebla, and Veracruz) that he examined. Davis and Smith (1953:137) found the same condition in three snakes from Morelos. The anterior nasal is in contact with the second supralabial on every specimen from Sinaloa. The contact of the anterior nasal and the second supralabial is reported to be characteristic of *S. grahamiae* by Smith (1939b:233), but is considered to be of little, if any, taxonomic importance by Charles M. Bogert (personal communication).

In the specimens from Sinaloa, the dorsolateral dark stripes terminate on the nape just posterior to the parietal and temporal regions. This characteristic distinguishes *S. bairdi* from *S. lineata*, in which the dorsolateral dark stripes diverge on the neck and pass through the temporal region to the eye. The Sinaloan specimens of *bairdi* also have a dark lateral stripe on the third scale row. The right maxilla of one specimen (KU 78918) has nine teeth anterior to the diastema that separates them from larger teeth at the posterior end of the jaw. In contrast, *S. grahamiae* lacks a dark lateral stripe on the third scale row and usually has ten maxillary teeth anterior to the fangs (Smith and Taylor, 1945:122). However, it is of interest to note that the anterior nasal and the second supralabial are separated in the southern part of the range of *bairdi* (away from the range of *grahamiae*) and the nasal and supralabial are in contact in the northern part of the range (close to the range of *grahamiae*).

Bogert and Oliver (1945:403) suggested that *S. bairdi* and *S. lineata* might intergrade in Hidalgo and Distrito Federal. Davis and Dixon (1957a:21-22) reported a specimen from Michoacán that was intermediate between *bairdi* and *lineata* and suggested that they are probably subspecies of a single species. However, Davis and Dixon regarded them as distinct species pending the availability of more material. Duellman (1961:108) found only one specimen that resembled *lineata* among 89 specimens from Michoacán. Our specimens are typical of *bairdi* in most characters but the overlap in some characters previously discussed suggests

the need for a detailed study of specimens obtained throughout the ranges of *Salvadora bairdi*, *grahamiae*, and *lineata*.

Distribution in Sinaloa.—Known from the northern and southern highlands; probably occurs throughout the highlands. See Fig. 83.

Specimens examined.—18 km. NNE Choix (° KU 68753); 2.2 km. NE (by hwy. 40) Santa Lucía, 1155 m. (° KU 78917; CSCLB 733); 19.2 km. NE (by hwy. 40) Santa Lucía, 1935 m. (° KU 78918).

Salvadora hexalepis deserticola Schmidt

Salvadora hexalepis deserticola Schmidt, Zool. ser., Field Mus. Nat. Hist., 24:146, May 31, 1940 (type locality, Government Spring, near Chisos Mountains, Brewster county, Texas).

Remarks.—One female and four males (two adults, two juveniles, with yolk scars) have the following characters, respectively: ventrals 190, 189, 187, 189, 193; subcaudals 72, 81, 81, 83, 83; dorsal scale rows 20-17-18, 19-17-15, 18-17-13, 18-17-13, 18-17-13; infralabials 10-10, 9-9, 9-10, 10-10, 10-10; preoculars 2-1, 2-2, 2-2, 3-3, 1-2; temporals 2 + 3/3 + 3, 2 + 3/2 + 3, 3 + 3/3 + 3, 3 + 3/3 + 3, 2 + 2/2 + 3; and loreals 2-2, 1-1, 1-1, 2-2, 1-1. All of the specimens examined have 9-9 supralabials, 2-2 postoculars, labials five and six entering the eye, the lateral black line on scale rows three and four, and the chin shields separated by a series of small scales. In one specimen with 2-2 loreals (KU 83412), the lower loreal on each side appears to be a fragment of supralabials 4-4. The supranal scales are smooth in the juvenile males (KU 83411-12) and keeled in the adults.

Smith (1941a:9) described *S. h. celeris* based on one female from San Blas, Sinaloa. According to Smith (1941a:11) the only difference between *deserticola* and *celeris* is in the ventral counts (200, 205 in *celeris*; 198 or fewer in *deserticola*). Bogert and Oliver (1945:366) placed *celeris* in the synonymy of *S. h. deserticola*. Two specimens from Vaca (KU 83411-12) examined by us have ventral counts typical of *deserticola*. The other scale counts are typical of both subspecies except that Smith (1941a:9) reported 11-11 infralabials in the holotype of *celeris*. We agree with Bogert and Oliver (1945:366) in referring *celeris* to the synonymy of *deserticola*. The status of this species is being studied by Charles M. Bogert, who is reviewing the genus *Salvadora*. This snake is a diurnal terrestrial species and inhabits the more open portions of forest.

Distribution in Sinaloa.—Throughout the lowlands and foothills, below about 500 meters. See Fig. 83.

Specimens examined.—Rosario, 150 m. (° KU 73626-27); San Ignacio (° LACM 7086); 13 km. NNE Vaca, 400 m. (° KU 83411-12).

Literature records.—Ahome (Bogert and Oliver, 1945:403); 9 mi. N Mazatlán, 100 ft. (Zweifel, 1954b:147); San Blas (Smith, 1941a:9 and 1943a:467); Yecorato (Smith, 1941a:11; Bogert and Oliver, 1945:403).

Additional records.—Culiacán (MVZ 70273); 16 mi. SE Los Mochis (SM 11153); 9 mi. N Mazatlán (MVZ 59287); 10 mi. S Villa Unión (MCZ 61428).

Sonora aemula (Cope)

Procinura aemula Cope, Proc. Amer. Philos. Soc., 18:262, 1879 (type locality, Batopilas, Chihuahua).

Sonora aemula, Bogert and Oliver, Bull. Amer. Mus. Nat. Hist., 83:371, March 30, 1945.

Remarks.—Charles H. Lowe, Jr., obtained an adult male north of Culiacán on September 1, 1956. On August 25, 1966, Lynn W. Robbins found an adult female (DOR) near Cerro Prieto at 1745 hours. These specimens are the first and second records for the state and have the following characteristics, respectively: 145 (?), 156 ventrals; 40, 36 subcaudals; 18-15-15, 17-15-15 dorsal scale rows; single, divided anal plate. Both specimens have 7-7 supralabials, 7-7 infralabials, 1-1 loreals, 1-1 preoculars, 2-2 postoculars, and 1 + 2 temporals. On one specimen (LACM 28714) the dorsal scales are smooth anteriorly with keeling apparent at about ventral number 125 and increasing posteriorly to the strongly keeled tail; the total length is 414.5, tail length 60, and tail length to total length ratio is 0.17. The other specimen has smooth anterior dorsal scales that become keeled at the sixth black band and are progressively more keeled to the tail; the nasal is complete.

The coloration and pattern of LACM 28714 is as follows: dorsum red, with black spot on most dorsal scales; red caudal scales nearly lacking black pigment; a single dyad, beginning at ventral 147 and continuing to ventral 152, consists of 2 black bands separated by a white band, each band two scales long on midline; tail tip white, preceded by a narrow (2 scales long) black band; ventrals white with slight reddish wash on lateral edges; slight black pigmentation at position of dorsal dyad; subcaudals uniform reddish, except where black band nearly encircles tail tip; black spot covers most of parietals, frontal, supraoculars, and encircles eye; three scales behind the parietals is a black band three scales wide extending $2\frac{1}{2}$ scales below angle of mouth; snout, labials, and chin white.

The other specimen has nine black bands, 3-6 scales long (longer posteriorly), on body with the second and third bands separated only by a dirty white band two and one-half scales long; the body bands are incomplete across the belly anteriorly, but complete at midbody and posteriorly. The interspaces between the black bands

are yellow, 11-16 scales long, and include faint indications of small black bands before and after each large black band; there are two black bands on the tail; the snout is pale yellowish white to the posterior third of prefrontals and contacts the black head-cap that extends nearly to posterior edge of parietals.

These specimens agree well with the specimens reported by Bogert and Oliver (1945:371-74) in all characters except coloration. As pointed out by Zweifel and Norris (1955:244), and supported by additional material from Sonora (Nickerson and Heringhi, 1966:136-138), the color pattern is variable. Specimens are known that are unicolor, that have one, two, or several dyads, and that are ringed in no definite color arrangement. The dyad may be two black rings separated by a white ring or two white rings separated by a black ring. These color patterns could provide interesting material for a study of natural selection and mimicry, especially with the sympatric occurrence of two potential models, *Micrurus distans* and *Micruroides euryxanthus*.

Stickel (1943:111) remarked that "the color pattern of *Procinura* is developed along a different line than that seen in any described form of *Sonora*." Wright and Wright (1957:672-73) discussed the many color variations of *Sonora episcopa*. The other character mentioned by Stickel to separate *Procinura* from *Sonora* is the modified caudal scales. We agree with Bogert and Oliver (1945:374) that the recognition of a monotypic genus based on a single character tends to obscure its relationship with *Sonora*.

One specimen (LACM 28714) contained the remains of a scorpion and a terrestrial orthopteran.

Distribution in Sinaloa.—Known only from the northern lowlands. See Fig. 81.

Specimens examined.—13 km. S Cerro Prieto on hwy. 15 (° LACM 28714); 46.6 mi. (by hwy. 15) N Culiacán (° UAZ 16533).

Storeria storerioides (Cope)

Tropidoclonium storerioides Cope, Proc. Acad. Nat. Sci. Philadelphia, 17: 199, 1865 (based on four specimens from the "Méxican plateau between the eastern ranges and the valley of México").

Storeria storerioides, Garman, Mem. Mus. Comp. Zool., 8:29, 1883.

Remarks.—One male has 129 ventrals, 41 subcaudals, 15-15-15 dorsal scale rows, 5-5 supralabials, 7-7 infralabials, 2-2 preoculars, 2-2 postoculars, 1 + 2/1 + 2 temporals, and labials two and three entering the eye on each side. This specimen was caught in pine-oak forest on August 5, 1963; a heavy rain fell on the previous day.

Distribution in Sinaloa.—Known only from the lower montane dry forest of the southern highlands. See Fig. 78.

Specimen examined.—19.2 km. NE Santa Lucía, 1935 m. (* KU 78922).

Additional record.—9.6 mi. SW El Palmito (UMMZ 123036).

Sympholis lippiens Cope

Sympholis lippiens Cope, Proc. Acad. Nat. Sci. Philadelphia, 13:524, 1862 (type locality, Guadalajara, Jalisco).

Remarks.—Six specimens have 207-227 (214.3) ventrals; 15-23 (19.8) subcaudals; 228-241 (236.3) total ventrals plus subcaudals; 5-6 (mode 5) supralabials; 6-7 (mode 6) infralabials; 1-1 postoculars in three, 1-0 postoculars in two, no postoculars in one. All specimens have 19-19-19 scale rows; 1-1 preoculars; third supralabial entering orbit. Dorsal body bands number 17-23 (20) and are 5-13 scales long on the middorsal line. The light interspaces are 2-4 scales long on the middorsal line; there are black flecks in the light dorsal interspaces of three specimens. Caudal bands number 2 or 3.

Humphrey and Shannon (1958:260), in a redescription of the species, suggested that specimens from Sinaloa and Nayarit (one each) might represent distinct subspecies. Hensley (1966:51) described a northern subspecies, *Sympholis lippiens rectilimbus*, as different from the nominal population in color pattern and head scutellation.

Specimens from Sonora and northern Sinaloa generally have a straight anterior margin of the white nuchal collar across the posterior edges of the parietals. Most specimens from southern Sinaloa and Nayarit have a loop-like extension of the light nuchal collar onto the frontal as figured by Hensley (1966:51). A specimen (LACM 6501) from near Mazatlán and a specimen (CSCLB 1389) from near San Blas, Nayarit, have a white spot on the frontal scale but a straight anterior margin of the nuchal collar. Hensley (1966:50, 54) interpreted this white spot as characteristic of *S. l. lippiens*. Two specimens from north of Mazatlán (KU 73628; UAZ 16309) have the same collar pattern as that figured for *S. l. lippiens* from near Tepic, Nayarit (Hensley, 1966:51). This variation in the southern segment of the population suggests a clinal trend northward, from the looped to the straight collar margin. There is no definite break in this character but rather a 240 kilometer range of the intermediate collar patterns. There is also some variation in the nuchal collar in northern specimens (Hensley, 1966:53). The ventral pattern varies in the condition of the dark bands on the ventrals. In some speci-

mens the margins of the dark bands are symmetrical and meet at the same point; in some specimens the margins are offset two or three ventral scales; in others the ventral extensions of the dorsal bands are separated by two or three white ventral scales; in some the dorsal band is continuous onto the ventral midline on one side, but extends only to the second scale row on the other side; some dorsal bands fuse laterally, others show indications of lateral splitting by light color. The dorsal dark bands of some individuals completely encircle the body to form rings; in others the dorsal band may be interrupted on the midventral line by a white area of varying width and shape. The length of the white interspaces on the middorsal line shows clinal variation increasing from two scales in the north to five scales in the south. The scales of the head exhibit a wide range of variation, a characteristic frequently associated with burrowing snakes. Inger and Marx (1965:14) demonstrated that variation in size and shape of the frontal scale and the ratios of frontal to supraocular scales increase with sample size in another burrowing snake of the genus *Calamaria*. We suspect the same is true in *Sympholis*. Fusions and divisions of the loreal, postocular, and supralabial scales are common. Other details of head scutellation show considerable variation.

Because of the lack of adequate material, the range of variation in certain characters of coloration and scutellation, and the clinal variation in other characters, we refrain from recognizing the subspecies of *Sympholis lippiens* described by Hensley (1966:51) at this time.

Distribution in Sinaloa.—Known from scattered localities throughout the lowlands of the state. See Fig. 65.

Specimens examined.—Alamos [Sonora] (° ASDM 1269); 18 mi. W Alamos [Sonora] (CSCLB uncatalogued); 4.8 mi. N Culiacán (° FAS 11374); 5 mi. S Culiacán (° CSCLB 1388); 31 km. SE Escuinapa (° KU 80760); 9 mi. N Mazatlán (° LACM 6501); 10.8 mi. N Mazatlán (° UAZ 16309); 56 km. N Mazatlán (° KU 73628); 39.2 mi. N Mazatlán (° CSCLB 1387); 14.7 mi. E San Blas [Nayarit] (° CSCLB 1389); 10 mi. E Tepic [Nayarit] (° LACM 6500); Terreros (° LACM 6502).

Literature records.—4 mi. N Culiacán (Humphrey and Shannon, 1958:257; Zweifel, 1959b:6).

Additional records.—36.7 mi. NW Río Culiacán (SU 24045); 13.3 mi. SE Río Presidio (SU 24046).

Tantilla calamarina Cope

Tantilla calamarina Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 320, 1866 (type locality, Guadalajara, Jalisco; type locality probably in error, see Peters, Occ. Papers, Mus. Zool., Univ. Michigan, 554:31-32, June 23, 1954).

Remarks.—*Tantilla bimaculata* was described by Cope (1874-1881:143) on the basis of a specimen from Mazatlán. Taylor (1936b:346) placed *T. bimaculata* in the synonymy of *T. calamarina*, a species that occurs in the lowlands of western México. A second specimen (MCZ 61430, a male) has a total length of 153; tail length, 38; 127 ventrals; 36 subcaudals; 6-6 supralabials; 6-6 infralabials; 1-1 preoculars; 1-1 postoculars. The body is tan above rather than gray and the lateral dark stripe is on the third and fourth scale rows. Other characteristics are as described by Smith (1942a:35).

Distribution in Sinaloa.—Known only from the southern coastal lowlands around Mazatlán. See Fig. 84.

Specimen examined.—29 km. N Mazatlán (° MCZ 61430).

Literature records.—Mazatlán (Cope, 1874-1881:143 and 1887:84; Smith, 1942a:35 and 1943a:474).

Tantilla yaquia Smith

Tantilla yaquia Smith, Zoologica, 27:41, April 30, 1942 (type locality, Guasaremos, Río Mayo, Chihuahua).

Remarks.—Zweifel and Norris (1955:243) proposed that *T. bogerti* Hartweg be considered a subspecies of *T. yaquia* on the basis of a single specimen from Mirasol, Sonora. They distinguished *yaquia* from *bogerti* by the presence (in *yaquia*) of more ventrals, more subcaudals, and a less extensive black cap. Tanner (1966:135) considered *bogerti* and *yaquia* subspecies of *Tantilla planiceps*. We agree with Tanner's proposal that *Tantilla yaquia* is allied to *T. planiceps* of Baja California, but we cannot accept his contention that *yaquia*, *atriceps* and *planiceps* represent the same species. Furthermore, we have found that the characteristics utilized by Tanner (1966:148) and Zweifel and Norris (1955:243) to distinguish between *bogerti* and *yaquia* show clinal variation. On this basis we place *T. y. bogerti* in synonymy with *T. y. yaquia*. A detailed study of *T. yaquia* will be presented elsewhere.

Seven specimens of *T. yaquia* have 134-150 (145.8) ventrals; 48-61 (52.8) subcaudals (except UIMNH 34921); 7-7 (7-8 in 1) supralabials; 6-6 infralabials; 1-1 preocular; 2-2 postoculars. The mental is separated from the chin shields in all specimens examined.

Distribution in Sinaloa.—Probably occurs throughout the state. See Fig. 84.

Specimens examined.—Costa Rica (° UIMNH 34921); 43.8 mi. S Culiacán (° UAZ 16310); 1 km. ENE El Cajon, 1000 m. (° KU 93500); Labrados (° CAS 64976); 5.8 mi. N Mazatlán (° LACM 6998) 16 mi. N Mazatlán (° JFC 62:53); Teacapán (° LACM 7001).

Literature record.—Costa Rica (Smith and Van Gelder, 1955:147).

Additional Record.—22.4 mi. SE Piaxtla, Río (SU 23788).

Thamnophis cyrtopsis collaris (Jan)

T[ropidonotus] collaris Jan, Elenco Sistematico degli Ofidi . . . , p. 69, 1863 (based on a specimen from "Messico"; type locality restricted to Guanajuato, Guanajuato by Smith, Copeia, no. 2:140, June 8, 1951).

Thamnophis cyrtopsis collaris: Webb, Tulane Studies Zool., 13:60, August 30, 1966.

Remarks.—Four males have 159, 164, 161, 167 ventrals; 109, 112 subcaudals (excluding KU 75632, 78928); 19-19-17, 19-18-17, 19-19-19, 19-19-18 dorsal scale rows; 8-8, 8-8, 8-8, 9-8 supralabials; 3-3, 3-3, 3-4, 3-3 postoculars; and 1 + 3/1 + 3, 1 + 3/1 + 3, 1 + 2/1 + 3, 1 + 3/2 + 3 temporals. All of the males have 10-10 infralabials, 1-1 preoculars, and the fourth and fifth supralabials entering the eye (except KU 78927 which has supralabials five and six entering the eye on the left). Nine females have 149-159 (153.4) ventrals and 98, 98, 99, 92 subcaudals (only KU 40349, 75633, 78924-25). There are 19 dorsal scale rows at the neck in six, 20 scale rows in two and 18 in one; 8-8 supralabials in eight and 8-9 in one; 10-10 infralabials in seven, 10-9 in one, and 10-11 in one; 3-3 postoculars in five, 3-4 in one, 4-4 in two, and 4-5 in one; 1 + 2/1 + 2 temporals in four, 1 + 2/1 + 3 in two, and 1 + 3/1 + 3 in three; 4-5/4-5 supralabials entering the eye in eight and 4-5/5-6 in one; all females have 1-1 preoculars. The vertebral stripe is confined to the vertebral scale row on all specimens examined.

Gloyd and Smith (1942:234) recognized *T. eques cyrtopsis* as distinct from *T. e. eques* by having 167 or more ventrals (86%) in males and 163 or more ventrals (100%) in females. Smith used this same character in a synonymy of the garter snakes (1942d:108). Later, Smith (1951:139) resurrected *Eutaenia cyrtopsis* Kennicott for the black-necked garter snakes referred to *T. eques* by Gloyd and Smith (1942:234); *T. eques* was applied by Smith to a different species that inhabits the Mexican plateau and is currently recognized. According to Milstead (1953:353), only *T. c. cyrtopsis* (= *T. eques cyrtopsis*, Gloyd and Smith, 1942:234) occurs in Sinaloa, with 161-184 ventrals in males and 152-177 ventrals in females (p. 371); and *T. cyrtopsis cyclides* (= *T. e. eques*, Gloyd and Smith, 1942:234) occurs on the southern part of the Mexican plateau, with 140-172 ventrals in males and 138-168 ventrals in females.

Chrapliwy and Fugler (1955:127) referred a specimen from Durango to *T. c. cyclides*, and Fouquette and Rossman (1963:197) referred a specimen from northern Sinaloa to *T. c. cyrtopsis*. Fitch and Milstead (1961:112) suggested that *Thamnophis dorsalis* is

the correct name by priority for *T. cyrtopsis*. However, according to Webb (1966:56), the name *dorsalis* probably belongs to the upper Río Grande population of *Thamnophis sirtalis* and would replace *T. sirtalis ornata* Baird. This would allow conservation of the name *cyrtopsis* for the snakes as understood by Smith (1951). Webb also stated (pp. 60-63) that *Tropidonotus collaris* Jan, 1863, is the earliest name for the population of *cyrtopsis* in the coastal lowlands and subtropical highlands of western México [Sinaloa]. Therefore, the Sinaloan population of black-necked garter snakes should be known as *Thamnophis cyrtopsis collaris*, one of five subspecies of *cyrtopsis* listed by Webb (p. 69). The other subspecies are *T. c. cyrtopsis* in the southwestern United States and Mexican plateau, *T. c. ocellata* in central Texas, *T. c. postremus* in Michoacán, and *T. c. pulchrilatus* in highland areas from Durango to Morelos and Veracruz.

Thamnophis has been collected in a variety of habitats in the state: along irrigation ditches near Los Mochis, in forest near Culiacán, and along rivers near Presidio. The species has successfully occupied the extensive agricultural areas of the Río Fuerte floodplain.

Distribution in Sinaloa.—Throughout the state from near sea level to about 2000 meters. See Fig. 85.

Specimens examined.—N edge Culiacán (CSCLB 1939); 4.7 mi. N Culiacán (CSCLB 1970); 23 km. N Culiacán (CSCLB 1945); 68.7 N Culiacán (LACM 7173); 4.2 mi. S Culiacán (LACM 7183); 5.5 mi. S Culiacán (LACM 7178); 6.7 mi. S Culiacán (LACM 7179); 6.9 mi. S Culiacán (LACM 7180); 17 km. S Culiacán (CSCLB 1944); 15 mi. S Culiacán (LACM 25936-37); 16.9 mi. S Culiacán (LACM 7181); 19 mi. S Culiacán (LACM 25935); 22 mi. S Culiacán (LACM 25934); 5 km. SW El Palmito, 1900 m. (° KU 75632-33, 80761); 8 mi. W El Palmito (LACM 25198-99); 8 mi. N Guamúchil (CSCLB 1940); 3.8 mi. N La Cruz turnoff, hwy. 15 (LACM 7172); 5.6 mi. E La Cruz (LACM 7174); 1.2 mi. N Los Mochis (CSCLB 1941); 47 km. N Los Mochis (° KU 67725); 2-3 mi. S Los Mochis (UCLA 12513); 7.3 mi. S Los Mochis (UAZ 9373-77); 13.6 mi. S Los Mochis turnoff, hwy. 15 (LACM 7177); 3.3 mi. SW Los Mochis (JFC 63:147); 5.3 mi. SW Los Mochis (JFC 63:146); 15 mi. S Mazatlán, Río Presidio (SU 18261-62); San José del Oro, 230 m. (° KU 83413); 1 km. NE Santa Lucía (CSCLB 1942); 2.2 km. NE Santa Lucía, 1155 m. (° KU 78923-24); 19.2 km. NE Santa Lucía, 1935 m. (° KU 78925-29); 1.5 km. E Santa Lucía, 1700 m. (° KU 40349); 4.1 mi. N Terreros (LACM 7176); 0.7 mi. S Terreros (LACM 7184); 15.7 mi. S Terreros (LACM 7175).

Literature records.—Copala (Webb, 1966:63); Costa Rica (Smith and Van Gelder, 1955:147; Webb, 1966:63); El Batel, 70 km. NE Mazatlán (Webb, 1966:63); El Dorado (Fugler and Dixon, 1961:16; Webb, 1966:63); 1 mi. NE El Fuerte; 8 mi. W El Palmito (Webb, 1966:63); 6.6 mi. S Guasave (Fouquette and Rossman, 1963:197); 70 km. NE Mazatlán (Milstead, 1953:372); Rosario (Smith, 1942d:108 and 1943a:479; Webb, 1966:63); 1 mi. E Santa Lucía (Webb, 1966:63).

Additional records.—4.8 mi. N Culiacán (FAS 11364); 26.7 mi. N Culiacán (FAS 11353); 44.6 mi. N Culiacán (FAS 17013); 44.8 mi. N Culiacán (FAS

9080); 10.3 mi. S Culiacán (FAS 12425); 31.3 mi. NW Culiacán, Río (SU 24078); 1.9 mi. W hwy. 15 on Culiacáncito road (SU 24079); El Dorado (AMNH 90753); 29.8 mi. N El Dorado (SU 24089); 29.9 mi. N El Dorado (SU 24088); 30.6 mi. N El Dorado (SU 24087); 31.3 mi. N El Dorado (SU 24085-86); 31.7 mi. N El Dorado (SU 24084); 32.0 mi. N El Dorado (SU 24082-83); 32.4 mi. N El Dorado (SU 24081); 9.6 mi. N Guamúchil (FAS 16998, 17016); 9.7 mi. N Mazatlán (UF 16537); 87.2 mi. N Mazatlán (FAS 12409); 6.4 mi. S Mazatlán (CAS 95755); 1.4 mi. WNW Mocerito, Río (SU 24077); 5.4 mi. WNW Mocerito, Río (SU 24076); 9.5 mi. WNW Mocerito, Río (SU 24075); 10.2 mi. WNW Mocerito, Río (SU 24074); 7.3 mi. E Navolato (SU 24080); 0.9 mi. N San Lorenzo, Río (SU 24090); 7.1 mi. NNE Topolobampo (SU 74073); 7.4 mi. NNE Topolobampo (SU 70072).

Trimorphodon lambda paucimaculata Taylor

Trimorphodon paucimaculatus Taylor, Univ. Kansas Sci. Bull., 24:527, February 16, 1938 (type locality, Mazatlán, Sinaloa).

Trimorphodon lambda paucimaculata: Fugler and Dixon, Publ. Mus. Michigan State Univ., Biol. ser., 2:17, July 20, 1961.

Remarks.—Taylor (1938:527) distinguished *T. paucimaculatus* from *T. biscutatus* by the presence in the former of preoculars separated from the frontal and the presence of dorsal spots "greatly elongated and fewer in number." *Trimorphodon paucimaculatus* is further distinguished from *T. biscutatus* by the absence of keels or ridges on the scales of males (Taylor, 1939b:360). Davis and Dixon (1957a:24) stated that *lambda* has fewer ventrals and darker dorsal blotches than *paucimaculatus*, and that intergradation between them probably occurs in Sinaloa north of Mazatlán. Duellman (1957b:240) suggested that more material may prove that the populations known as *T. paucimaculatus*, *T. lambda*, and *T. biscutatus* are subspecies. Fugler and Dixon (1961:17) concluded that *paucimaculata* is a subspecies of *lambda* and that the "zone of intergradation probably lies to the north of El Dorado, perhaps in the coastal plain between El Dorado and Alamos, Sonora." Fouquette and Rossman (1963:198-99) reported an intergrade with 240 ventrals from 30.7 miles north of Culiacán.

Six females have 250-259 (253.8) ventrals and 73-81 (77.3) subcaudals. The dorsal scale rows at the neck are 21 in two, 22 in one, 23 in one, 24 in one, and 25 in one; the scale rows at midbody are 24 in three, 25 in two and 27 in one; the scale rows at the vent are 17 in two, 18 in two, 19 in one, and 20 in one. The supralabials are 8-9 in one and 9-9 in five; infralabials 12-12 in one, 13-13 in two, ?-13 in one, 14-13 in one, and 13-14 in one; preoculars 3-3 in three, 3-4 in one, and 3-4 in two (one preocular on right very small); postoculars 3-3 in five, and 3-4 in one; temporals 3 + 3/2 + 3 in one, 3 + 3/4 + 3 in one, 3 + 4/3 + 4 in two, and 3 + 4/3 + 5 in two. Supralabials 4-5/4-5 enter the eye in five, and 5-6/5-6 in one; the

preoculars touch the frontal in three and the preoculars are separated from the frontal in three; 21-24 (22.2) dorsal dark body blotches (KU 78930 excluded); 9-11 (9.8) dorsal dark tail blotches (KU 78930 excluded).

One male (KU 37592) has 21-22-17 dorsal scale rows; the head is missing so no other counts are available. Characters of seven additional males are as follows: ventrals, 243-249 (246.9); subcaudals, 81-87 (84.3) (KU 83416 excluded); dorsal scale rows at neck, 21 in two, 22 in three, and 23 in two; scale rows at midbody, 23 in three, and 24 in four; scale rows at vent, 16 in one, 17 in two, 18 in three, and 19 in one; supralabials, 8-8 in one, 9-9 in five, and 9-10 in one; infralabials, 12-12 in three, and 13-13 in four; preoculars, 3-3 in seven; postoculars, 3-3 in six, and 4-3 in one; temporals, 2 + 3/3 + 3 in one, 3 + 3/3 + 4 in one, 3 + 4/3 + 4 in two, 3 + 3/3 + 3 in two, and 4 + 3/4 + 3 in one. Supralabials 4-5/4-5 enter the eye; the preoculars contact the frontal in one, the preoculars do not contact the frontal in six. Dorsal dark body blotches, 17-25 (21.7), and dorsal dark tail blotches, 11-14 (12.0) (KU 80765, 83416 excluded).

A female and male from the vicinity of Badiraguato (KU 83415-16) have more ventrals (251 and 248) than the intergrade reported by Fouquette and Rossman (1963:198-99). Two of the specimens examined from the southern half of Sinaloa (KU 73638, 80765) have 243 and 244 ventrals. If these specimens and one from 13 miles north of the Sinaloa-Sonora state line (Dixon, Sabbath, and Worthington, 1962:98) are intergrades, then the zone of intergradation would include most of Sinaloa northward from Mazatlán, as pointed out by Davis and Dixon (1957a:24). A zone of intergradation covering more than 500 kilometers is a condition untenable to most biologists. Although we refer all Sinaloan specimens to *T. l. paucimaculata* we recognize that clinal variation is probably a more reasonable explanation of evolutionary divergence in *Trimorphodon* in western México. In addition we suspect that a detailed study of *Trimorphodon biscutatus*, *lambda*, *lyrophanes*, *paucimaculata* and *vandenburghi* will show that these nominal populations are all representative of a single species.

Trimorphodon is a nocturnal species that is frequently found in or about rocky areas. Two specimens from San Ignacio were found about 3 meters above the ground in the rock foundation of a bridge.

Distribution in Sinaloa.—Throughout the state below about 1200 meters. See Fig. 86.

Specimens examined.—1.5 km. N Badiraguato, 230 m. (* KU 83415); 20 km. N, 5 km. E Badiraguato, 560 m. (* KU 83416); 6.5 mi. NE Concordia (CSCLB 557); 30 mi. N Culiacán (LACM 7094); 18 mi. S Culiacán (CSCLB 554); 78 mi. S Culiacán (LACM 7095); 26.7 mi. S Escuinapa (CSCLB 1375); 34.1 mi. S Escuinapa (CSCLB 1376); 6 km. S Guamúchil (LACM 28716); 0.1 mi. E La Cruz (LACM 7089); 5 mi. E La Cruz (LACM 7090); 18.5 mi. N La Cruz turnoff [hwy. 15] (LACM 7102); 7.9 mi. S La Cruz turnoff [hwy. 15] (LACM 7098); 16 km. NNW Los Mochis (* KU 37592); 7.3 km. SW Matatán, 155 m. (* KU 78931); 5 mi. N Mazatlán (CSCLB 556); 6.5 mi. N Mazatlán (UAZ 16311); 12.6 mi. N Mazatlán (JFC 62:143); 18.6 mi. N Mazatlán (LACM 7100); 21.1 mi. N Mazatlán (UAZ 16312); 21.3 mi. N Mazatlán (LACM 7093); 25.5 mi. N Mazatlán (LACM 7099); 26 mi. N Mazatlán (LACM 7087); 27.3 mi. N Mazatlán (LACM 7091); 48 km. N Mazatlán (* KU 73636); 50 km. N Mazatlán (* KU 73638); 33.6 mi. N Mazatlán (LACM 7101); 66 km. N Mazatlán (* KU 73637); 41.5 mi. N Mazatlán (LACM 7088); 53.3 mi. N Mazatlán (UAZ 16313); 67.3 mi. N Mazatlán (CSCLB 1374); 110 km. N Mazatlán (* KU 73639); Panuco, 625 m. (* KU 83414); 1 mi. W hwy. 15 along Río Piaxtla (CSCLB 2966); 15.9 mi. N Rosario (CSCLB 558); 17.5 mi. N Rosario (CSCLB 1379); 1 km. W Rosario, 30 m. (* KU 29496); San Ignacio, 210 m. (* KU 73635; LACM 7092); Santa Lucía (CSCLB 1378); 4.8 km. NE (by hwy. 40) Santa Lucía, 1315 m. (* KU 78930); 4.1 mi. S Terreros (LACM 7097); 5 mi. S Terreros (LACM 7096); 12 mi. N Tropic of Cancer (CSCLB 555); 8 km. N Villa Unión, 140 m. (* KU 80764); 12 km. N Villa Unión, 120 m. (* KU 80765).

Literature records.—6 mi. N Coyotitán, 300 ft. (Davis and Dixon, 1957a:23); 30.7 mi. N Culiacán (Fouquette and Rossman, 1963:198); El Dorado (Fugler and Dixon, 1961:17); Mazatlán (Boulenger, 1896:54; Van Denburgh, 1898:464); 24 mi. N Mazatlán, 150 ft.; 36 mi. N Mazatlán, 500 ft.; 6 mi. E Mazatlán, 50 ft. (Davis and Dixon, 1957a:23); 2-36 mi. NNW Mazatlán (Duellman, 1957b:240); Presidio (Boulenger, 1896:54; Smith, 1941c:155).

Additional records.—17 mi. S Coyotitán (AMNH 87613); 37.5 mi. N Culiacán (FAS 9079); 8.5 mi. S Culiacán (AMNH 77523); 11 mi. S Culiacán (AMNH 77522); 65.4 mi. S Culiacán (FAS 12411); 95.4 mi. S Culiacán (FAS 12424); 1.8 mi. W hwy. 15 on Culiacáncito road (SU 24052); El Dorado (AMNH 90754-56); Escuinapa (AMNH 4310); 14.5 mi. SE Escuinapa (SU 24062); 5.1 mi. NW Escuinapa (SU 24063); 20.2 mi. N Guamúchil (UF 16786); 4.9 mi. E La Cruz (SU 24057); 0.6 mi. SE La Cruz road on hwy. 15 (SU 24056); 17.4 mi. SE La Cruz road on hwy. 15 (SU 24058); 2.1 mi. NW La Cruz road on hwy. 15 (SU 24055); 49.6 mi. N Los Mochis (SU 24051); 19.9 mi. N Mazatlán (CAS 95809); 27.4 mi. N Mazatlán (UF 12832); 51.5 mi. N Mazatlán (FAS 14461); 53.5 mi. N Mazatlán (FAS 14743); 75 mi. N Mazatlán (FAS 16884); 94.1 mi. N Mazatlán (FAS 14715); 43.9 mi. NW Mazatlán (SU 24059); 23.0 mi. N Rosario (CAS 95822); 14.8 mi. NW Rosario (SU 24061); 12.1 mi. SE San Lorenzo, Río (SU 24053); 15 mi. SE San Lorenzo, Río (SU 24054); 2.2 mi. E hwy. 15 (Villa Unión) on hwy. 40 (SU 24060).

Trimorphodon tau Cope

Trimorphodon tau Cope, Proc. Amer. Philos. Soc., 11:151, 1869 (type locality, Quiotepec, Oaxaca according to Smith, Proc. U. S. Nat. Mus., 91:166, 1941, not "Tehuantepec").

Remarks.—Eight males have 217-229 (222.3) ventrals (excluding LACM 9510); 78-84 (81.0) subcaudals; 16-21 (18.4) dark body blotches; 9-12 (9.6) tail blotches. A single female (CSCLB 553) has 227 ventrals, 66 subcaudals, 19 dark body blotches, and 8 caudal blotches. All specimens of this group from Sinaloa, including the

two specimens reported as *T. latifascia* by Fouquette and Rossman (1963:199), are tentatively assigned to *T. tau*, pending completion of a study of the *tau* group of *Trimorphodon* by Norman J. Scott and the second author. All specimens were collected on the highway at night.

Distribution in Sinaloa.—Foothills in north. See Fig. 87.

Specimens examined.—16 km. NNE Choix, 520 m. (° KU 68754); 22.1 mi. N Culiacán (° CSCLB 553); near Terreros (° LACM 7112, 9510); 2.5 mi. N Terreros (° LACM 7108); 5 mi. N Terreros (° LACM 7109); 7 mi. N Terreros (° LACM 7111); 10 mi. N Terreros (° LACM 7110); 10.2 mi. S Terreros (° LACM 7113).

Literature records.—8.3 mi. N Guacamil [Guamúchil]; 1.6 mi. S Guacamil [Guamúchil] (Fouquette and Rossman, 1963:100).

Additional records.—15.5 mi. N Culiacán (FAS 16995); 29.9 mi. N Culiacán (FAS 16996); 4 mi. NNE El Fuerte (FMNH 71531); 8 mi. NNE El Fuerte (FMNH 71532-33).

Tropidodipsas annulifera Boulenger

Tropidodipsas annulifera Boulenger, Catalogue of the Snakes in the British Museum (Natural History), 2:297, 1894 (based on a specimen of unknown provenance).

Remarks.—One female and two males have smooth dorsal scales in 15 rows without apical pits; 146, 149, 152 ventrals; 42, 44, 41 subcaudals; 6-6 supralabials; 7-7, 7-7, 6-7 infralabials; 1-1, 0-0, 0-0 preoculars; 2-2 postoculars; 1 + 2/1 + 2 temporals; anal entire (only KU 75621); nasal divided; loreal and supralabials 3 and 4 enter the eye; mental separated from chin shields; pupil vertically elliptical. The dorsal coloration is black with eight and 12 lateral white spots or rings (about two scales wide) anterior to the vent.

Most specimens were collected at night in July, during and immediately after a hard rain, probably the first hard rain of the season. One specimen (KU 75621) was found above ground in daylight on July 15, 1963.

Greer (1965b:237) reported *T. malacodryas* from the lowlands north of Culiacán. Scott (1967:281) referred *T. malacodryas* Shannon and Humphrey and four of the specimens reported as *T. occidentalis* (UCLA 14640-43) by Campbell and Simmons (1962:198) to *T. annulifera*.

Distribution in Sinaloa.—Occurs below 1200 meters in the lowland thorn woodland and tropical deciduous forest in the southern two-thirds of the state. See Fig. 87.

Specimens examined.—7 mi. S Escuinapa (LACM 7115); 16.2 mi. N Espinal (° UCLA 14643); 10.5 mi. N Mazatlán (CSCLB 565); 13.7 mi. N Mazatlán (° UCLA 14642); 19.5 mi. N Mazatlán (CSCLB 566); Santa Lucía, 1100 m. (° KU 75621).

Literature records.—36.7 mi. NW Culiacán (Greer, 1965b:237); 13 mi. S Escuinapa (Scott, 1967: 285); 16.2 mi. N Espinal (Campbell and Simmons, 1962:198); about 10 mi. N Mazatlán; 10.5 mi. N Mazatlán (Scott, 1967:285); 13.7 mi. N Mazatlán (Campbell and Simmons, 1962:198); 19.5 mi. N Mazatlán (Scott, 1967:285).

Tropidodipsas philippii (Jan)

Leptognathus philippii Jan, Elenco sistematico degli Ofidi . . . , p. 101, 1863 (type locality, Mazatlán, Sinaloa).

Tropidodipsas philippi: Boulenger, Catalogue of the Snakes in the British Museum (Natural History), 2:295, 1894.

Remarks.—One male has 193 ventrals; 87 subcaudals; 7-7 supralabials; 8-8 infralabials; 15 dorsal scale rows at midbody and 18 black bands on the body and tail. The male reported by Greer (1965b:237) has fewer ventrals (188), subcaudals (81), and white rings (17).

Tropidodipsas freiae was described from a single specimen by Shannon and Humphrey (1959b:220) and placed in the synonymy of *T. philippii* by Scott (1967:284). Nearly all known specimens were collected at night during or after a light rain.

Distribution in Sinaloa.—Known only from the southern lowlands of the state. See Fig. 87.

Specimens examined.—Between Escuinapa and Palmillas (LACM 7117); 31.6 mi. N Mazatlán (LACM 7119); 58 km. N Mazatlán (* KU 73640); 53 mi. N Mazatlán (LACM 7118); Teacapán (LACM 7116).

Literature records.—3.5 mi. NW Elota (Greer, 1965b:237); 63.5 mi. N Mazatlán (Shannon and Humphrey, 1959b:220).

Additional record.—57 mi. NW Mazatlán (TMM 36932).

Family Elapidae

Micruroides euryxanthus neglectus Roze

Micruroides euryxanthus neglectus Roze, Amer. Mus. Novitates, 2287:4, April 13, 1967 (type locality, sixteen and three-tenths miles north-northwest of Mazatlán, Sinaloa).

Remarks.—Duellman (1957b:240) reported an adult male of *M. euryxanthus* from the vicinity of Mazatlán that has fewer ventrals (210) and more dorsal red scales (113) than those reported in the original description of *M. e. australis* Zweifel and Norris. Also, none of the white rings are more than one scale wide, whereas all of the white rings of the holotype of *australis* (Zweifel and Norris, 1955: plate 1, lower left) appear to be more than one scale wide. Roze (1967:4) used the Sinaloan specimen (UMMZ 114637) as the holotype of *M. euryxanthus neglectus*. Joseph F. Copp kindly supplied data on a second specimen (JFC 62:56), a paratype of *neg-*

lectus (Roze, 1967:4): adult male; ventrals 208; subcaudals 25; dorsal scales 17-15-?; supralabials 7; infralabials 7; preocular 1; postoculars 2; temporals 1 + 2. The snake has 12 red and 12 black body rings; no black markings in the red rings; 107 red scales along the midline; two black and three white tail rings including the tip. This specimen is similar to the holotype in having fewer ventrals than *M. e. australis*, but is more like *australis* in the number of red scales along the midline. The holotype is the southernmost known specimen of the genus *Micruroides*.

Distribution in Sinaloa.—Known only from near Mazatlán, but probably occurs in the northern lowlands. See Fig. 88.

Specimen examined.—20 mi. N Mazatlán (JFC 62:56).

Literature record.—Type locality (Duellman, 1957b:240, *M. e. australis*).

Micrurus distans distans (Kennicott)

Elaps distans Kennicott, Proc. Acad. Nat. Sci. Philadelphia, 12:338, 1860 (type locality, Batosegatchie, Chihuahua).

Micrurus distans distans: Zweifel, Amer. Mus. Novitates, 1954:7, June 26, 1959.

Remarks.—Zweifel (1959c:7) commented on the nomenclatural history of this species. According to Zweifel, *M. d. distans* can be identified by the presence of "immaculate scales of the red rings, presence of pale coloration on the anterior supralabials and (usually) snout, and a broad pale head ring with its rear margin behind the posterior tips of the parietal scales."

A male and two females have the following characters, respectively: ventrals, 213, 235, 222; subcaudals, 51, 44, ?; black tail rings, 6, 5, ?. All specimens have 7-7 supralabials; 7-7 infralabials; 1-1 preoculars; 2-2 postoculars; 1 + 1/1 + 1 temporals; and 14 black body rings. On all specimens some of the black body rings are constricted laterally, the anterior supralabials are pale, the pale head band includes the tips of the parietals, and the scales of the red rings lack black tips.

Specimens were collected at night on several occasions following light rains, at air temperatures of 24.2° to 26.3°C, indicating the species is active at lower temperatures than most other snakes from the state.

Distribution in Sinaloa.—Throughout the lowlands. See Fig. 88.

Specimens examined.—9.1 mi. NE Concordia (LACM 7186); 6.5 km. SW Concordia (° KU 73641); El Salado, 90 m. (° KU 95971); La Cruz turnoff, hwy. 15 (LACM 7189); 2.5 mi. E La Cruz (LACM 7187); 9 mi. E La Cruz (LACM 7188); 11.6 mi. N Mazatlán (LACM 7190); Rosario, 150 m. (° KU 73642).

Literature record.—12 mi. SE Los Mochis (Bogert and Oliver, 1945:407).
Additional records.—9.9 mi. N Mazatlán (FAS 14479); Sinaloa [state?] (AMNH 3928-31, 62264).

Family Hydrophiidae

Pelamis platurus (Linnaeus)

Anguis platura Linnaeus, Syst. Nat., 12th ed. p. 391, 1766 (based on a specimen from Pine Island, Pacific Ocean).

Pelamis platurus: Gray, Ann. Philos., p. 15, 1825.

Remarks.—Two specimens are black above and yellow below, and the two colors are sharply defined. This is pattern type one according to M. Smith (1926:118). One specimen (KU 63430) has lateral black spots posteriorly and represents pattern type four.

Two specimens (KU 63430, 63741) were found on the beach on February 15 and March 1, 1961, respectively. Other individuals were taken in October and June.

Distribution in Sinaloa.—This sea-snake is known from the ocean adjacent to southern and extreme northern Sinaloa and from an estuary near Teacapán. See Fig. 81.

Specimens examined.—Isla Lechuguilla "near Río del Fuerte" (RSF 473); Mazatlán (* KU 63430; LACM 7231); 1 mi. N Mazatlán (* KU 63741); Teacapán (LACM 7232).

Literature records.—Mazatlán (Smith, 1943a:458); 15 mi. offshore between Mazatlán, Sinaloa and San Blas, Nayarit (Burt and Burt, 1932:572).

Additional record.—Sinaloa? (USNM 65833).

Family Viperidae

Agkistrodon bilineatus bilineatus (Günther)

Ancistrodon bilineatus Günther, Ann. Mag. Nat. Hist., ser. 3, 12:364, 1863 (type locality, Pacific Coast of Guatemala).

Agkistrodon bilineatus bilineatus: Burger and Robertson, Univ. Kansas Sci. Bull., 34:213, October 1, 1951.

Remarks.—Two males have 133, 131 ventrals; 24, 24 single and 42, 39 divided subcaudals; 25-23-20, 24-23-19 dorsal scale rows; 8-8, 8-8 supralabials; 11-11, 11-11 infralabials; 2-2, 2-2 preoculars; 2-2, 2-2 postoculars; 2-2, 2-2 suboculars; and 4 + 4/4 + 4, 3 + 5/3 + 5 temporals. The lower white line on the side of the head is bordered below by a dark line posterior to the second supralabials (see Burger and Robertson, 1951:214, diagnosis) and the body and tail blotches are indistinguishable. Two specimens of unknown sex (KU 73643-44) have 133, 131 ventrals, and 23 scale rows at mid-body.

Several individuals were collected at night on the road in areas

of heavy forest and in regions cleared for agriculture. One was found alive near San Ignacio about 60 meters from a stream. Although uncommon, this snake is known and feared throughout the coastal lowlands.

Distribution in Sinaloa.—Coastal lowlands south of Culiacán. Specimens from Sonora (Bogert and Oliver, 1945:393) suggest the species inhabits the foothills of northern Sinaloa. See Fig. 89.

Specimens examined.—49 mi. S Culiacán (LACM 7193); 7.5 mi. N Mazatlán (LACM 7192); 1 mi. S Rancho Huanacastle (LACM 7191); Rosario, 150 m. (° KU 73644); San Ignacio, 210 m. (° KU 73643).

Literature records.—Escuinapa; Mazatlán (Gloyd, personal communication); Mazatlán (Bogert and Oliver, 1945:393); Presidio (Boulenger, 1896:522).

Additional record.—Escuinapa (AMNH 4002-05).

Crotalus atrox Baird and Girard

Crotalus atrox Baird and Girard, Cat. North Amer. Rept., part 1, p. 5, 1853 (type locality, Indianola, Calhoun county, Texas).

Remarks.—According to Klauber (1952:102) there were no valid records of *C. atrox* from Sinaloa. Dixon, Sabbath, and Worthington (1962:98) reported the sympatric occurrence of *atrox* and *C. basiliscus* in Sinaloa.

Two males and two females have the following characters: ventrals, 168, 172, 173, 178; subcaudals, 25, 26, 20, 19; dorsal scale rows, 25-25-23, 27-25-22, 23-24-23, 27-25-22; supralabials, 15-14, ♀-15, 15-14, 14-14 (excluding left side of KU 67738); infralabials, 18-17, ♀-16, 16-16, 16-15 (excluding left side of KU 67738); preoculars or postoculars, 2-2 in each specimen; suboculars, 3-4, 4-4, 2-3, 4-4; width of black tail rings (in scales), 3.5, 3.0, 3.0, 2.0; and width of white tail rings (in scales), 3.5, 4.0, 3.0, 3.0.

Distribution in Sinaloa. Known only from the northern lowlands. See Fig. 89.

Specimens examined.—El Carrizo, 12 m. (° KU 83418); 5 km. NW El Carrizo, 12 m. (° KU 83417); 48 km. N Los Mochis, 15 m. (° KU 67738); Santa María Island, 3 m. (° KU 69938).

Additional records.—15.5 mi. N Fuerte, Río (SU 24092); 33.2 mi. N Los Mochis (FAS 14678).

Crotalus basiliscus basiliscus (Cope)

Caudisona basilisca Cope, Proc. Acad. Nat. Sci. Philadelphia, 16:166 (type locality, Colima).

Crotalus basiliscus basiliscus: Gloyd, Nat. Hist. Misc., 17:1, April 23, 1948.

Remarks.—Nine males, seven females, and four specimens of unknown sex have the following characters, respectively: ventrals, 179-188 (183.9), 182-198 (189.3), 187, 187, 184, 185; subcaudals,

27-31 (28.8), 22-24 (23.1), 28, 28, 30, 22; dorsal scale rows at neck, 25-29 (26.8), 26-29 (27.4), 28, 29, 26, 28; dorsal scale rows at mid-body, 25-29 (26.3), 25-27 (26.4), 27, 27, 25, 27; dorsal scale rows at vent, 21-23 (21.8), 21-23 (21.7), 22, 21, 21, 23; supralabials, 13-17 (14.9), 14-17 (15.3), 14/15, 15/15, 13/16, 16/15; infralabials, 15-19 (16.1), 14-17 (15.4) (excluding left side of KU 67740), 17/17, 16/17, 16/17, 17/18; dorsal body blotches, 32-35 (33.4) (excluding KU 80770, 29513, 83419, and 78966), 31-38 (33.4) (excluding KU 40364 and 83420), 33, 33, 33, ?; tail rings 8-10 (8.9) (excluding KU 29513), 7-9 (7.7) (excluding KU 40364); 9, 9 (excluding KU 80767, 80769). The proximal rattle is gray in all except three which have damaged tails (KU 67739-40, 80767). The characters of these specimens agree with characters given by Klauber (1952:79-84) for the subspecies and with those given by Fugler and Dixon (1961:21) for *basiliscus* in central Sinaloa.

Crotalus basiliscus is one of the more common snakes in the state, and has been collected in both the wet and the dry seasons. On July 25, a litter of 20 baby *C. basiliscus* was located on the southwestern slope above a river near Escuinapa. The snakes were found in a small clearing in dense forest sunning themselves near a burrow. These specimens were the first young encountered during the field work in that season, and because of their concentration near the burrow were probably recently born. Through late September, baby rattlesnakes were frequently collected at night on the highway.

Distribution in Sinaloa.—Throughout state at elevations from near sea-level to about 2000 meters. See Fig. 90.

Specimens examined.—21 km. ESE Badiraguato, 240 m. (° KU 83419-20); 16 km. NE Choix, 520 m. (° KU 73645); 7.9 mi. N Coyotitán (JFC 65:146); 1.9 mi. S Coyotitán (JFC 65:147); 3 mi. S Coyotitán (JFC 65:148); 19 km. N Culiacán, 120 m. (° KU 40364); 50 km. N Culiacán (° KU 73648); 15 mi. S Culiacán (JFC 62:59); 17 mi. S Culiacán (JFC 62:58); 19 mi. S Culiacán (CSCLB 1204); 21.3 mi. S Culiacán (LACM 7197); 27 mi. S Culiacán (JFC 62:57); El Carrizo (LACM 7223); 2 mi. N El Salado (CSCLB 1205); 5 km. NW Escuinapa, 150 m. (° KU 73647); 5.4 mi. NW Escuinapa (LACM 7202-18); 2.7 mi. N Guamúchil (CSCLB 1973); 7.4 mi. W Guamúchil (CSCLB 1209); N Guasave (LACM 8660); Labrados (CAS 64974); 10.4 mi. N La Cruz turnoff [hwy. 15] (LACM 7199); 2 mi. NE La Cruz turnoff [hwy. 15] (LACM 7222); 58 mi. S Los Mochis turnoff [hwy. 15] (CSCLB 1216); 48 km. N Los Mochis, 15 m. (° KU 67739); 56 km. N Los Mochis (° KU 67740); 3 mi. N Mazatlán (UAZ 16314); 4.4 mi. N Mazatlán (UAZ 16315); 5.5 mi. N Mazatlán (UAZ 16316); 10.9 mi. N Mazatlán (UAZ 16317); 15.8 mi. N Mazatlán (UAZ 16318); 17.5 mi. N Mazatlán (JMS osteo. coll.); Rosario 150 m. (° KU 73646; LACM 7219); 10.4 mi. N Rosario (CSCLB 1206); 22.2 mi. N Rosario (CSCLB 1207); 2.7 mi. S Rosario (CSCLB 1208); San Ignacio (LACM 7200-01); 6 km. NE San Lorenzo, 150 m. (° KU 83421); Santa Cruz, 120 m. (° KU 83422); Santa Lucía 1135 m. (° KU 75637-38, 78965; CSCLB 1218); 5 km. NE Santa Lucía 1520 m. (° KU 80767); 19.2 km. NE Santa Lucía, 1940 m. (° KU 78966); Teacapán (LACM 7224); Terreros (CSCLB 1217); 28 mi.

N Terreros (LACM 7220); 115 mi. N Terreros (LACM 7221); 3 mi. S Terreros (JMS osteo. coll.); 16 mi. S Terreros (LACM 7198); 25.5 mi. S Terreros (JMS osteo. coll.); 4 mi. S Tropic of Cancer (JFC 63:163); 13 km. NNE Vaca, 400 m. (* KU 80770); 8 km. N Villa Unión, 140 m. (* KU 80768-69); 25.5 mi. NE Villa Unión [hwy. 40] (JMS osteo. coll.); 3 km. W Villa Unión (* KU 29513).

Literature records.—6 km. W Costa Rica (Smith and Van Gelder, 1955:145); 2 mi. S Coyotitán, 300 ft.; 12 mi. S Culiacán, 300 ft. (Davis and Dixon, 1957a:25); El Dorado (Fugler and Dixon, 1961:21); Labrados (Gloyd, 1940:145); 30 mi. N Los Mochis, 100 ft.; 16 mi. N Mazatlán, 200 ft. (Davis and Dixon, 1957a:25); Presidio (Günther, 1895:195); Retes (Gloyd, 1940:145).

Additional records.—2 mi. N Agua Nuevo (SDSNH 41204); Costa Rica (UIMNH 34923); Culiacán (SDSNH 3034); 16-20 mi. N Culiacán (FAS 11370, 11372); 46.6 mi. N Culiacán (FAS 17003); 57.9 mi. N Culiacán (FAS 14407); El Dorado (AMNH 90757-59); 8 mi. NNE El Fuerte (FMNH 95982; SDSNH 42427); 2.4 mi. SE Elota, Rio (SU 24094); 4.4 mi. S Espinal (FAS 17001); 1.2 mi. E La Cruz (SU 24093); 35 mi. S Los Mochis (USNM 151780); 5 mi. N Mazatlán (AMNH 75892); 14 mi. N Mazatlán (MCZ 61431); 28.4 mi. N Mazatlán (FAS 12430); 32.5 mi. N Mazatlán (UIMNH 39184); 14.4 mi. NNW Mazatlán (UMMZ 114666); 18 mi. NNW Mazatlán, 200 ft. (UMMZ 114593); 19 mi. NNW Mazatlán (UMMZ 114667); Palos Blancos (SDSNH 3133-35); 12.1 mi. N Pericos (FAS 10408); Retes (SDSNH 3061); 9.8 mi. N Rosario (CAS 95765); 5.9 mi. NW Rosario (SU 24095); 2.8 mi. NW Villa Unión (AMNH 94809).

Crotalus lepidus (Kennicott)

Caudisona lepida Kennicott, Proc. Acad. Nat. Sci. Philadelphia, 13:206, 1861 (based on specimens from Presidio del Norte and Eagle Pass, Texas).

Crotalus lepidus: (part), Cope, Proc. Acad. Nat. Sci. Philadelphia, 35:13, 1883.

Remarks.—Two juveniles of unknown sex have 169, 159 ventrals; 23, 28 subcaudals; 26-23-21, 23-23-17 dorsal scale rows; 12-12, 12-12 supralabials; 11-11, 11-10 infralabials; 33, 35 dorsal body blotches. One specimen has the upper preocular split in a manner typical for the species, but the other specimen (KU 79232) has undivided upper preoculars that curve over the canthus rostralis. Both specimens have a pair of black occipital spots and a distinct black stripe from the eye to the angle of the jaw.

Although these specimens are from the western edge of the range of *C. l. klauberi* they possess high numbers of dorsal blotches that are characteristic of *C. l. morulus* from Tamaulipas; they also have postocular stripes and separated occipital blotches that are characteristic of *C. l. lepidus* from the eastern part of the Mexican plateau. Klauber (1956:37, footnote 16) has commented that *C. lepidus* from this general area require further study. For these reasons we use no subspecific designation for the Sinaloan specimens.

Distribution in Sinaloa.—Known only from the southern highlands. See Fig. 88.

Specimens examined.—5 km. SE Palmito, Durango (*in Sinaloa*), 1880 m. (* KU 79232); 19.2 km. NE Santa Lucía, 1940 m. (* KU 78973).

Literature record.—7 and 9 mi. (by road) NE El Batel (Zweifel, 1954:149).

Crotalus molossus molossus Baird and Girard

Crotalus molossus Baird and Girard, Catalogue of North American reptiles, p. 10, 1853 (type locality, Fort Webster, Santa Rita del Cobre, New Mexico).

Crotalus molossus molossus: Gloyd, Occ. Pap. Mus. Zool. Univ. Michigan, 325:2, January 28, 1936.

Remarks.—Klauber (1952:87) reported that specimens of *Crotalus basiliscus* and *C. molossus* from southern Sonora show intergradation in several characters, and that no actual overlap in the ranges of the two species had been demonstrated.

A female, collected near El Fuerte, has 181 ventrals, 20 subcaudals, 25-25-22 dorsal scale rows, 17-16 supralabials, 16-16 infra-labials, 32 dorsal body blotches, and six tail rings. The dorsal blotches are open laterally (see Klauber, 1936:259, fig. 78), and the tail is nearly solid black. The tail length is 5.3 per cent of the total length. Our specimen shares certain characters with *C. basiliscus*, but because of the low number of ventrals and subcaudals, the distinctive dorsal pattern, the nearly solid black tail, and a knowledge of *C. basiliscus* from the same general area we assign the specimen to *C. molossus*.

Specimens of *C. basiliscus* have been taken within about 50 kilometers southwest (near sea-level) and about 50 kilometers northeast (about 520 meters elevation) of the locality of this specimen of *molossus* (elevation about 150 meters). It is probable that the two species are sympatric in northern Sinaloa. We leave the final clarification of the relationships between *C. basiliscus* and *C. molossus* to future workers.

Distribution in Sinaloa.—Known only from the northern foothills. See Fig. 89.

Specimen examined.—6 km. NE El Fuerte, 150 m. (* KU 78964).

Crotalus stejnegeri Dunn

Crotalus stejnegeri Dunn, Proc. Biol. Soc. Washington, 32:214, 1919 (type locality, Plomosas, Sinaloa).

Remarks.—One male of this rare species has 175 ventrals, 42 subcaudals, 28-27-22 dorsal scale rows, 14-14 supralabials, 14-16 infra-labials, 2-2 preoculars, 4-3 postoculars, 3-3 suboculars, 38 dorsal body blotches, about 12 tail bands (indistinct on posterior part of tail); the tail length is 13.9 per cent of body length. The color pattern

and scale characteristics agree with the description by Klauber (1952:107-09).

Distribution in Sinaloa.—Southern highlands in tropical deciduous forest. See Fig. 88.

Specimen examined.—2.2 km. NE Santa Lucía, 1155 m. (° KU 78972).

Literature records.—Plomosas (Gloyd, 1940:232; Smith, 1943a:414).

Order CROCODYLIA

Family CROCODYLIDAE

Crocodylus acutus Cuvier

Crocodylus acutus Cuvier, Ann. Mus., 10:55, pls. I, II, 1807 (based on a specimen from Santo Domingo, West Indies).

Remarks.—The crocodile occurs in the lowland drainages, coastal lagoons, and estuaries of southern Sinaloa. Residents of Culiacán have reported “caimanes” from near Altata, but verification of these accounts must await the securing of specimens. Recently hatched young were reported from near Teacapán on August 10 (Scott, 1962:84). A large specimen from near Teacapán measured 3 meters.

Distribution in Sinaloa.—Known only from extreme south. See Fig. 91.

Specimens examined.—Palmillas (LACM 6558, 6560); 4 mi. SE Teacapán (LACM 6559).

Literature records.—Mazatlán (Boulenger, 1889:281; Cope, 1900:175; Zweifel, 1959a:3); Presidio (Boulenger, 1889:281).

Additional records.—Mazatlán (AMNH 15162-63; USNM 72342).

SPECIES OF QUESTIONABLE OCCURRENCE

Records of several species that have been reported from Sinaloa are doubtful for various reasons. Five such species are discussed below.

Rana montezumae Baird

Rana montezumae Baird, Proc. Acad. Nat. Sci. Philadelphia, 7:61, 1854 (type locality, City of México, Distrito Federal).

There is a single specimen in the collections of the Museum of Comparative Zoology (MCZ 8629) recorded from Mazatlán. Dunn (1922:222) reported this specimen as *Rana pustulosa*. Oliver (1937:7-8) re-examined the frog and assigned it to *Rana montezumae*. We have examined the specimen and agree with Oliver that the frog definitely is not *R. pustulosa*. The presence of paired lateral vocal sacs and dorsolateral glandular folds indicate the specimen is a member of the *pipiens* group. Certain characteristics suggest the frog might represent *Rana megapoda*, but because of its poor condition we follow Oliver and refer the specimen to *Rana montezumae*. Because both *Rana montezumae* and *Rana megapoda* are restricted to the Mexican plateau and because Mazatlán represents a habitat distinct from those known for the species, we do not include *Rana montezumae* in the fauna of the state.

Kinosternon hirtipes Wagler

Cinosternon hirtipes Wagler, *Naturl. Syst. der Amphibien*, p. 137, pl. 5, figs. 29, 30, 1830 (based on a specimen from México).

In 1885-1902, Günther (page 15, plates 12-15) reported specimens of *Kinosternon* from Mazatlán, Sinaloa, and from the Tres Mariás Islands as *K. hirtipes*. Boulenger (1889:42) referred the same specimens to *K. integrum*. Subsequent authors (Taylor, 1938:529; Smith and Taylor, 1950b:25) reported *K. hirtipes* from Sinaloa. Zweifel (1960:94) referred the Tres Mariás *Kinosternon* to the species *integrum*. Our work in Sinaloa complements Zweifel's work on the fauna of the Tres Mariás Islands and we agree that all specimens of *Kinosternon* from Sinaloa are typical *integrum*. On this basis we reject the records and reports of *K. hirtipes* from Sinaloa, and suggest that these records are based on misidentified specimens of *K. integrum*. Additional information pertaining to the differences between *K. integrum* and *K. hirtipes* are presented in the account for *K. integrum*. It should be pointed out that the wholesale restrictions of type localities, as exemplified by the restriction of the type locality for *K. hirtipes* to Mazatlán by Smith and Taylor (1950a:343) have no validity and such restrictions should be ignored. This is especially relevant in the above instance where the type locality is restricted to a place where the species apparently does not occur.

Anolis nebuloides Bocourt

Anolis nebuloides Bocourt, *Mission scientifique au Mexique . . .*, *Etudes sur les reptiles*, livr. 2, pp. 74-75, pl. 13, fig. 10, 1873 (type locality, Putla, Oaxaca).

An examination of specimens of *Anolis* from Sinaloa has convinced us that the reports of *Anolis nebuloides* are based on misidentified specimens of *Anolis nebulosus*. In addition, all specimens examined had, to the best of our knowledge, an orange dewlap. *Anolis nebuloides* has a pink dewlap.

Gerrhonotus imbricatus ciliaris Smith

Gerrhonotus levicollis ciliaris Smith, *Proc. U. S. Nat. Mus.*, 92:365, 1942 (type locality, Sierra Gaudelupe, Coahuila).

Gerrhonotus imbricatus ciliaris: Stebbins, *Amer. Mus. Novitates*, 1883:23, March 21, 1958.

There is a specimen of *Gerrhonotus imbricatus ciliaris* in the American Museum of Natural History (AMNH 585) collected by Paul R. Ruthling at "Escuinapa." The lizard was re-examined and the identity confirmed as reported by Tihen (1949:245) and Smith and Taylor (1950b:202). According to Tihen (1949:252), Stebbins (1958:18, fig. 4), and Duellman (1961:88) *Gerrhonotus imbricatus* is found at relatively high altitudes usually in pine forests. Escuinapa is located on the coastal plain at less than 50 meters elevation in tropical dry or deciduous forest. Because of the obvious differences in habitat between Escuinapa and other localities at which *Gerrhonotus imbricatus* has been collected, and because of the provenance of certain other specimens from the Ruthling collection, we do not consider Escuinapa, Sinaloa, to be the

likely collecting site for this specimen. For this reason we do not consider *Gerrhonotus imbricatus ciliaris* as a member of the Sinaloan herpetofauna. Future collecting in the pine-oak forest to the east of Escuinapa may reveal its presence in the state.

***Thamnophis melanogaster melanogaster* (Peters)**

Tropidonotus melanogaster Peters, Monatsb. Akad. Wiss. Berlin, pp. 389-390, 1864 (based on two specimens from México).

Thamnophis melanogaster melanogaster: Smith, Zoologica, 27:116, 1942.

Two specimens (AMNH 19526-27) of this snake were purportedly collected by Paul R. Ruthling at Mazatlán. The amount of black on the belly of these specimens, a characteristic of the central Mexican plateau race of *T. melanogaster*, necessitates a rejection of Mazatlán as the collecting site. Roger Conant examined the specimens and arrived at the same conclusion concerning the probable origin of these specimens.

SUMMARY

The herpetofauna of Sinaloa consists of 137 taxa, including 131 species. Reported from Sinaloa for the first time are 21 species or subspecies as follows: *Eleutherodactylus hobartsmithi*, *Syrrophus modestus*, *Rana pustulosa*, *Hyla smaragdina*, *Chrysemys scripta hiltoni*, *Hemidactylus frenatus*, *Phyllodactylus h. homolepidurus*, *Sceloporus m. magister*, *Cnemidophorus tigris*, *Gerrhonotus kingii ferrugineus*, *G. l. liocephalus*, *Heloderma s. suspectum*, *Coniophanes l. lateritius*, *Dryadophis melanolomus stuarti*, *Geophis dugesii*, *Leptodeira septentrionalis polysticta*, *Phyllorhynchus decurtatus*, *Salvadora bairdi*, *Sonora aemula*, *Storeria storerioides*, and *Crotalus m. molossus*.

Based on more extensive systematic studies of several species the following taxonomic changes are proposed. Each synonym is followed by the name recognized in this paper.

Phrynohyas latifasciata Duellman (1956) equals *Phrynohyas venulosa* (Laurenti, 1768)

Sceloporus clarkii uriquensis Tanner and Robison (1959) equals *Sceloporus clarkii boulengeri* Stejneger (1893)

Sceloporus nelsoni barrancorum Tanner and Robinson (1959) equals *Sceloporus nelsoni* Cochran (1923)

Gyalopion quadrangularis desertorum (Taylor, 1936) equals *Gyalopion quadrangularis* (Günther, 1893)

Pseudoficimia frontalis hiltoni Bogert and Oliver (1945) equals *Pseudoficimia frontalis* (Cope, 1864)

Tantilla yaquia bogerti Hartweg (1944) equals *Tantilla yaquia* Smith (1942)

The following polytypic species are not assigned to subspecies in Sinaloa at this time: *Syrrhophus modestus*, *Ctenosaura hemilopha*, *Masticophis bilineatus*, *Phyllorhynchus browni*, *P. decurtatus*, and *Sympholis lippiens*.

Several species are not included in the fauna of Sinaloa even though some have been reported from the state and others are likely to be found there in the future; these are: *Leptodactylus melanonotus*, *Rana montezumae*, *Anolis nebuloides*, *Hysiglena ochrorhyncha*, *Kinosternon hirtipes*, *Gerrhonotus imbricatus ciliaris*, and *Thamnophis melanogaster melanogaster*.

Each species that occurs in the state is discussed in terms of its taxonomic status, habitat, and geographical distribution. In addition, information on life history, ecology, and morphological variation are presented when such facts are known or are pertinent.

No new taxa are described in this paper.

GAZETTEER

The following names of places and geographical features are those to which reference is made in this paper. The spellings are based principally on Gazetteer number 15 for México prepared by the United States Board on Geographic Names and published by the Department of the Interior (1956). Latitude north of the equator is followed by longitude west of Greenwich. There are many places in Sinaloa with identical or similar names. Where several coordinates are given for a single name, the first one listed is the one used in this paper. Numbers in brackets refer to the position of the places on the accompanying map (Fig. 12, p. 224).

- Abuya 24 09 N, 107 04 W (not shown on Fig. 12)
Acaponeta [Nayarit] 22 30 N, 105 22 W [99]
Agua Caliente 23 09 N, 106 06 W; 23 27 N, 106 06 W; 24 03 N, 106 38 W; 24 38 N, 106 46 W; 24 56 N, 107 23 W; 25 58 N, 108 08 W; 26 22 N, 107 49 W; 26 31 N, 108 22 W; 26 49 N, 108 23 W [85]
Aguaje 25 22 N, 108 02 W [32]
Agua Nuevo 24 05 N, 106 50 W; 24 45 N, 107 14 W; 26 42 N, 108 27 W [58]
Aguapepe 25 04 N, 107 39 W; 25 07 N, 107 10 W; 25 27 N, 108 16 W [38]
Ahome 25 55 N, 109 11 W [18]
Altamura, Isla 25 00 N, 108 10 W [42]
Altata 24 38 N, 107 55 W [49]
Bacubirito 25 49 N, 107 55 W [15]
Badiraguato 25 22 N, 107 31 W [33]
Barrón, Río Presidio 23 07 N, 106 17 W [86]
Caitime 25 21 N, 107 56 W [34]
Camino Real 23 52 N, 106 39 W [64]
Cañas, Río (at hwy. 15) 23 32 N, 106 29 W [70]
Carrizalejo 25 42 N, 107 50 W; 24 49 N, 107 19 W [23]
Casa Blanca 26 16 N, 108 48 W [8]
Cerro Prieto Approximately 26 07 N, 109 03 W [9]
Charay 26 01 N, 108 50 W [13]
Chele 23 13 N, 105 53 W [80]
Chivos, Isla 23 11 N, 106 26 W [84]
Choix 26 43 N, 108 17 W [4]
Chupaderos 23 22 N, 105 58 W [77]
Colonia de la Reforma Approximately 25 12 N, 108 17 W [37]
Concepción 22 32 N, 105 28 W [98]
Concordia 23 17 N, 106 04 W [78]
Copala 23 23 N, 105 56 W [75]
Cosalá 24 23 N, 106 41 W [52]
Costa Rica Approximately 24 33 N, 107 23 W [50]
Coyotitán 23 47 N, 106 35 W [66]
Crucero de Piaxtla 23 49 N, 106 36 W [65]
Culiacán 24 48 N, 107 24 W [46]
El Batel 23 27 N, 105 49 W [72]
El Burrion 25 34 N, 108 24 W [28]
El Cajón 26 52 N, 108 20 W; 23 21 N, 106 02 W [1]
El Carrizo 25 58 N, 108 57 W; 26 15 N, 109 03 W; 23 04 N, 105 35 W [16]
El Dorado 24 17 N, 107 21 W; 25 32 N, 108 28 W [53]
El Fuerte 26 25 N, 108 39 W [6]

- El Limón 23 44 N, 106 31 W; 24 16 N, 106 44 W; 24 16 N, 107 04 W; 24 43 N, 107 08 W; 26 06 N, 108 46 W; 26 56 N, 108 28 W [68]
- Elota 23 58 N, 106 42 W [60]
- El Palmito [Durango] (=Palmarito) 23 35 N, 105 49 W; 23 45 N, 106 28 W; 24 36 N, 106 55 W; 25 32 N, 108 16 W; 25 38 N, 107 46 W [69]
- El Quelite (=Quelite) 23 32 N, 106 28 W [70]
- El Salado 23 53 N, 106 49 W [62]
- El Venadillo 23 17 N, 106 24 W (not Kellogg, 1932:138, 188) [79]
- Escuinapa 22 51 N, 105 48 W [91]
- Espinal (=El Espinal) 23 47 N, 106 24 W; approximately 24 04 N, 106 54 W [67]
- Estero la Ballena This is a locality for *Urosaurus ornatus lateralis* (UAZ 9585-87) presumably from the coastal lowlands just north of Ahome (not shown on Fig 91).
- Guacamil This is the northwest edge of Guamúchil according to Howard W. Campbell (personal communication).
- Guamúchil 25 28 N, 108 06 W; 22 35 N, 105 36 W; 22 54 N, 105 45 W; 23 07 N, 105 51 W; 23 55 N, 106 37 W; 24 07 N, 106 45 W; 24 54 N, 108 06 W; 25 14 N, 107 42 W; 25 22 N, 108 22 W; 25 27 N, 108 06 W; 25 58 N, 109 18 W [31]
- Guasave 25 34 N, 108 27 W [26]
- Guayvo Approximately 26 02 N, 109 23 W [11]
- Higuera de Zaragoza 25 59 N, 109 16 W [14]
- Higueras 24 14 N, 107 02 W; 23 04 N, 105 56 W (Higueras); 23 41 N, 106 06 W (Las Higueras); 24 25 N, 107 21 W; 24 15 N, 107 19 W (Higueral); 25 22 N, 108 28 W; 25 23 N, 108 32 W; 25 56 N, 108 59 W [55]
- Ixpalino 23 54 N, 106 38 W [64]
- La Boca 24 12 N, 107 12 W; 24 56 N, 107 25 W [56]
- Labrados 23 24 N, 106 01 W; 23 03 N, 106 07 W [76]
- La Concha 22 45 N, 105 34 W [93]
- La Cruz 23 55 N, 106 54 W; 24 20 N, 107 19 W; 24 40 N, 107 38 W; 25 58 N, 108 54 W [61]
- La Noria 23 30 N, 106 18 W; 22 53 N, 105 54 W [71]
- Las Teposanas 24 03 N, 106 42 W [59]
- Las Trancas 24 43 N, 107 44 W [48]
- Los Mochis 25 45 N, 109 03 W [21]
- Madero (=ejido Francisco Madero) 25 35 N, 108 37 W [27]
- Mármol Approximately 23 30 N, 106 29 W [70]
- Matatán 23 02 N, 105 45 W [88]
- Mazatlán 23 13 N, 106 25 W [82]
- Mocorito 25 29 N, 107 55 W [30]
- Navolato 24 47 N, 107 42 W [47]
- Obispo 24 18 N, 107 06 W; 24 17 N, 107 09 W [54]
- Ohura, Bahía de 25 38 N, 108 58 W [24]
- Palmar 24 56 N, 107 07 W; 23 39 N, 106 02 W; 25 11 N, 107 23 W [45]
- Palmer de Sepulveda (=Palmar de Sepúlveda) 25 43 N, 107 55 W [22]
- Palmillas 22 48 N, 105 36 W; 23 16 N, 106 18 W [92]
- Palmito de la Virgen, Isla 23 00 N, 106 10 W [90]
- Palmito del Verde, Isla 22 39 N, 105 48 W [95]
- Palos Blancos 24 54 N, 107 46 W; 23 41 N, 106 18 W; 25 08 N, 107 56 W; 25 35 N, 108 21 W [44]
- Pánuco 23 25 N, 105 55 W [75]
- Pericos 25 03 N, 107 42 W; 26 06 N, 107 28 W [39]
- Piactla 23 52 N, 106 39 W [64]
- Playa Visnaga Approximately 26 02 N, 109 18 W [12]
- Plomosas 23 04 N, 105 29 W [87]
- Potrerrillos 23 27 N, 105 52 W; 23 02 N, 105 56 W; 25 28 N, 108 19 W [74]
- Presidio 23 14 N, 106 08 W; 23 09 N, 106 13 W [83]

- Quelite 23 32 N, 106 28 W; 25 20 N, 108 14 W [70]
Rancho Huanacastle 22 36 N, 105 36 W [96]
Rancho de los Pocitos 25 02 N, 107 51 W [40]
Rancho Rosalito Approximately 26 53 N, 108 01 W [2]
Retes Locality unconfirmed, but according to Gloyd (1940:145, map 10) it appears to be in the vicinity of 25 02 N, 107 20 W [41]
Rincón de Urías 23 14 N, 106 23 W [82]
Rosario 23 00 N, 105 52 W [89]
San Benito 25 32 N, 107 45 W [29]
San Blas 26 05 N, 108 46 W [10]
San Francisco [Nayarit] 22 44 N, 105 30 W; 25 36 N, 108 16 W; 26 20 N, 108 56 W [94]
San Ignacio 23 55 N, 106 25 W; 25 25 N, 108 54 W (San Ignacio, Isla [100]) [63]
San José del Oro 25 21 N, 107 16 W [35]
San Lorenzo 24 25 N, 107 07 W; 25 41 N, 108 04 W [51]
San Miguel 25 56 N, 109 03 W; 23 02 N, 105 32 W; 25 41 N, 108 06 W; 25 48 N, 108 40 W; 25 59 N, 108 22 W [17]
San Pedro Approximately 26 25 N, 108 30 W [5]
Santa Cruz 25 36 N, 108 26 W; 25 35 N, 107 33 W [28]
Santa Lucía 23 27 N, 105 53 W [74]
Santa Rita 23 28 N, 105 50 W (= Rancho Santa Rita); 23 04 N, 105 31 W; 23 12 N, 106 15 W [72]
San Rosa 24 59 N, 107 20 W; 25 59 N, 108 26 W; 26 31 N, 107 53 W [43]
Sinaloa 25 50 N, 108 14 W [20]
Tazon 24 07 N, 107 06 W [57]
Teacapán 22 33 N, 105 45 W [97]
Tecorito 25 01 N, 107 23 W [41]
Terreros 25 14 N, 107 55 W; 25 12 N, 107 58 W; Approximately 26 23 N, 108 42 W [36]
Topolobampo 25 36 N, 109 03 W [25]
Tropic of Cancer (at hwy. 15) Approximately 23 28 N, 106 28 W [73]
Tule 25 52 N, 108 31 W; 25 28 N, 108 39 W [19]
Vaca 26 48 N, 108 25 W [3]
Venados, Isla 23 14 N, 106 29 W [84]
Villa Unión 23 12 N, 106 14 W [81]
Yecorato 26 22 N, 108 18 W [7]

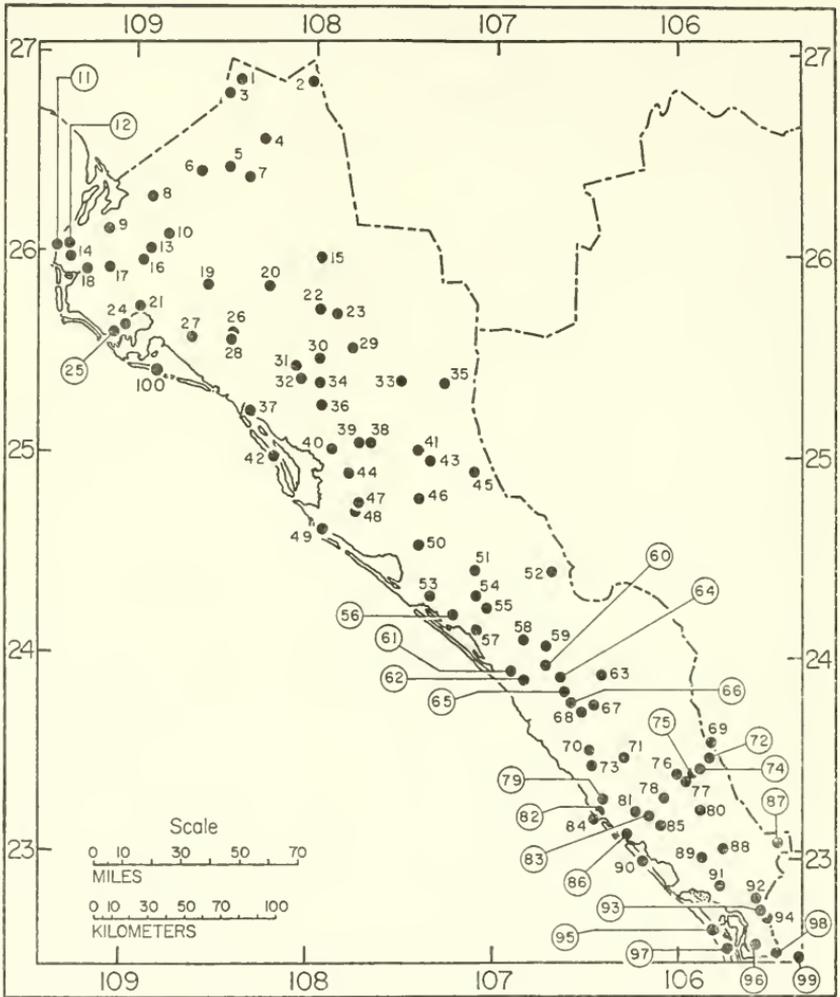
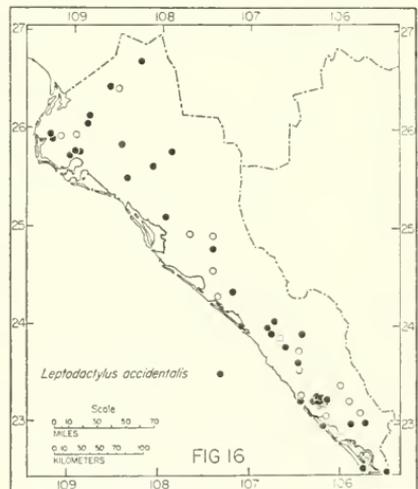
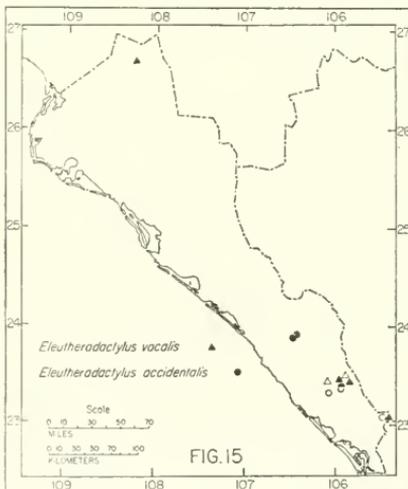
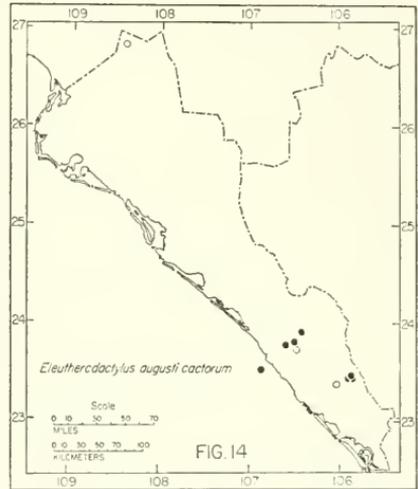
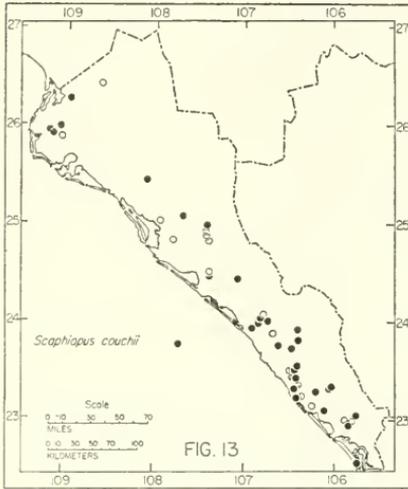


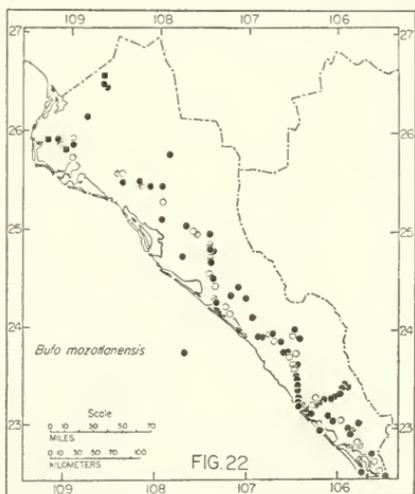
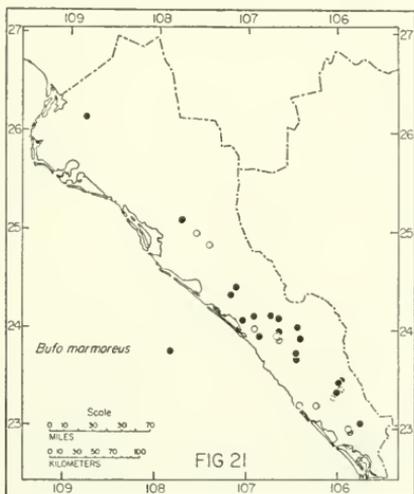
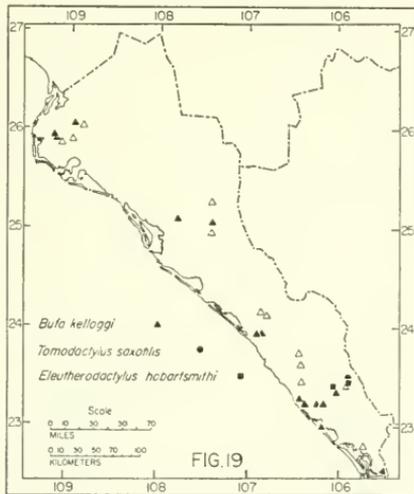
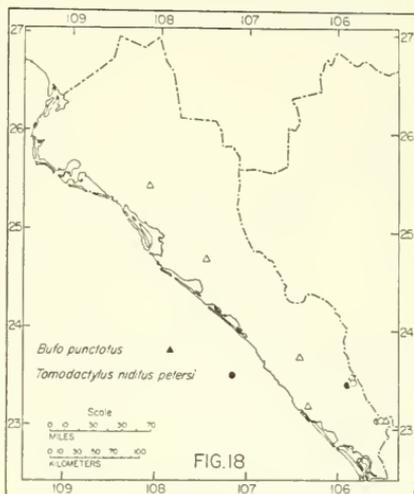
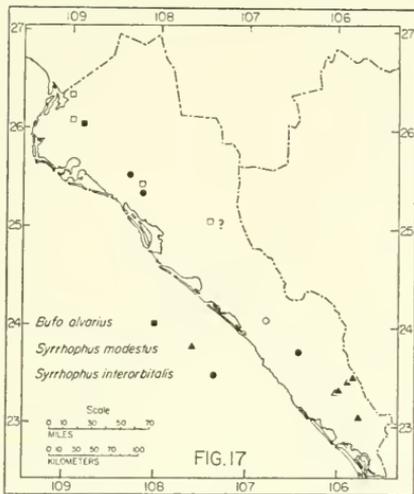
FIG. 12. Map of Sinaloa showing named places and geographic features referred to in this paper. In the numerical sequence north takes precedence over south. Each number represents a single dot, but each dot may represent one or more localities.

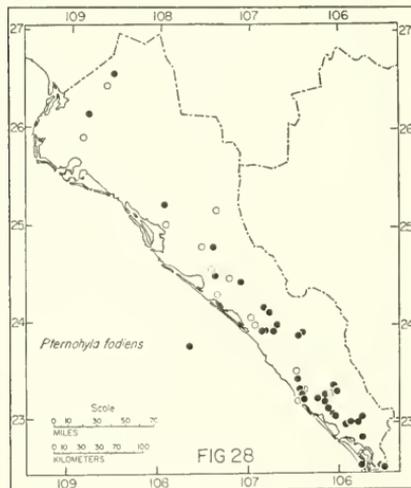
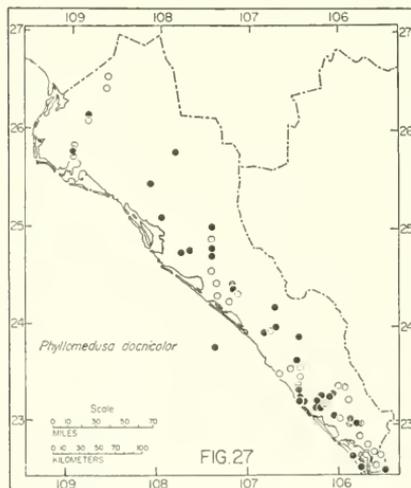
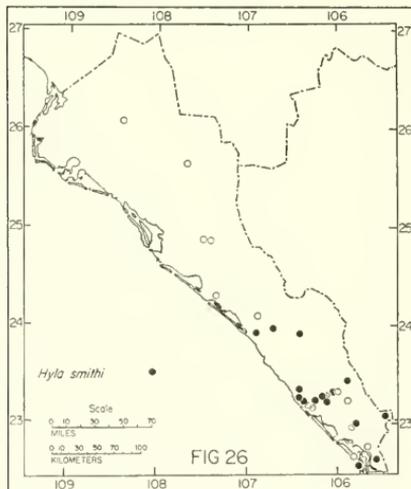
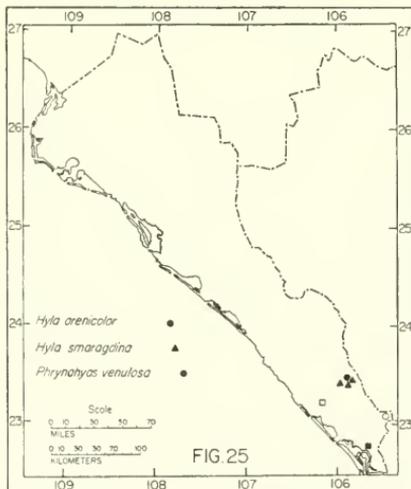
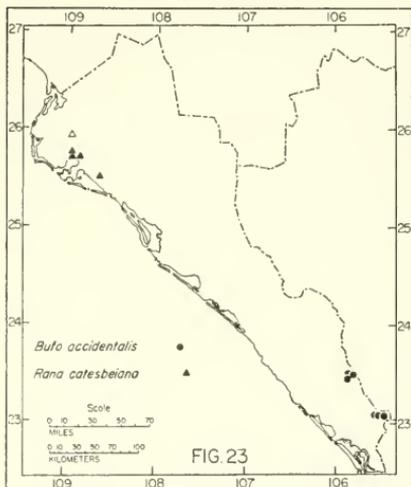
1. El Cajón
2. Rancho Rosalito
3. Vaca
4. Choix
5. San Pedro
6. El Fuerte
7. Yecorato
8. Casa Blanca
9. Cerro Prieto
10. San Blas
11. Guayvo
12. Playa Visnaga
13. Charay
14. Higuera de Zaragoza
15. Bacubirito
16. El Carrizo
17. San Miguel
18. Ahome
19. Tule
20. Sinaloa
21. Los Mochis
22. Palmer de Sepulveda
23. Carrizalejo
24. Ohura, Bahía de
25. Topolobampo
26. Guasave
27. Madero
28. El Burrion
Santa Cruz
29. San Benito
30. Mocorito
31. Guamúchil
32. Aguaje
33. Badiraguato
34. Caitime
35. San José de Oro
36. Terreros
37. Colonia de la Reforma
38. Aguapepe
39. Pericos
40. Rancho de los Pocitos
41. Retes
Tecorito
42. Altamura, Isla
43. Santa Rosa
44. Palos Blancos
45. Palmar
46. Culiacán
47. Navolato
48. Las Trancas
49. Altata
50. Costa Rica
51. San Lorenzo
52. Cosalá
53. El Dorado
54. Obispo
55. Higuera
56. La Boca
57. Tazon
58. Agua Nuevo
59. Las Tepepanas
60. Elota
61. La Cruz
62. El Salado
63. San Ignacio
64. Camino Real
Ixpalino
Piactla
65. Crucero de Piactla
66. Coyotitán
67. Espinal
68. El Limón
69. El Palmito [Durango]
70. Cañas, Río
El Quelite
Marmol
Quelite
71. La Noria
72. El Batel
Santa Rita
73. Tropic of Cancer (at hwy. 15)
74. Potrerillos
Santa Lucía
75. Copala
Panuco
76. Labrados
77. Chupaderos
78. Concordia
79. El Venadillo
80. Chele
81. Villa Unión
82. Mazatlán
Rincón de Urías
83. Presidio
84. Chivos, Isla
Venados, Isla
85. Agua Caliente
86. Barrón
87. Plomosas
88. Matatán
89. Rosario
90. Palmito de la Virgen, Isla
91. Escuinapa
92. Palmillas
93. La Concha
94. San Francisquito [Nayarit]
95. Palmito del Verde, Isla
96. Rancho Huanacastle
97. Teacapán
98. Concepción
99. Acaponeta [Nayarit]

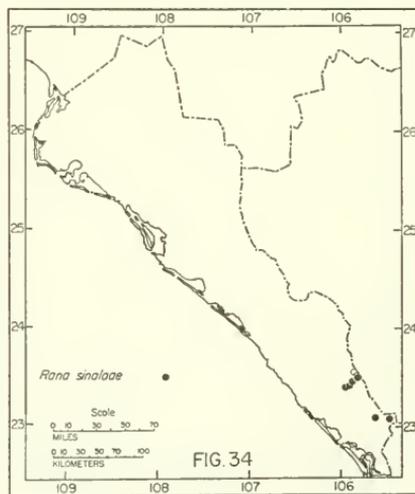
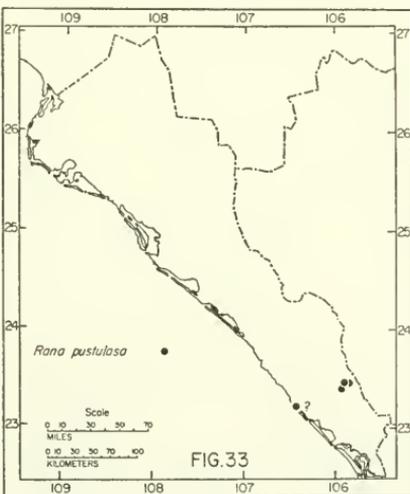
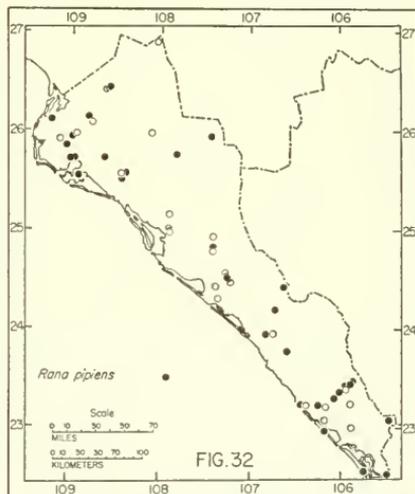
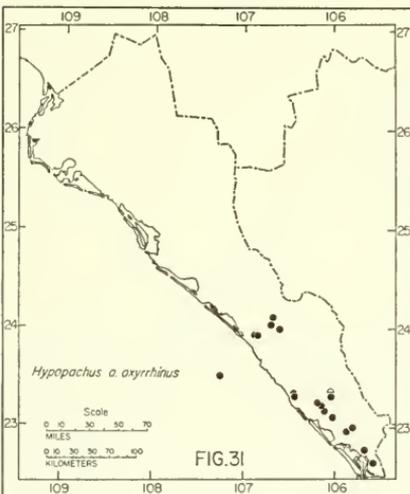
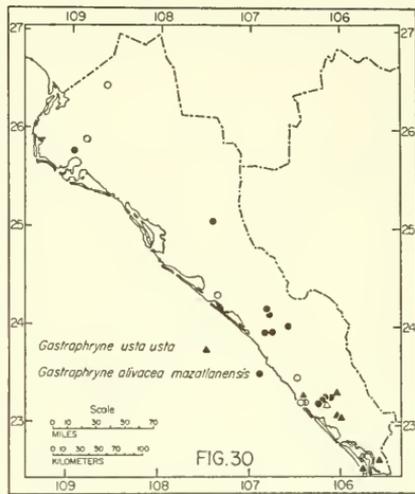
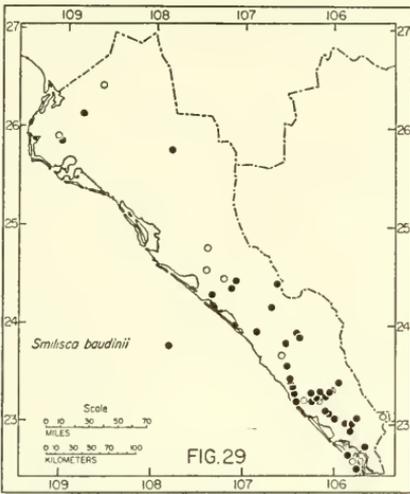
EXPLANATION OF DISTRIBUTION MAPS

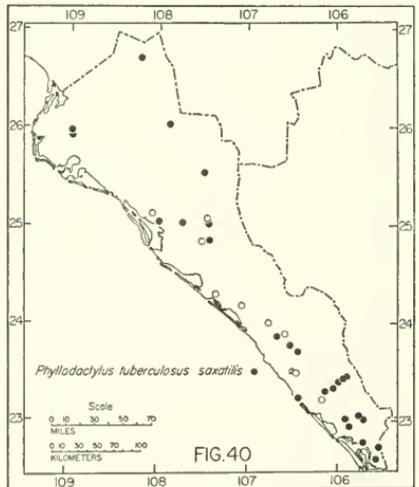
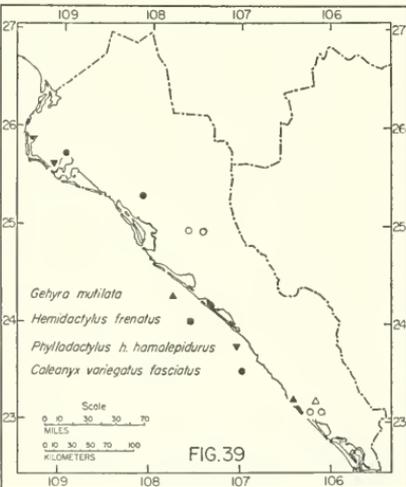
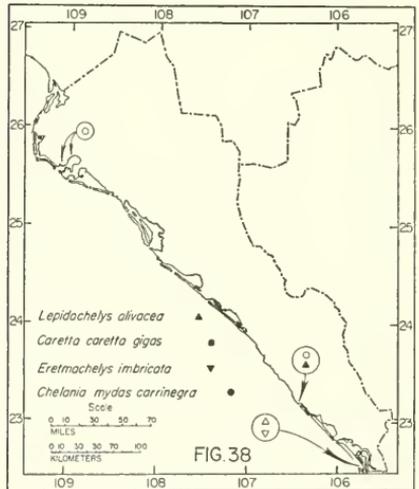
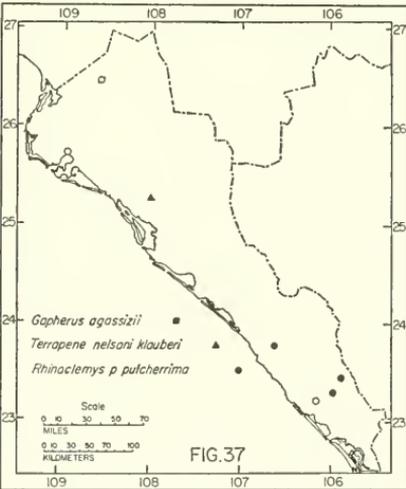
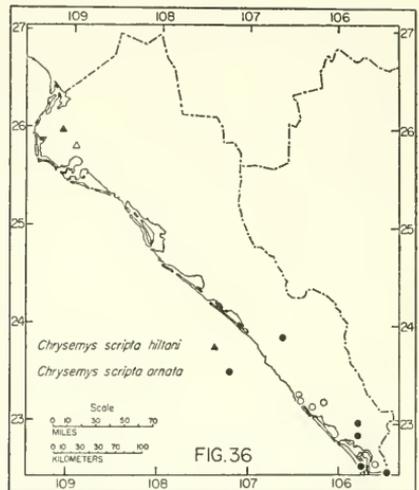
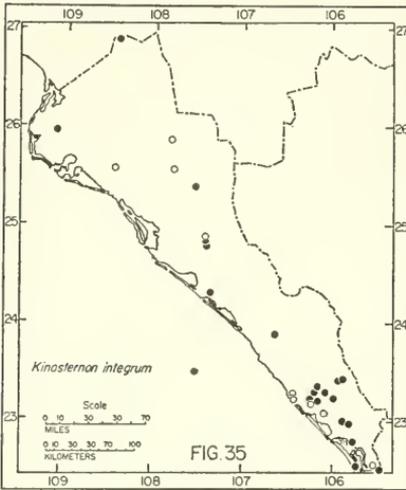
On distribution maps that follow (Figs. 13-91), solid symbols indicate localities of capture for specimens examined by us; open symbols indicate records for which we have not seen specimens.

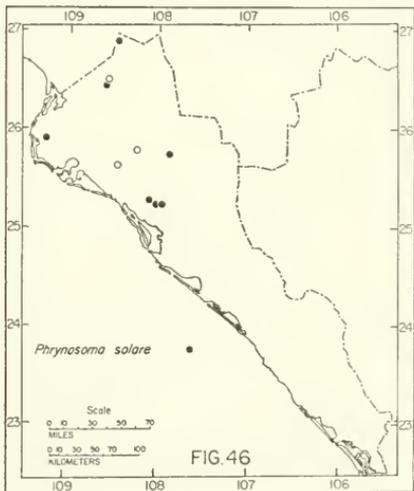
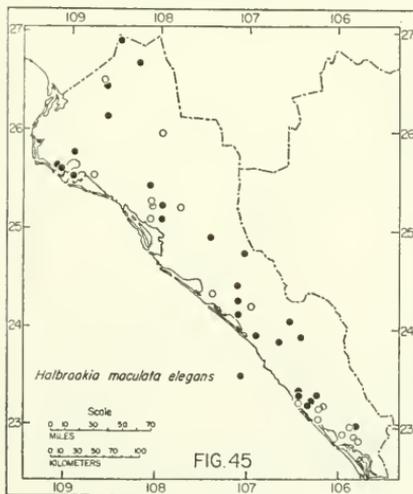
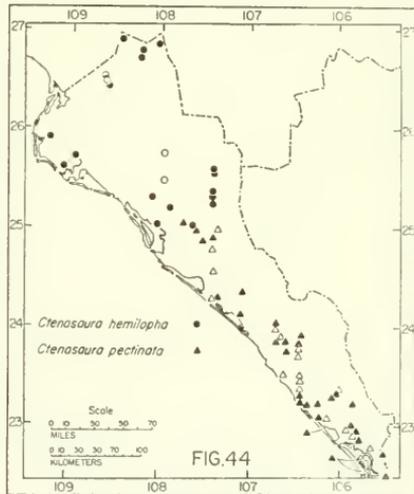
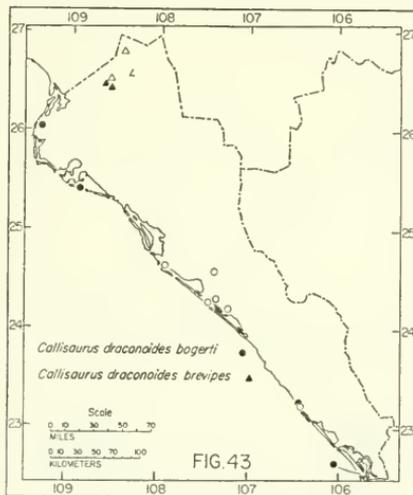
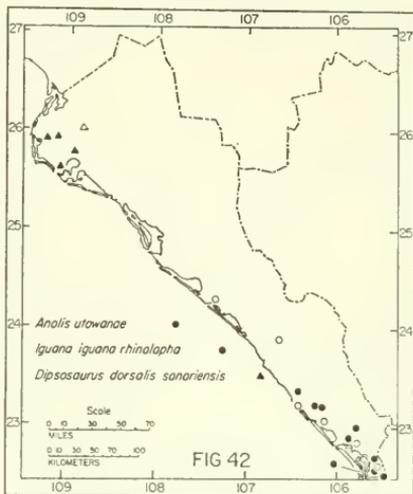
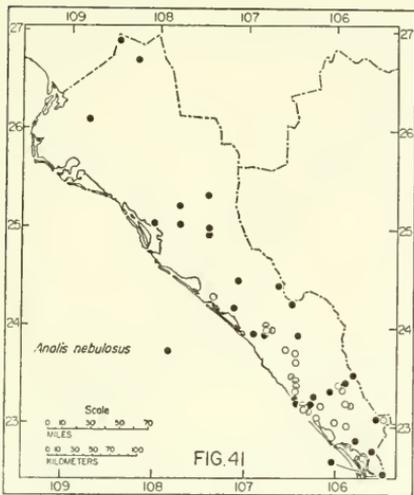


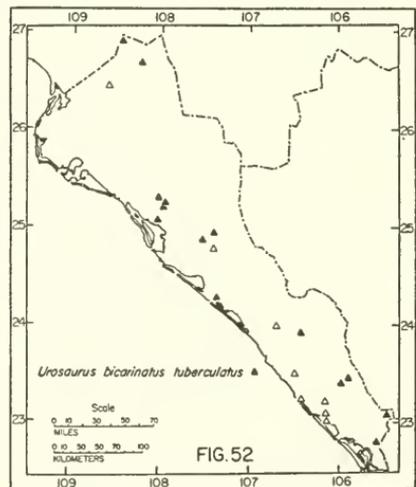
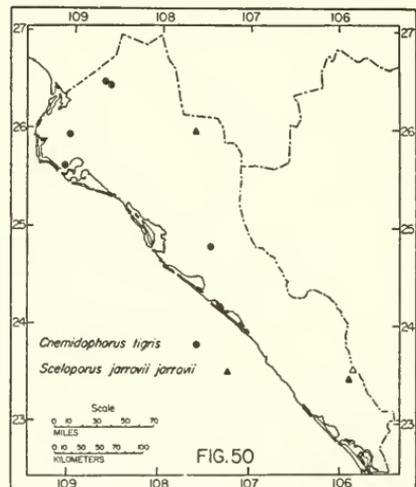
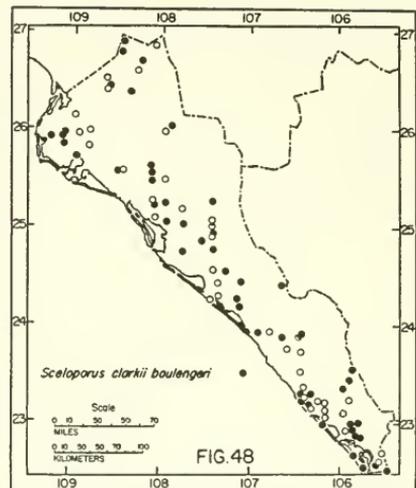
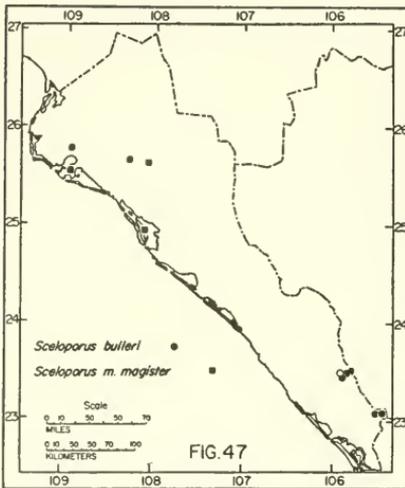


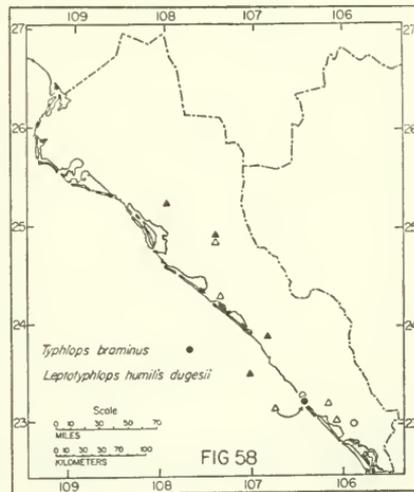
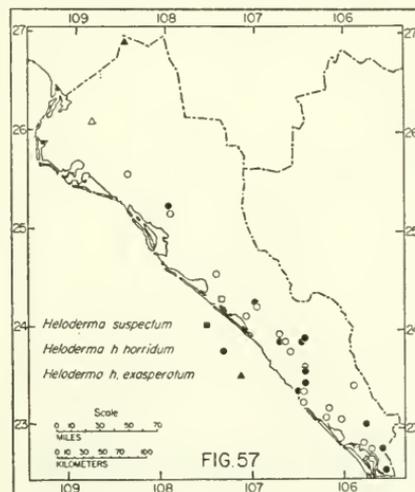
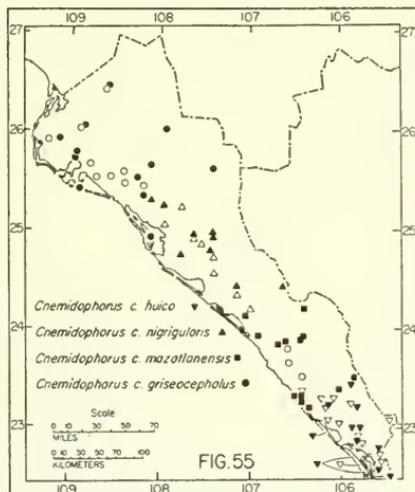
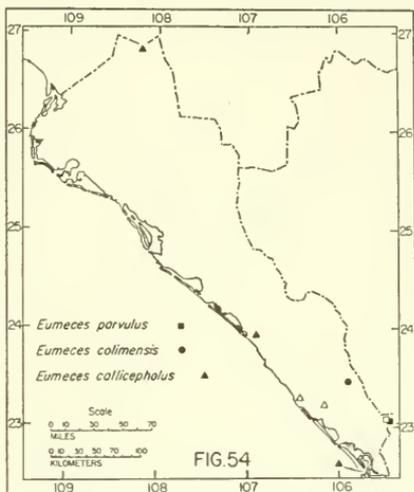
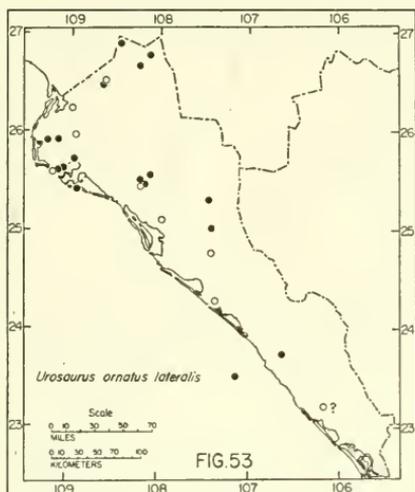


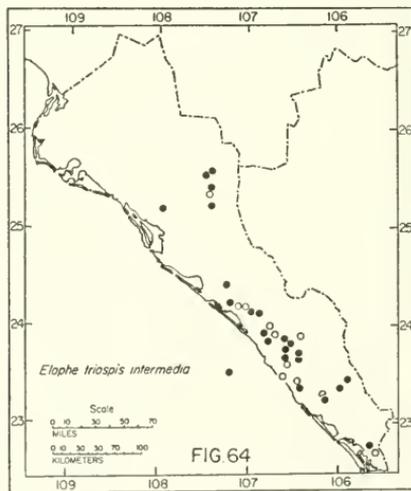
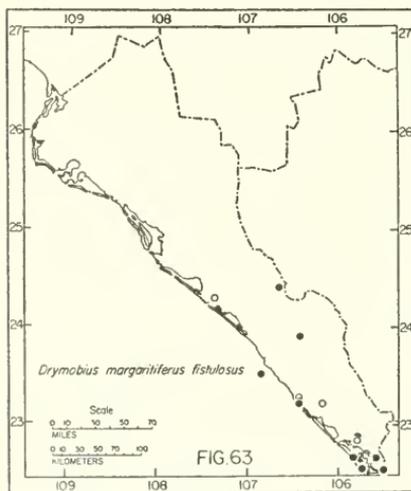
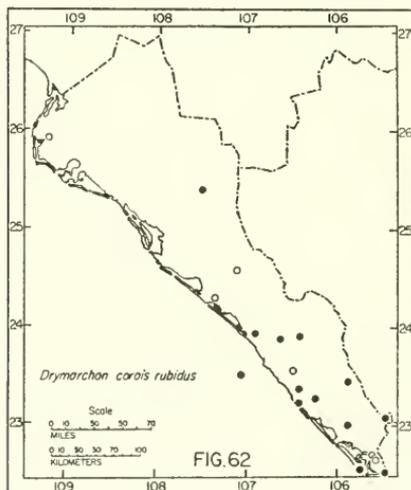
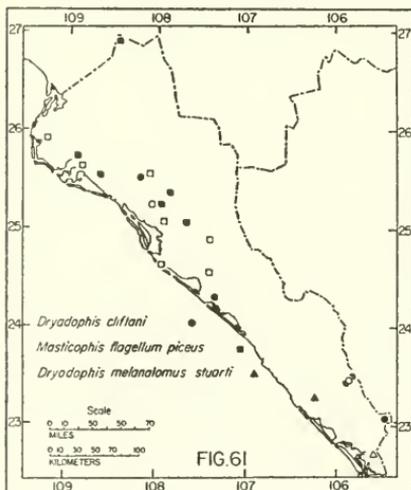
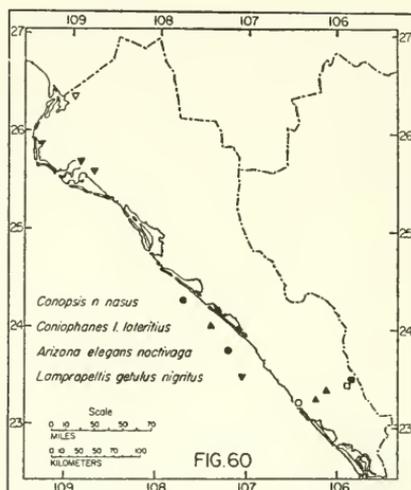
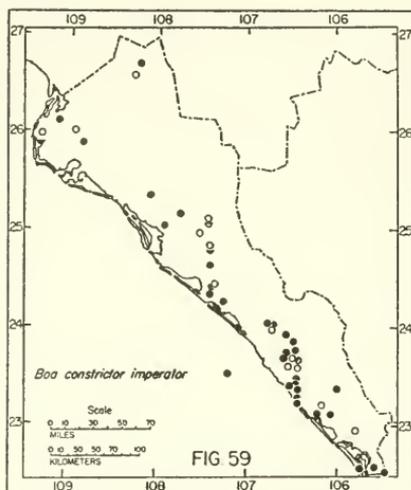


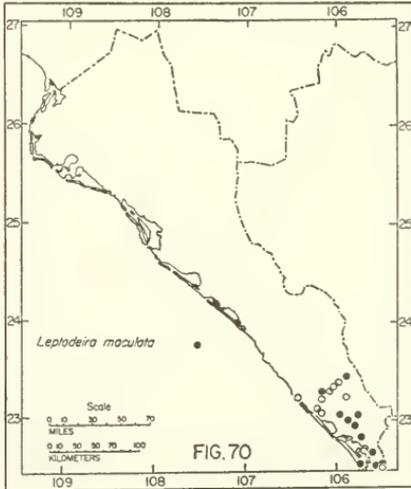
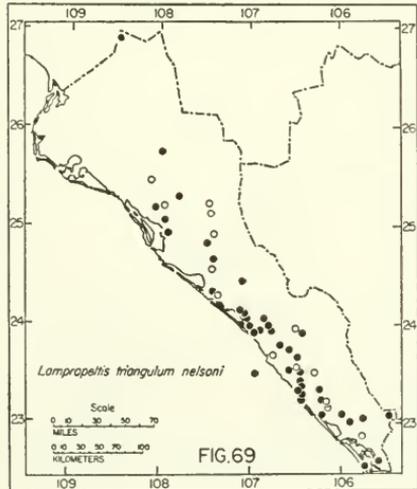
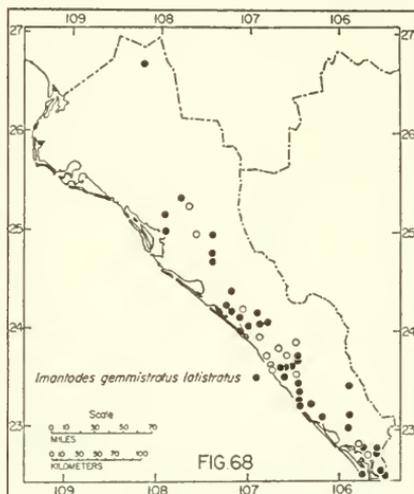
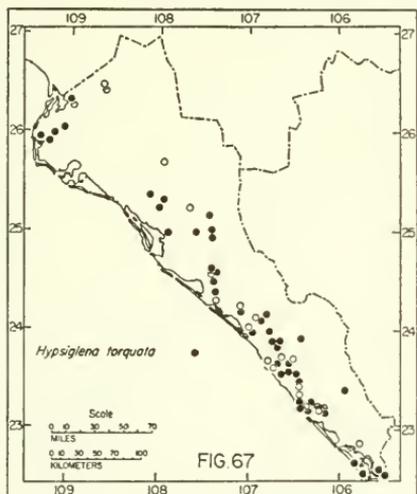
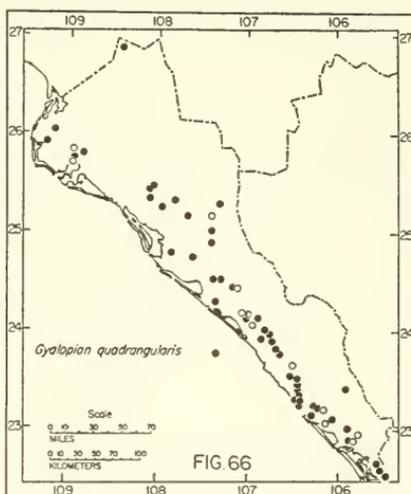
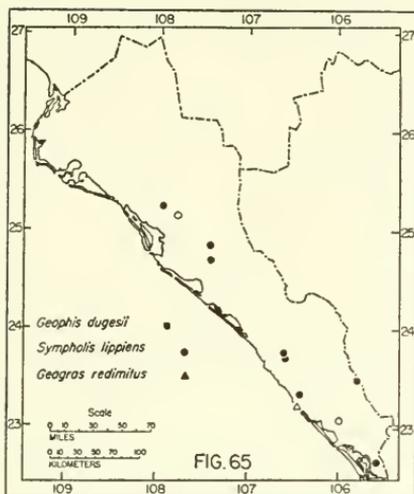


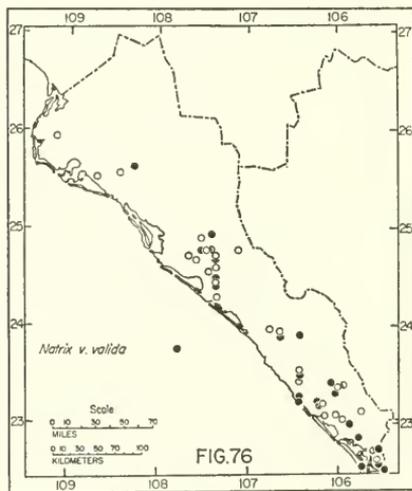
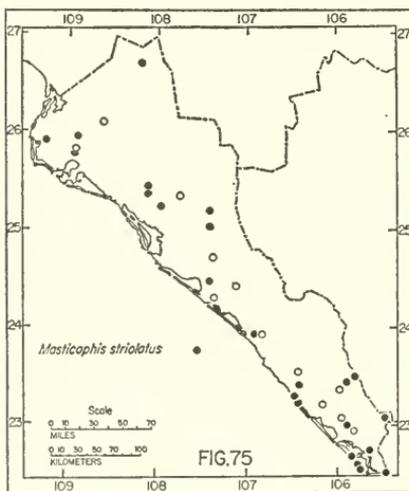
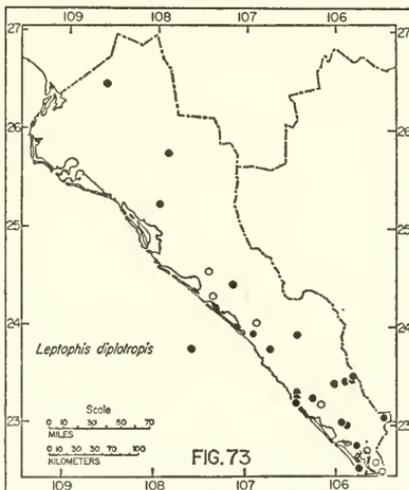
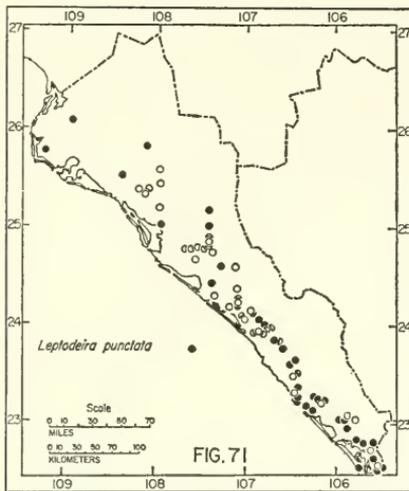


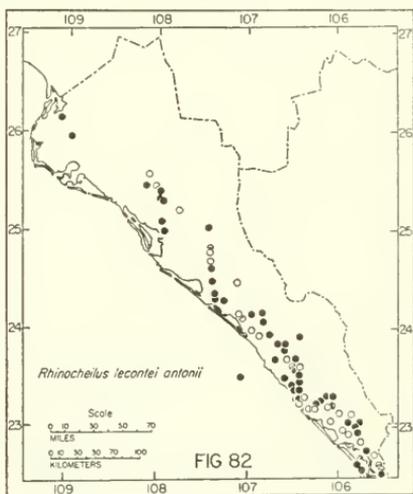
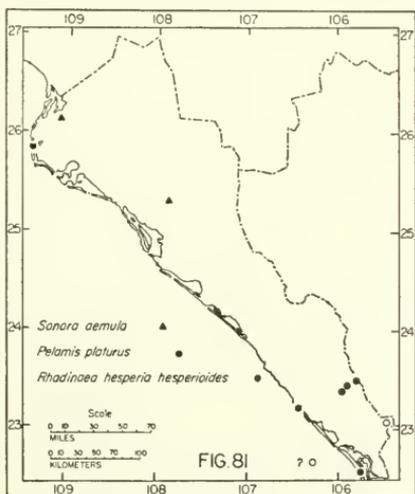
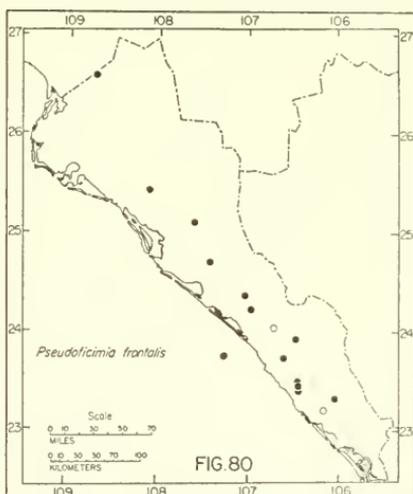
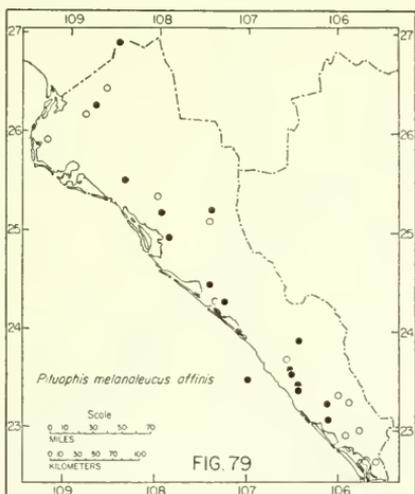
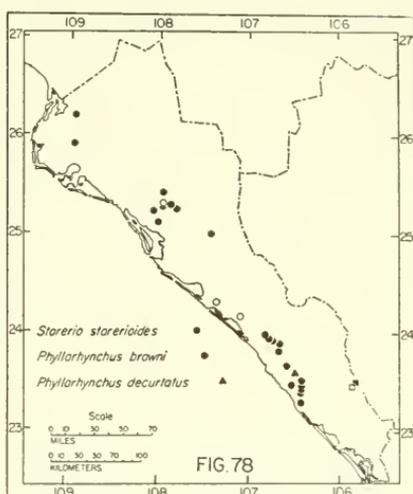
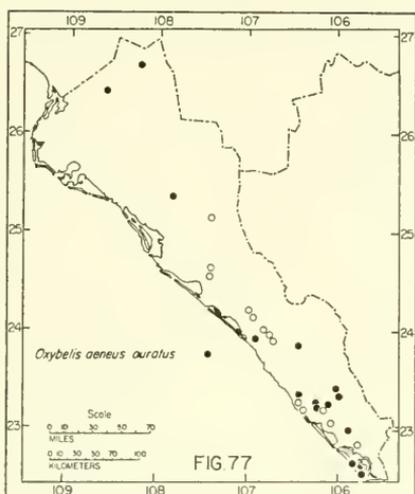


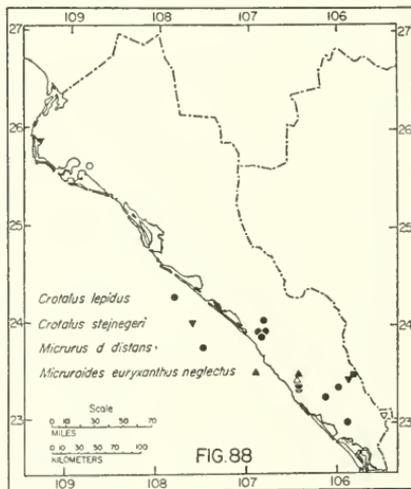
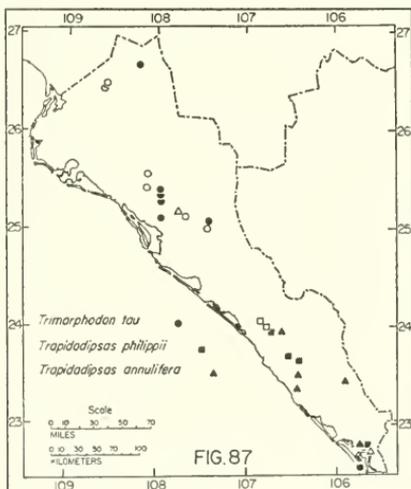
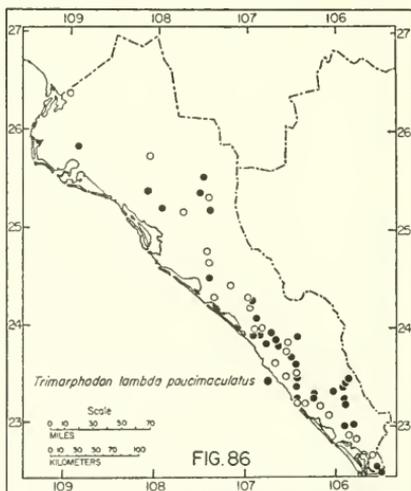
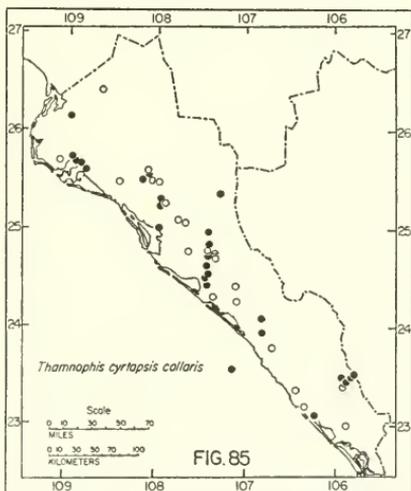
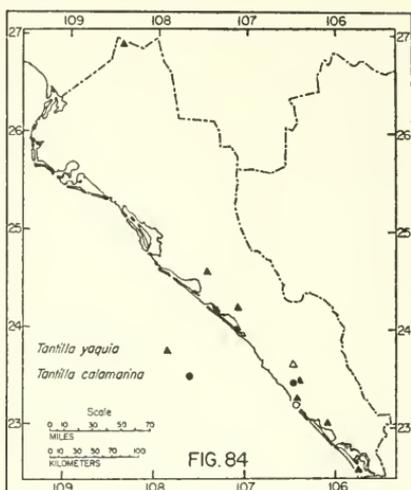
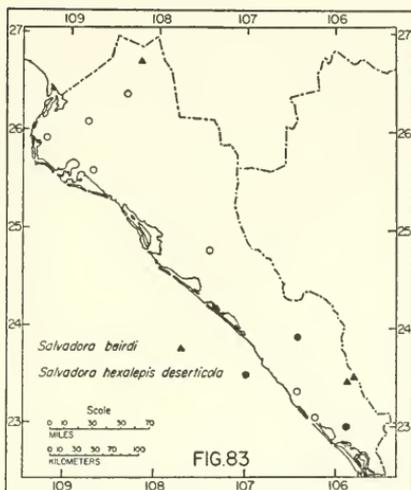


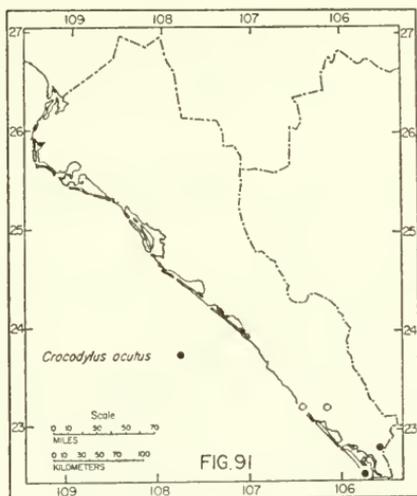
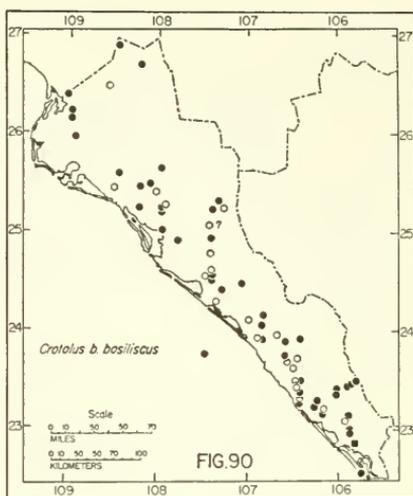
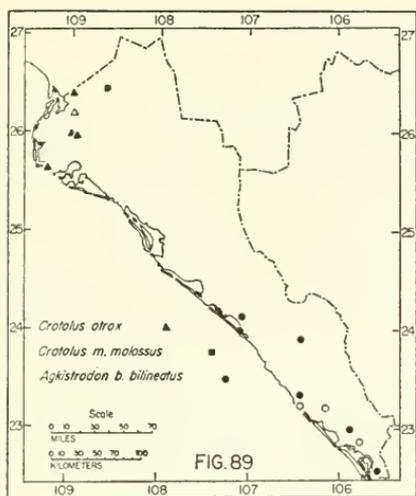












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When the research reported here was conducted, Hardy was associated with the Museum of Natural History, University of Kansas, Lawrence, Kansas 66044 (later with the Department of Biology, University of New Mexico, Albuquerque, New Mexico 87106); McDiarmid was associated with the Department of Biological Sciences, University of Southern California, Los Angeles, California 90007. Their present addresses are, respectively, the Department of Biological Sciences, Louisiana State University at Shreveport, Shreveport, Louisiana 71105, and the Collegiate Division of Biology, University of Chicago, Chicago, Illinois 60637.



PLATE 1



FIG. 1. Tropical Thorn Woodland at five kilometers northeast of El Fuerte, 60 meters elevation. Photograph by Percy L. Clifton on December 26, 1961.



FIG. 2. Tropical Thorn Woodland in the dry season near Tule, Sinaloa. June 18, 1963.

PLATE 2



FIG. 1. Xeric coastal vegetation in Tropical Thorn Woodland at Topolobampo, Sinaloa. June 17, 1963.



FIG. 2. Tropical Thorn Woodland, 24 kilometers south of Guasave, Sinaloa. Photograph by Percy L. Clifton on March 14, 1962.

PLATE 3



FIG. 1. Tropical Semiarid Forest, 13 kilometers north-northeast of Vaca, Sinaloa, 400 meters elevation. Photograph by Percy L. Clifton on November 26, 1963.



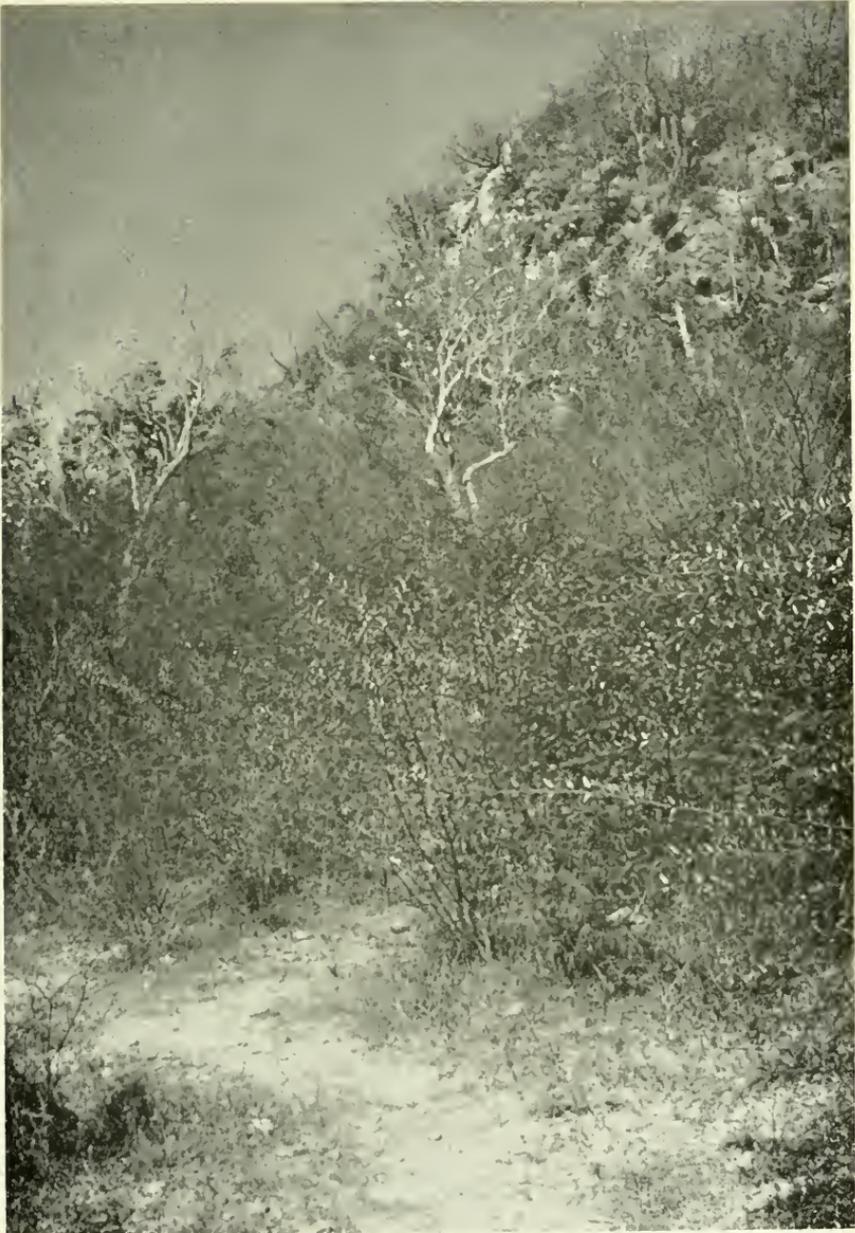
FIG. 2. Tropical Semiarid Forest about 10 miles north of Culiacán, Sinaloa. Open areas of forest are the result of cattle grazing. Photograph by James R. Dixon, September, 1960.

PLATE 4



Tropical Semiarid Forest about 20 miles south of Culiacán in the dry season. The columnar cacti, *Pachycereus pecten-arborinum*, is abundant in this formation. Photograph by Richard B. Loomis; June, 1962.

PLATE 5



Trail through Tropical Semiarid Forest near Río Piaxtla, Sinaloa. *Acacia cymbispina* is the dominant plant in this area. Photograph by Richard B. Loomis on December 28, 1964.

PLATE 6



Tropical Dry Forest in the dry season one kilometer south of Panuco, Sinaloa.
Photograph by Richard B. Loomis on December 9, 1964.

PLATE 7



FIG. 1. Tropical Dry Forest eight kilometers north of Villa Unión, Sinaloa, 45 meters. Photograph by Percy L. Clifton, October 20, 1963.



FIG. 2. Mountain stream through Subtropical Dry Forest, 2.2 kilometers north-east of Santa Lucía, Sinaloa, 1100 meters. July 30, 1963.

PLATE 8

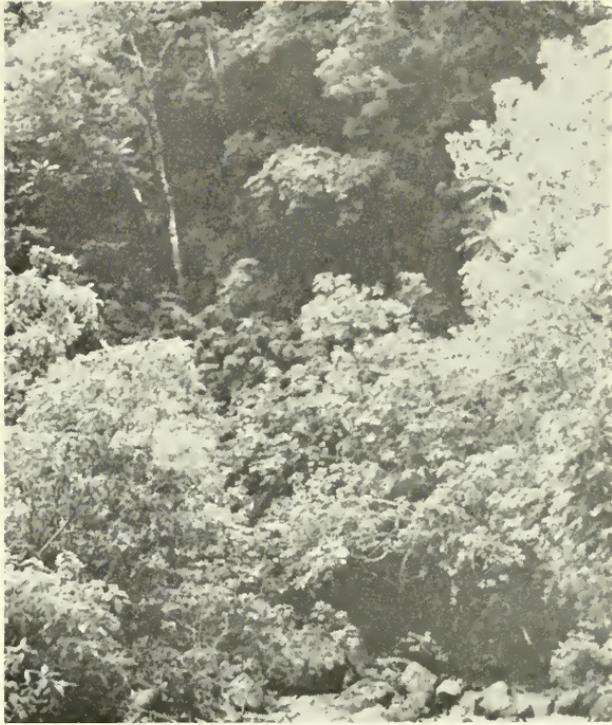


FIG. 1. Subtropical Dry Forest in a canyon, 2.2 kilometers northeast of Santa Lucia, Sinaloa. July 30, 1963.



FIG. 2. Lower Montane Dry Forest five kilometers southwest of El Palmito (Durango), 1850 meters, Sinaloa. Photograph by Percy L. Clifton, July 19, 1963.

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Natural History of the Hognose Snakes
Heterodon platyrhinos and
Heterodon nasicus

BY

DWIGHT R. PLATT

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INTRODUCTION

Because of their peculiar morphology and interesting behavior, hognose snakes, genus *Heterodon*, have been extensively featured in popular literature. Even so, little is known about many aspects of their ecology and most of what is known is to be found in scattered notes. Some of the more important contributions to our knowledge of hognose snakes are those of Surface (1906), Uhler *et al.* (1939), Clark (1949), and Hamilton and Pollack (1956) on the food of the eastern hognose snake; of Hay (1892a), Clark (1952a, 1952b), and Kennedy (1961) on reproduction of that species; of Munro (1949b, 1949c) on reproduction of a western hognose snake; of Davis (1946) on burrowing of the eastern hognose; of Edgren (1952a, 1952b; 1955; 1957; 1961) on geographical variation, taxonomy, evolution, and natural history of hognose snakes; and of Weaver (1965) on their cranial anatomy.

There are three species in the genus *Heterodon*. The eastern hognose snake (*Heterodon platyrhinos*) is found over much of eastern North America and west through parts of the prairie. The range of the western hognose snake (*H. nasicus*) is in the Great Plains from Mexico into southern Canada. The southern hognose snake (*H. simus*), not included in this report, is restricted to the southeastern coastal regions of the United States from southern North Carolina to south-central Florida. There is no evidence of hybridization between the eastern hognose and the western hognose in their area of sympatry.

Although hognose snakes are not abundant over much of their range, they are known to farmers and other persons who spend much time outdoors. The peculiar defensive "bluffing" behavior of the eastern hognose, involving hissing, expanding the neck, and mock strikes, is notorious. This behavior and the broad triangular head have given rise to many stories concerning the venomous nature of hognose snakes. In certain localities the eastern hognose is sometimes mistaken for the copperhead (*Agkistrodon contortrix*), or thought to be closely related to this venomous species. (See p. 366; Hay, 1892a:116; Morse, 1904:127; Ditmars, 1905:104; Netting, 1927:30-31; Myers, 1929:101; Welter and Carr, 1939:129; Brimley, 1941:23; Wheeler, 1947:165.) Although such fallacious ideas persist, I found that many lay persons who have had experience with hognose snakes recognize that they are harmless. More than 50 common names have been given to the eastern hognose, the ma-

majority reflecting a belief in its venomous nature (Schneck, 1878:586; Strecker, 1928:14; McCauley, 1945:63; Wright and Wright, 1957:306). More than 20 common names have been used for the western hognose (Wright and Wright, 1957:297, 302).

The objectives of my study were: (1) to determine the ecological niches occupied by sympatric populations of eastern and western hognose snakes in two natural communities in south-central Kansas; (2) to compare the adaptations, ecology, population dynamics, and life history of the two species, and to attempt to determine the biological significance of differences and similarities; (3) to determine factors limiting the geographic distributions of the two species; (4) to determine the nature and degree of morphological variability of hognose snakes.

Because of their burrowing habits and their lack of aggregation behavior during hibernation, hognose snakes usually cannot be collected in large numbers. The present report is based primarily upon records obtained by live-trapping snakes on two study areas, Harvey County Park and Graber Pasture, in the sand prairies of south-central Kansas, from May 6, 1959, to November 18, 1963. In five seasons 241 western hognose snakes were captured 314 times on the two study areas. A total of 124 eastern hognose snakes were captured 144 times. Live-trapping on the study areas was supplemented by collecting in the surrounding sand prairie area.

It was not possible to make intensive studies of other populations of hognose snakes in the center of the allopatric portions of the range of each species. However, the study in central Kansas was supplemented by visits to other localities where hognose snakes have been found in Kansas, southeastern Missouri, Illinois, Iowa, and North Carolina. Also, information was obtained from the literature and from persons familiar with these snakes in other parts of their ranges.

ACKNOWLEDGMENTS

Many persons and organizations have aided in this study. Dr. Henry S. Fitch has been especially helpful. He gave me the opportunity to work as an assistant in his research on the ecology of snakes and has given many helpful suggestions at all stages of the project. Special thanks are also due to the following persons: Dr. A. Byron Leonard and Mr. James W. Bee for advice on histological technique and photography; Dr. William E. Duellman for helpful counsel, editorial suggestions, and use of his personal library; Dr. Lloyd C. Hulbert for helpful suggestions and data concerning the plant communities on the study areas; and Dr. Edward Batschelet, Mr. G. M. Jolly, and Dr. Arnold M. Wedel for suggestions concerning statistical methods. Without the help of these persons, the study would have been much less adequate. However, any errors or misinterpretations are the responsibility of the author.

Mr. Roy W. Henry, Dr. W. Dale Horst, and Mr. Howard L. Schrag assisted with the field work in Harvey County, Kansas. Identifications of parasites were made by Dr. S. L. Loewen (trematodes) and Mr. W. W. Becklund (nematodes). Dr. John L. Buckley and Mr. William H. Stickel of the U. S. Fish and Wildlife Service Patuxent Wildlife Research Center made available the data in their files concerning the food of and predation on hognose snakes. Mr. Charles H. Rousell, Mr. Robert C. Waltner, Mr. Harvey Holzrichter, and the late Mr. Ralph Woods collected specimens for me in south-central Kansas. Mr. Tom Swearingen advised and assisted in the preparation of graphs and maps. The following persons have supplied information on or specimens of hognose snakes from other parts of the ranges of the eastern and western species: the late Mr. Paul Anderson, Dr. Richard J. Baldauf, Dr. Monroe H. Bartel, Dr. W. J. Breckenridge, Dr. Bryce C. Brown, Dr. Kenneth D. Carlander, Mr. Roger Conant, Mr. Francis R. Cook, Dr. Donald C. Dunlap, Dr. Carlos S. Folger, Dr. John W. Forsyth, Dr. Carl Gans, Dr. Claude W. Hibbard, Mr. H. T. Hiemstra, Mr. W. Charles Kerfoot, Mr. E. B. S. Logier, Mr. Robert J. Mangile, Dr. T. Paul Maslin, Mr. Herbert Milnes, Dr. Sherman A. Minton, Jr., Dr. Gerald G. Raun, Dr. Philip W. Smith, Mr. Ernest C. Tanzer, Dr. Donald W. Tinkle, Mr. I. L. Traill, Dr. Robert G. Webb, and Dr. George C. Wheeler.

I am grateful to curators of herpetological collections in the following institutions who either provided information concerning specimens or allowed me to examine specimens: Chicago Academy of Sciences, Field Museum of Natural History, Fort Hays Kansas State College, Kansas State Teachers College at Emporia, Kansas State University, Stanford University Natural History Museum, Texas Cooperative Wildlife Museum, United States National Museum, University of Kansas Museum of Natural History, and University of Michigan Museum of Zoology.

I thank Mr. Harry Graber and Mr. John Randall for permission to trap snakes and pursue other studies on their properties. Mr. George Hawkes, caretaker, kindly allowed me to establish a study area in Harvey County Park.

I am particularly grateful to the National Science Foundation for giving financial assistance to my study. Much of the field work from 1959 to 1962 was financed by National Science Foundation grants G-6158 and G-16104 to Dr. Henry S. Fitch of The University of Kansas Department of Zoology. I was employed as research assistant on the project supported by these funds in 1959 and 1960. From 1960 to 1962 I was assisted by a National Science Foundation Cooperative Graduate Fellowship.

My wife, LaVonne Platt, has aided me by copying notes, typing, assisting in statistical computations, and editing; and has encouraged me in all phases of the work.

METHODS

Natural populations of hognose snakes in Harvey County, Kansas, were studied primarily by live-trapping, marking, releasing, and recapturing. Cylindrical traps of galvanized wire "hardware cloth" of quarter-inch mesh with funnel entrances were used (Fitch, 1951; 1960b:93-94). Each trap station consisted of a straight drift fence 15 to 20 feet long and 8 to 12 inches high of wood or galvanized "hardware cloth" with a funnel trap fitted on either end. These trap stations were located in shade and where they would be protected from disturbance by cattle. The same trap stations were normally maintained from year to year, but some had to be relocated because of flooding, lack of sufficient shade, or disturbance by cattle. In 1959, 24 trap stations were used in Harvey County Park. From 1960 to 1962, 27 trap stations in Harvey County Park and 22 trap stations in Graber Pasture were maintained and checked from late April or early May to late October or November. In 1963 trapping was done from April 17 to July 12 and from September 11 to November 18.

The traps were checked once or twice a week, depending on the weather. Mortality among various mammals, wrens, and amphibians incidentally trapped was high, but only three eastern and 10 western hognose snakes died in the traps. Active snakes, such as blue racers (*Coluber constrictor*), sometimes escaped from the traps through the entrance, but there was no evidence that adult hognose snakes escaped. Dargan and Stickel (1949:266) reported that hognose snakes were unable to escape from funnel traps. Eastern hognose snakes of all sizes were caught in the traps, but few hatchlings of the western species were caught.

In 1959 and 1960 snakes were released immediately after data were recorded in the field. From 1961 to 1963 the snakes were carried to the laboratory to be measured and were released on the next visit to the study area. With a few exceptions, the snakes were released near the trap station at which they had been caught. The following data were taken from each snake: (1) Snout-vent length and tail length measured with the snake stretched along a metal tape or meter stick until it relaxed. The error in measurement of these live snakes probably did not exceed three per cent. (2) Weight to the nearest one-tenth gram on a laboratory balance or to the nearest two grams on spring scales in the field. (3) Sex, determined by probing for the hemipenial sacs. (4) Parasites, including flukes in the mouth and mites on the skin. (5) Food items in the stomach were forced up into the gullet for identification. Then, if possible, they were forced back into the stomach. Fecal material was forced out onto paper toweling, wrapped, labeled, and allowed to dry. Later, these scats were washed and examined microscopically for hair, reptile scales, feathers, skeletal parts, and other remains from food items. (6) The cloacae of most males and some females were washed with Ringer's solution. Samples of this fluid were examined microscopically to ascertain the presence of spermatozoa. (7) Numbers of large ova in gravid females were counted by palpation. (8) Counts of dorsal blotches, ventral scales, subcaudal scales, and dorsal scale rows. (9) Behavior in defense or after release.

From some individuals data were also recorded concerning temperature, rate of heart beat, number of azygous scales, length of head, and width of head.

Each snake was marked and given a number by cutting out two subcaudal scales as described by Fitch (1963:360-361). Little regeneration of clipped scales was noted. For the few instances in which doubt existed as to the identity of the clipped scales in a recaptured snake, other data on scale counts and dorsal blotches provided evidence that confirmed the identity.

A trailer taped to the tail was used to trace movements of some snakes after they were released. The trailer fed out fine nylon thread as the snake moved.

Some snakes were kept in cages in the laboratory for experimental studies of feeding, digestion, burrowing, temperature tolerances, moulting, and growth. In 1960, 1961, and 1962, snakes kept in a rectangular outdoor pen, 11 by 19 feet, provided data concerning temperature preference, diel and seasonal cycles of activity, moulting, and use of burrows. The pen was partly shaded and partly in full sun.

Fifty-five hognose snakes, collected outside of the study areas, were dissected. They were examined for internal parasites and contents of digestive tracts. The condition of the reproductive organs of females was noted. Testes, reproductive ducts, and kidneys of males were fixed in ten per cent formalin or Bouin's fluid, embedded in paraffin, sectioned at ten microns, and stained with hematoxylin and eosin. These sections were studied to determine the spermatogenic cycle. Gravid females were brought to the laboratory and each kept in a cage until she laid a clutch of eggs. The eggs were incubated partially buried in moist sand in cans.

In this report, statistical mean values are accompanied by one standard error or by the range. In tables, values of *t* or chi-square that are significant at the five per cent level of significance are designated with one asterisk, those that are significant at the one per cent level are designated with two asterisks, and those that are significant at the one-tenth per cent level are designated with three asterisks. Yates' correction for continuity was used in calculating chi-square with small samples (Simpson *et al.*, 1960:189-191).

The term hatchling is used in this report for snakes between hatching and first hibernation. Juveniles (adj. juvenal) are snakes that are not yet sexually mature. First-year snakes are those in their first full season of activity. Harvey County in this report refers to Harvey County, Kansas.

DESCRIPTION OF STUDY AREAS

General

The areas in Graber Pasture and Harvey County Park on which studies of populations of snakes were made are in the eastern edge of the Hutchinson Dune Tracts, a strip of sand dunes two to eight miles wide that extends 50 miles, from north of Burrton in Harvey County, west into Reno County, and then northwest to a point east of Saxman in Rice County. The sand dunes in Harvey County probably were formed during late Pleistocene and Recent times by wind deposition of sand picked up from the Arkansas River valley by the predominantly south and southwesterly winds (Williams and Lohman, 1949:71, 82). This area of sand dunes was settled between 1870 and 1890 and has since been used mainly for grazing.

Climate.—The climate of Harvey County is characterized by variability in precipitation and temperature. The mean annual precipitation is approximately 30 inches. Between April 1 and September 30 in two out of three years 30 or more consecutive days of drought occur. The normal annual mean air temperature is 56.1°F, with a normal mean temperature of 80°F in July and of 31°F in January. The average maximum temperature in July is 93°F. An average of 15 to 20 days each year have maximum temperatures above 100°F. The average length of the growing season is 184 (145 to 223) days with the last killing frost in spring expected between April 17 and 20, and the first killing frost in autumn between October 18 and 20 (Flora, 1948). The period in which my study was made was abnormally cool and wet (Table 1).

TABLE 1. Deviations From Long-term Averages of Weather Conditions at Newton, Harvey County, Kansas, in the Period From 1959 to 1963 (Data From Robb, 1959 to 1964).

Year	Mean July temperature (deviation, degrees F)	Annual precipitation (deviation, inches)
1959.....	-6.2	+ .12
1960.....	-4.0	+14.98
1961.....	-2.2	+6.50
1962.....	-1.2	+4.25
1963.....	+1.6	-5.15

Soil.—On the study areas the surface layer is a medium-fine sand with little organic matter or soil development (Table 10). This sand deposit, thin in swales but many feet deep on dunes, is underlain by a fine-textured subsoil that is only 0.3 per cent as pervious to water as the sand and 2.2 per cent as pervious as garden loam (Doell, 1938:117).

Topography.—The topography is hummocky, and on Graber Pasture there are a few sand blowouts. Because surface drainage is poorly developed and

the subsoil is relatively impervious, small temporary or permanent ponds and marshes are present in many of the swales between dunes.

Vegetation.—The sand prairie differs from the better-drained mixed grass prairie on nearby loam soils in the large number of marshes and ponds and the prevalence of shrubs and trees. The study areas are in the easternmost extension of the Sandsage-Bluestem Prairie as mapped by Küchler (1964). However the dominant climax plants are those of the Bluestem Prairie (Küchler, 1964), although many of the associated forbs and grasses are restricted to sandy areas. Doell (1938) has described the vegetation of the sand prairies of western Harvey County.

The two study areas are approximately one mile apart. The study area in Harvey County Park was in an ungrazed, unmowed grassland, part of which appears to be near climax. The study area in Graber Pasture was in a heavily-grazed pasture.

Harvey County Park

Approximately 25 of the 383 acres in Harvey County Park were cultivated and the remainder grazed at the time of acquisition by the county in 1938. The eastern part of the park along the Little Arkansas River is now a recreation area, but the western part is a wildlife refuge that has been ungrazed and little disturbed since it was acquired by the county. Before 1940 a shelterbelt was planted along the south, west, and north edges of the wildlife refuge. The study area of approximately 50 acres was in the southwest part of the wildlife refuge.

A permanent 21-acre lake in the northern part of the study area first formed in a borrow pit after earth was removed for use on the park roads in 1939. It was enlarged in 1953 and 1954 by placing a dam across a drainageway. Much of the area near the lake was disturbed by the earthwork.

The scientific names of plants in the following discussion are from Fernald (1950) or Harrington (1954), while the common names follow Anderson (1961). The names of plant communities are my own, used only with reference to the study areas.

The plant communities on the study area are primarily related to topography and previous treatment (Fig. 1). The vegetative cover is dense and moderately tall on much of the study area. On the uplands climax grasslands (Tall Grassland and Little Bluestem Grassland), weedy grasslands (Weedy Little Bluestem Grassland, Weedy Lovegrass, and Weedy Upland Grass) and weedy communities occur. The dominant grasses of the Tall Grassland are big bluestem (*Andropogon gerardi*), little bluestem (*A. scoparius*), switchgrass (*Panicum virgatum*), and indiagrass (*Sorghastrum nutans*), growing in dense stands up to six feet tall (Pl. 1, Fig. 1). The surface is heavily mulched. Little Bluestem Grassland, found on higher or more disturbed sites, is dominated by clumps of little bluestem, with shorter grasses and forbs and some open sand present between these clumps. Switchgrass and indiagrass are common in parts of this grassland, but big bluestem is scattered and dwarfed.

More disturbed sites support Weedy Little Bluestem Grasslands with the bluestem clumps widely spaced and much sand exposed. The grasses Kearney threeawn (*Aristida intermedia*), scribner panicum (*Panicum oligoanthos* var. *scribnerianum*), fall witchgrass (*Leptoloma cognatum*), fringeleaf paspalum (*Paspalum ciliatifolium*), and sand dropseed (*Sporobolus cryptandrus*) and

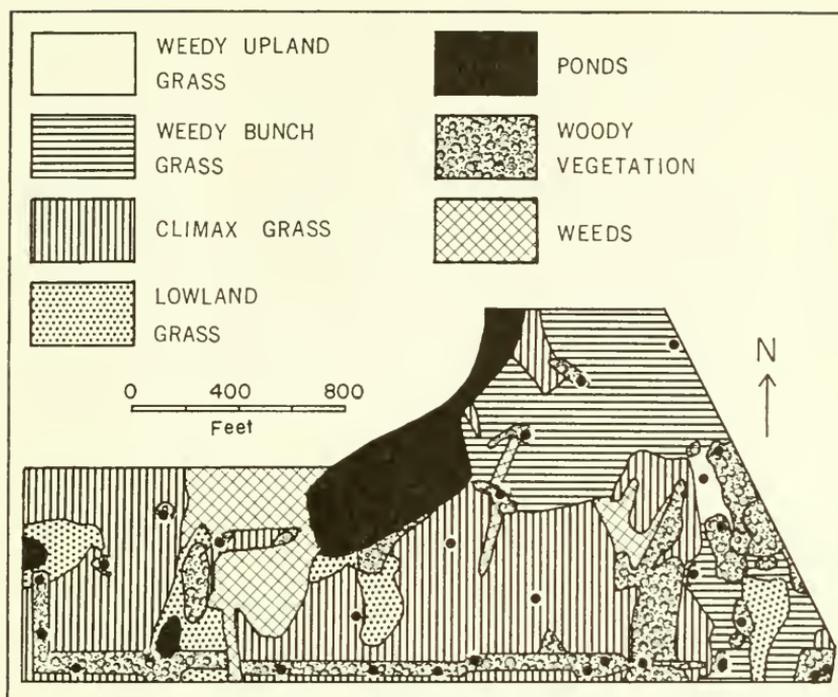


FIG. 1. Map of the Harvey County Park study area located in the south half of section six, township 23S, range 2W in Harvey County, Kansas. Weedy bunch grass includes the Weedy Little Bluestem and Weedy Lovegrass communities. Climax grass includes the Tall Grassland and the Little Bluestem Grassland. Woody vegetation includes the shelterbelt, groves of trees and Upland and Lowland Shrub communities. Trapping stations are indicated by dots.

the forbs and succulents dayflower (*Commelina* sp.), snakecotton (*Froelichia* sp.), pricklypear (*Opuntia* sp.), common eveningprimrose (*Oenothera biennis*), prairie sunflower (*Helianthus petiolaris*), and western ragweed (*Ambrosia psilostachya*) are common. The Weedy Lovegrass community is dominated by sand lovegrass (*Eragrostis trichodes*) but includes many other short weedy grasses and forbs (Pl. 1, Fig. 2). This community with little or no sand lovegrass is the Weedy Upland Grass community. More disturbed sites near the lake support Upland Weed communities dominated by sweetclover (*Melilotus* sp.), prairie sunflower, and horseweed (*Erigeron canadensis*).

Chickasaw plum (*Prunus angustifolia*) dominates shrubby areas on the uplands. Groves of American elm (*Ulmus americanus*), red mulberry (*Morus rubra*), green ash (*Fraxinus pennsylvanica*), boxelder (*Acer negundo*), and black walnut (*Juglans nigra*) trees grow along the east side of the study area. Along the south, west, and north sides there is a shelterbelt of eastern cottonwood (*Populus deltoides*), green ash, common honeylocust (*Gleditsia triacanthos*), catalpa (*Catalpa speciosa*), and redcedar (*Juniperus virginiana*) trees. Small clumps of black willow (*Salix nigra*) and eastern cottonwood trees are scattered through the study area on lower sites.

Prairie cordgrass (*Spartina pectinata*) and/or switchgrass dominate the Lowland Grass community. Coyote willow (*Salix exigua*) is scattered in the

grassland and in places forms dense Lowland Shrub communities. The Lowland Weed communities are dominated by lambsquarter (*Chenopodium album*), smartweed (*Polygonum* sp.), prairie sunflower, and western ragweed. These lowland communities are flooded during some rainy periods.

Graber Pasture

The 50-acre study area was in the northeast part of the 640-acre Graber Pasture. As far as is known, this tract has been grazed but never cultivated. The study area is rough with many low swales that were flooded for long periods during my study. The upland plant communities are disturbed by grazing and the vegetative cover is low and sparse. Both uplands and lowlands are shrubby.

The distribution of plant communities is primarily related to topography and drainage; and, because of the roughness of the terrain, samples of the communities are small and interspersed closely (Fig. 2). The vegetation of the Weedy Upland Grass community is much shorter than in the similar plant

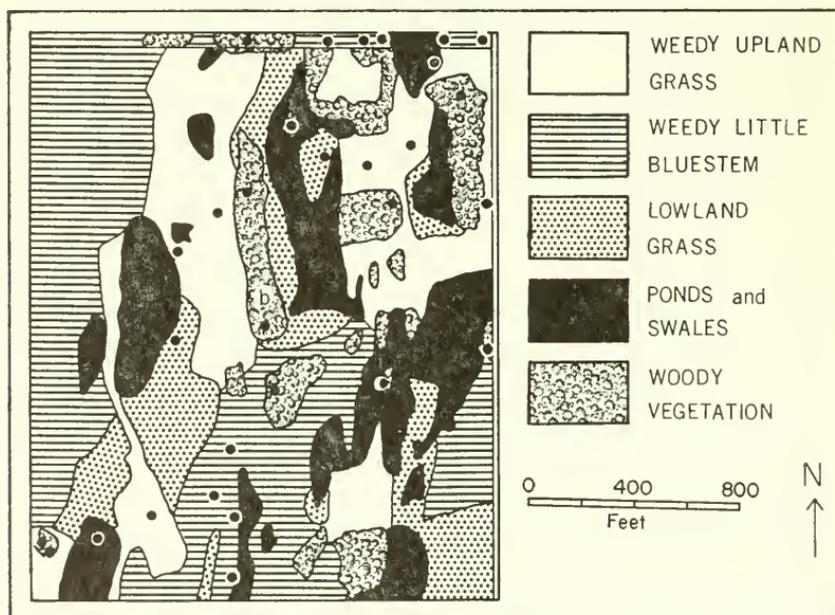


FIG. 2. Map of the Graber Pasture study area located in the northeast quarter of section one, township 23S, range 3W in Harvey County, Kansas. Weedy Little Bluestem also includes the similar Sumac-Little Bluestem community. Woody vegetation includes Willow Groves, large groves of other trees, Chickasaw Plum Thickets, and a large Buttonbush Marsh (indicated by b). Trapping stations are indicated by dots.

community in Harvey County Park. Coverage is poor and, on steep ridges, there are open sand exposures (Pl. 2, Fig. 1). Common plants include those in the Weedy Upland Grass in Harvey County Park, with the exception of prairie sunflower, and, in addition, flatsedge (*Cyperus schweinitzii*), cristatella (*Cristatella jamesii*), croton (*Croton glandulosus*), butterfly milkweed (*As-*

clepias tuberosa), gromwell (*Lithospermum carolinense*), rough buttonweed (*Diodia teres*), and camphorweed (*Heterotheca subaxillaris*).

Weedy Little Bluestem Grassland is found on the least disturbed uplands. It resembles the similar community in Harvey County Park, but has poorer coverage, lacks prairie sunflower, and includes a number of additional weedy plants. Sumac-Little Bluestem Grassland is a modification of the preceding community with low shoots of smooth sumac (*Rhus glabra*) scattered between the clumps of grass. Chickasaw plum invades both types of upland grass and forms Chickasaw Plum Thickets and Chickasaw Plum Grassland. Trees scattered alone or in small groups on the uplands are principally red mulberry, boxelder, black willow, and eastern cottonwood.

The lowland communities are distributed in relation to drainage. The Weedy Swales and Buttonbush Marshes are often flooded for long periods. A slightly higher *Spartina* Grassland is flooded for short periods. Willow Groves and Lowland Grass occur in the higher lowlands.

The open ponds found in the Weedy Swales are important breeding sites for frogs when they are flooded. When not flooded, the Weedy Swales are covered with a sparse to dense growth of low weedy and moisture-loving plants. Common buttonbush (*Cephalanthus occidentalis*) grows on the margins of many Weedy Swales and also in dense shrubby marshes. Buttonbush Marshes and Weedy Swales in many places are surrounded by a narrow band of dense tall prairie cordgrass, the *Spartina* Grassland. Black willow trees border many small swales above the *Spartina* Grassland, form small groves on slight rises in the swales, and are scattered in the Lowland Grass community. The Lowland Grass community is a moderately dense grassland up to three feet tall with switchgrass and prairie cordgrass as the dominant plants (Pl. 2, Fig. 2). On slightly higher sites it contains much little bluestem, indiagrass, and some big bluestem.

MORPHOLOGY

Size

Heterodon platyrhinus. This is the largest of the three species of hognose snakes. Edgren (1952a:2, 20-22, 25) measured 1200 preserved specimens in which the average total length of adults was 650 to 850 millimeters (mm.) (maximum 1082) in females and 500 to 650 (maximum 970) in males. He found a cline of increasing maximum length from south to north. Klau (1948:60) reported that adult males from northern regions were larger than those from southern regions, but that there was no significant difference in females.

In Harvey County, total lengths ranged between 584 and 892 mm. in adult females, and 568 and 819 mm. in adult males.

The longest known eastern hognose with precise measurements is a female measured by me from the Cimarron River, Beaver County, Oklahoma, that had a total length of 1155 mm. and a weight of 761 grams. Mr. H. T. Hiemstra (*in litt.*) reported a female that was "about 46 in. long" from Elgin County, Ontario, Canada. Other large specimens and their lengths are: a female from Kelleys Island, Erie County, Ohio, 1149 mm. (Conant, 1966:54); a female from Oxford County, Ontario, Canada, 43½ inches (1105 mm.; Milnes, 1946:2); a female from Moose Lake, Pine County, Minnesota, 1092 mm. and

a weight of 1191 grams (Breckenridge, 1942:128); and a snake from Pennsylvania, 1003 mm. (Netting, 1927:30-31).

Heterodon nasicus. The longest known western hognose is a male from Hale County, Texas, that had a length of 895 mm. (Bowers, 1967:61). Edgren (1952a:2, 20-21, 24) measured 300 preserved specimens of the western hognose in which the average total length of adults was 500 to 700 mm. in females and 350 to 500 in males. The largest female in his study had a total length of 823 mm. (from Washington County, Kansas) and the largest male 608 (from Rawlins County, Kansas). He found a cline of increasing maximum length from south to north.

In Harvey County more than two-thirds of the adult females captured had total lengths between 450 and 575 mm., and more than two-thirds of the adult males were between 375 and 525 mm. The longest female had a total length

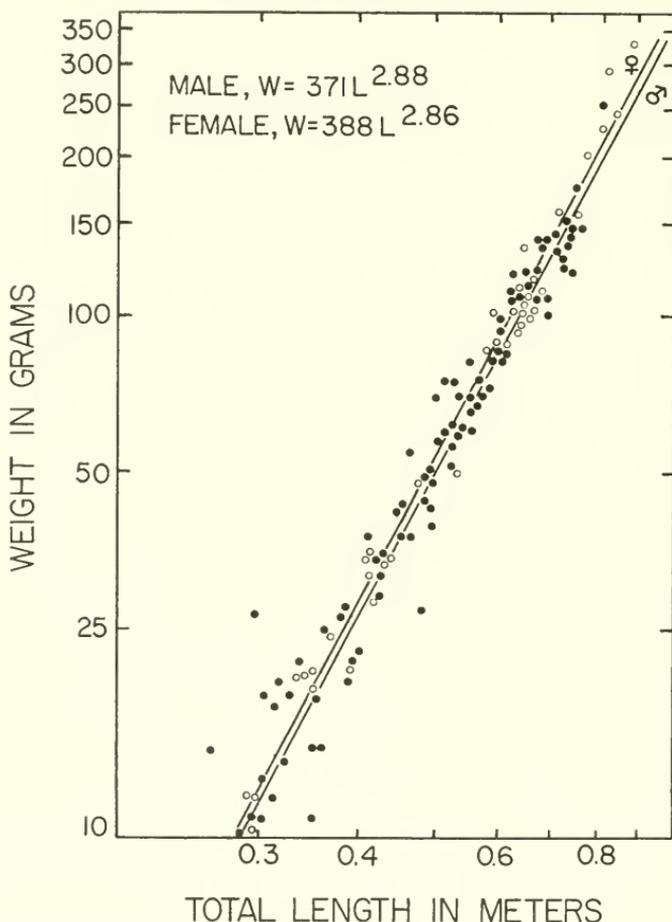


FIG. 3. Regression of weight on length as fitted by Bartlett's method (Simpson, *et al.*, 1960:232-233, 401) to measurements of 103 male and 57 female eastern hognose snakes from Harvey County, Kansas. Males are represented by dots and females by circles. Both the abscissa and ordinate are in logarithmic scale.

of 800 mm. and a weight of 210 grams. The longest male had a total length of 663 mm. and a weight of 118 grams.

Bodily Proportions and Sexual Dimorphism

Secondary sexual differences exist in bodily proportions and size of hognose snakes. Secondary sexual differences in coloration, anal ridges, knobbed anal keels, or chin tubercles are lacking. Eastern and western hognose snakes differ from one another in certain characteristics of bodily proportion.

Hognose snakes are stout and heavy-bodied. Klauber (1956:150, 305) con-

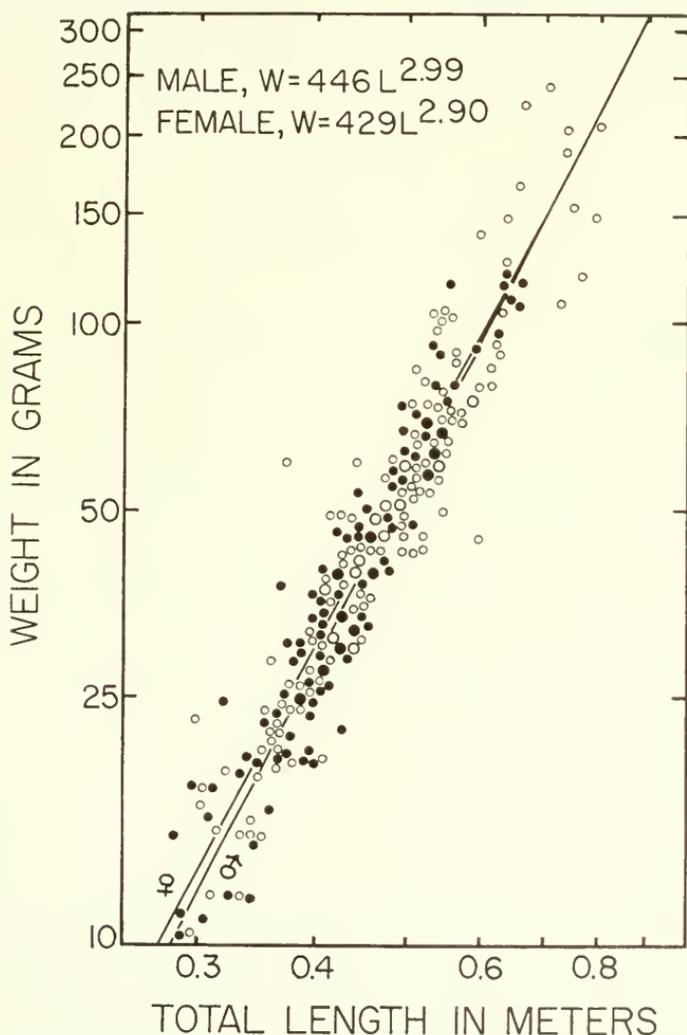


FIG. 4. Regression of weight on length as fitted by Bartlett's method to measurements of 158 male and 167 female western hognose snakes from Harvey County, Kansas. Males are represented by dots and females by circles. Small symbols represent a single record and larger symbols represent two to four records. Both the abscissa and ordinate are in logarithmic scale.

cluded that the relation between total length and weight is the best criterion of relative bulk of the body of snakes. He found that the regression line of weight on length for rattlesnakes was of the form $W = CL^P$, where W is weight, L is total length, and C and P are constants characteristic for each species. Regression lines of this form were fitted to the data on weight in grams and total length in meters for the snakes from Harvey County (Figs. 3 and 4).

TABLE 2. Bodily Proportions of Hognose Snakes From Harvey County, Kansas. The Males in the Samples Were 400 to 500 Millimeters in Snout-vent Length and Females 500 to 600 Millimeters.

	Western Hognose Snake		Eastern Hognose Snake		t (comparison of species)
	Number in sample	Ratio	Number in sample	Ratio	
MALES					
Weight in gms./total length in dms. ³	29	0.465 ± .012	29	0.411 ± .011	3.3**
Tail length/snout-vent length...	30	0.218 ± .0004	29	0.218 ± .005	0.0
Head width/head length...	20	0.662 ± .014	18	0.564 ± .003	5.5***
Head width/snout-vent length.....	20	0.020 ± .0004	18	0.021 ± .0004	1.8
Head length/snout-vent length.....	20	0.031 ± .0004	18	0.037 ± .0004	9.7***
FEMALES					
Weight in gms./total length in dms. ³	16	0.460 ± .287	15	0.395 ± .011	1.6
Tail length/snout-vent length...	16	0.141 ± .004	15	0.177 ± .002	8.3***
Head width/head length.....	10	0.658 ± .019	7	0.542 ± .015	4.5***
Head width/snout-vent length.....	10	0.017 ± .0006	7	0.018 ± .0005	1.4
Head length/snout-vent length.....	10	0.026 ± .001	7	0.034 ± .0005	7.3***

Hognose snakes are less heavy-bodied than prairie rattlesnakes (*Crotalus viridis*) (Klauber, 1937:46) but almost twice as heavy as common garter snakes (*Thamnophis s. sirtalis*) at comparable lengths (Carpenter, 1953:148). Both rattlesnakes and hognose snakes increase in weight approximately as the cube of the length. Klauber (*loc. cit.*) pointed out that a value of P exceeding three indicated that rattlesnakes become somewhat heavier-bodied with age if a constant specific gravity is assumed. Both eastern and western hognose snakes remain constant in bodily proportions or become slightly less heavy-bodied as they grow longer.

Adult male western hognose snakes are significantly heavier than male eastern hognose snakes of comparable lengths. Female western hognose snakes are also heavier but are so variable in weight that the difference is not statistically significant (Table 2). There is no consistent sexual dimorphism in length-weight relationships in either species.

The number of somites in a snake can be determined approximately by adding the number of ventral plates and the number of subcaudal plates. Hognose snakes are short-bodied and have relatively low numbers of somites. Female eastern hognose snakes from Harvey County have significantly more somites than males (Table 3). Edgren (1958:3) studied the number of somites in five populations of the eastern species from Florida, Michigan, Louisiana, and New York. He found significant sexual dimorphism with regard to this character only in the population from Alachua County, Florida. Western hognose snakes from Harvey County are not sexually dimorphic in number of somites (Table 3).

TABLE 3. Number of Somites in Hognose Snakes From Harvey County, Kansas.

Sex	Western Hognose Snakes		Eastern Hognose Snakes		t (comparison of species)
	Number in sample	Mean number of somites	Number in sample	Mean number of somites	
Male.....	70	181.8±.43	44	186.2±.63	7.0***
Female.....	84	182.6±.44	26	191.7±.81	10.0***
t (comparison of sexes)..		1.3		5.3***	

Both males and females of the eastern species have more caudal somites (subcaudal plates) than do western hognose snakes (Fig. 5). The significant difference between the two species in total number of somites (Table 3) is due to the difference in number of caudal somites, since the number of body somites (ventral plates) in the two species in Harvey County is similar (Fig. 5). However, from a study of specimens from all parts of their ranges, Edgren (1952a:151, 155) reported that the western species had more ventrals than the eastern.

Male hognose have fewer ventrals and more subcaudals than females.

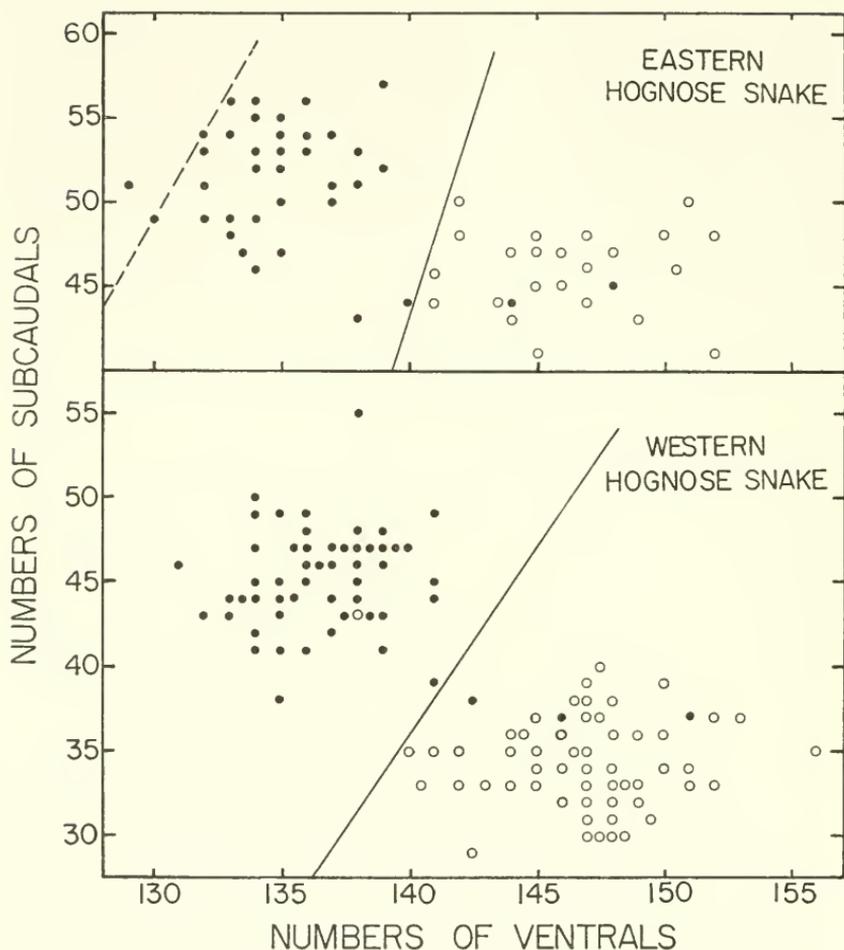


FIG. 5. Numbers of subcaudal plates and numbers of ventral plates in 67 specimens of the eastern hognose snake and 148 specimens of the western hognose snake from Harvey County, Kansas. Males are represented by dots and females by circles. The solid lines divide most of the male records from most of the female records in these samples. The dashed line would divide most of the male records from all of the female records in a sample of 94 eastern hognose snakes from Florida (Edgren, 1952a:110).

Although counts obtained for the two sexes overlap, sex can be reliably determined from the count of ventrals and subcaudals. On the graph of these two characters for the western species from Harvey County, the plotted values are in two clusters representing males and females (Fig. 5). The line separates 96 per cent of the males from 99 per cent of the females. This same line would separate 98 per cent of the males from all females in a sample of 135 western hognose snakes studied by Edgren (1952a:73-74).

The eastern species in Harvey County has less pronounced secondary sexual differences in scale counts, particularly in numbers of subcaudals (Fig. 5). Separation on the basis of number of ventrals is almost as reliable as the com-

bination of the two counts. The solid line on the graph for the eastern species separates 95 per cent of the males from all females. Edgren (1952a:110) reported the numbers of ventrals and subcaudals in 94 eastern hognose snakes from Florida. They had fewer ventrals than those from Harvey County, Kansas (Fig 5).

The numbers of ventrals and the numbers of subcaudals in male hognose snakes from Harvey County have a slight negative correlation (significant only at the five per cent level), while the counts on females show no correlation (r is -0.346 for males and $+0.003$ for females of the eastern species; -0.244 for males and $+0.003$ for females of the western species). Possibly the two sexes differ in the genetic or ontogenetic mechanisms that produce variation in these characters. Edgren (1952a:100) found little or no correlation between the numbers of caudals and the numbers of ventrals on snakes of one sex in populations that he studied.

Sexual dimorphism in numbers of ventrals and subcaudals is due, at least in part, to differences in the position of the vent, leaving the total number of somites unchanged (Table 3). The differences between individuals of the same sex are not primarily due to the degree of development of sexual dimorphism. If these differences were caused by the same mechanisms that are responsible for sexual dimorphism, the numbers of subcaudals and of ventrals would show a strong negative correlation.

Edgren (1958) reported sexual dimorphism in position of the umbilical scar in hognose snakes. The few measurements of umbilical scar positions made in my study supported Edgren's findings.

The number of dark middorsal blotches on the body is sexually dimorphic in the western species. Edgren (1952a:65) reported that females of the western species have an average of five more dorsal blotches on the body than males. The difference in means in the sample from Harvey County was 4.1 blotches (mean value for males was 34.8; for females was 38.9). In both males and females the number of dorsal blotches is positively correlated with the number of ventral plates, indicating that variability is due in part to variations in the basic length of the body (r for males is $+0.31$; for females is $+0.36$). Both values differ significantly from zero at the one per cent level). Dorsal blotches may be fused or separated in different patterns, also contributing to the variability.

The eastern species has a low degree of sexual dimorphism in numbers of middorsal blotches. For those populations from which Edgren (1961:126) had samples of at least 20 individuals, the mean number of dorsal blotches on females varied from two more dorsal blotches than on males to the same number of dorsal blotches as on males. The difference in mean number of blotches between the two sexes in 89 male and 40 female eastern hognose snakes from Harvey County was 2.8. The number of dorsal blotches is correlated with the number of ventral plates in males but shows little correlation in females (r for males is $+0.52$; for females is $+0.10$).

The sexually dimorphic characters reported above for the western species are due, at least in part, to more posterior positions of the vent and umbilicus in females than in males. Females of eastern hognose snakes, at least in the Harvey County population, have more somites, in addition to a more posterior placement of the vent and umbilicus, relative to males. These differences are also reflected in the ratio of length of tail to snout-vent length or total length.

Length of tail in the western species from Harvey County is approximately 21 per cent of snout-vent length in males and 14 per cent in females, *versus* 22 per cent in males and 18 per cent in females in the eastern species.

The relationship between tail length and total length can be fitted satisfactorily by regression lines of the form $Y = BX + A$, in which Y is the tail length, X is total length, and B and A are constants characteristic of a specific pattern of growth (Figs. 6 and 7). The slope of the regression line calculated for males of the western species from Harvey County differs significantly (at one-tenth per cent level) from the value calculated for females (t is -3.6 with 300 degrees of freedom). The secondary sexual difference in relative tail length becomes more marked with increasing size (Fig. 6). However, even in snakes less than 250 mm. in snout-vent length, the difference between the mean ratios of tail length to snout-vent length in males ($0.183 \pm .005$) and in females ($0.147 \pm .009$) is significant at the one-tenth per cent level (t is 4.0 with 22 degrees of freedom).

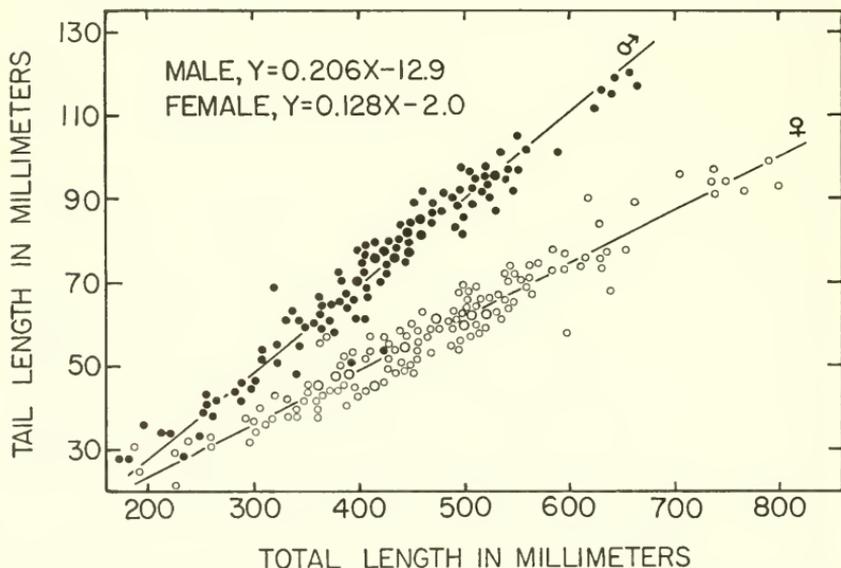


FIG. 6. Regression of tail length on total length as fitted by Bartlett's method to measurements of 157 male and 149 female western hognose snakes from Harvey County, Kansas. Males are represented by dots and females by circles. Small symbols represent a single record and larger symbols represent two to four records.

The regression line of tail length on total length for males of the eastern species also differs from that of females, but to a lesser degree than in the western species. This reduced sexual difference is due to a relatively longer tail in females, probably related to the larger number of caudal somites. The slope of the regression line is significantly different (at one-tenth per cent level) in males and females of the eastern species from Harvey County (t is -3.7 with 155 degrees of freedom). The sexual difference in relative tail length becomes more marked with increasing size (Fig. 7). However, in those snakes of less than 300 mm. snout-vent length, the mean ratio of tail

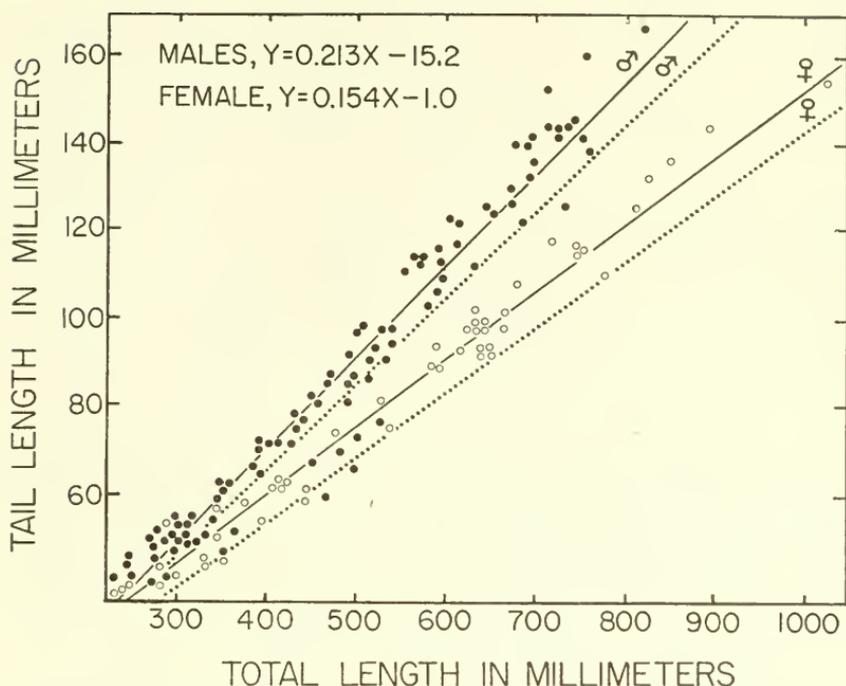


FIG. 7. Regression of tail length on total length as fitted by Bartlett's method to measurements of 104 male and 57 female eastern hognose snakes from Harvey County, Kansas. Males are represented by dots and females by circles. The solid regression lines and the regression formulas were calculated from my data, and the dotted lines are the regression lines reported by Edgren (1952a:29).

length to snout-vent length is $0.208 \pm .003$ for males and $0.184 \pm .004$ for females. The difference is significant at the one-tenth per cent level (t is 4.4 with 46 degrees of freedom).

The regression lines of tail length on total length reported by Edgren (1952a:29) show a similar sexual dimorphism. His regression lines for the eastern species indicate shorter tails than in the same species in Harvey County (Fig. 7). The difference is partly due to the effects of preservation, although geographic variation in this bodily proportion has not been studied. The regression lines reported by Edgren (*loc. cit.*) for the western hognose were obviously in error.

Males of the two species of the same adult size do not differ significantly in mean ratio of tail length to snout-vent length, but females of the eastern species have relatively longer tails than females of the western species in Harvey County (Table 2).

In young male western hognose snakes up to 450 mm. in snout-vent length, the tail has positive allometric growth relative to the body (Table 4). In males of the eastern species, the tail appears to grow faster than the body in all except the largest snakes, but the differences are not statistically significant. The tails of female hognose snakes grow at a rate proportional to that of the body.

TABLE 4. Mean Ratio of Tail Length to Snout-vent Length in Male Western Hognose Snakes From Harvey County, Kansas.

Snout-vent length	Number in sample	Ratio	t (comparison of size groups)
250 mm. and less.....	16	0.183 ± .005	4.8*** 2.7** 1.3
251-350 mm.....	57	0.208 ± .003	
351-450 mm.....	75	0.217 ± .002	
451-550 mm.....	12	0.209 ± .007	

Hognose snakes have broad, somewhat triangular heads. Length of the head was measured from the anterior end of the rostral scale to the posterior end of the interparietal suture. Width of the head was measured between the edges of the supraocular scales at a point above the center of the eye. This is approximately half the maximum width of the head. The western

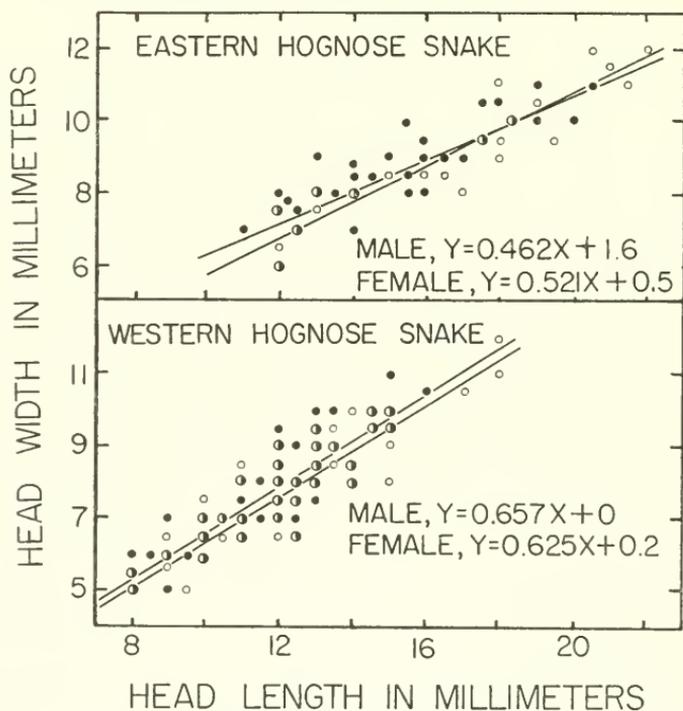


FIG. 8. Regression of head width on head length as fitted by Bartlett's method to measurements of 64 male and 29 female eastern hognose snakes and 103 male and 104 female western hognose snakes from Harvey County, Kansas. Each symbol represents one to six individuals with identical measurements. Males are represented by dots and females by circles. Half circles represent both male and female records.

species has a "chunkier" head than the eastern. As indicated by the ratios between head measurements and snout-vent length, the difference between the two species is in the relative length of the head (Table 2). Both my data and those of Edgren (1952a:28) indicate that adult females of both species have relatively shorter heads than males. However, the differences are not statistically significant.

Regression lines of the form $Y = BX + A$ fitted to the relationship of head length and head width of snakes from Harvey County are similar to regression lines reported by Edgren (1952a:31) on the basis of a study of preserved specimens from many geographic regions (Fig. 8).

Young have relatively larger heads in both dimensions than older snakes (Table 5). The differences between size groups are statistically significant at the one per cent level. In western hognose snakes there is no significant change in the ratio of head width to head length as the snake grows. In the eastern species the head becomes relatively narrower and longer with increase in size (Table 6).

In the samples from Harvey County, mean length of males is 90.7 per cent of the mean length of females in the western species and 90.0 per cent in the eastern species. Figure 9 shows the distribution, according to size groups based on total length. Edgren (1952a:20-22) reported that females attain a larger size than males in all three species of hognose snakes.

The mode of the sample of female western hognose snakes from Harvey

TABLE 5. Ratios of Dimensions of Head to Snout-vent Length for Hognose Snakes of Different Snout-vent Lengths From Harvey County, Kansas.

	Small snakes	Medium snakes	Large snakes
	Less than 351mm.	351 to 500 mm.	More than 500 mm.
EASTERN HOGNOSE SNAKES			
Head length—Males . . .	0.046 ± .0007	0.037 ± .0004	0.034 ± .0005
Females	0.046 ± .0019	0.036 ± .0007	0.032 ± .0007
Head width—Males . . .	0.027 ± .0005	0.021 ± .0004	0.019 ± .0003
Females	0.026 ± .0009	0.019 ± .0007	0.018 ± .0004
	Less than 351 mm.	351 to 450 mm.	More than 450 mm.
WESTERN HOGNOSE SNAKES			
Head length—Males . . .	0.038 ± .0009	0.032 ± .0003	0.029 ± .0004
Females	0.036 ± .0012	0.030 ± .0002	0.027 ± .0004
Head width—Males . . .	0.024 ± .0006	0.021 ± .0002	0.019 ± .0006
Females	0.023 ± .0008	0.019 ± .0002	0.018 ± .0003

TABLE 6. Mean Ratios of Head Width to Head Length for Eastern Hognose Snakes of Different Sizes From Harvey County, Kansas.

Snout-vent length	Number in sample	Ratio	t (comparison of size groups)
350 mm. and less.....	41	0.586 ± .007	2.1* 3.4**
351-500 mm.....	30	0.563 ± .008	
501 mm. and over.....	23	0.549 ± .006	

County falls in a larger size group than the mode of males, and the larger size groups contain a larger percentage of the female sample (Fig. 9). A test of homogeneity (Simpson *et al.*, 1960:324-326) on the male and female samples indicated significant differences at the one per cent level (chi-square is 22.3 with six degrees of freedom for the Harvey County samples and 25.6 with five degrees of freedom for Edgren's sample).

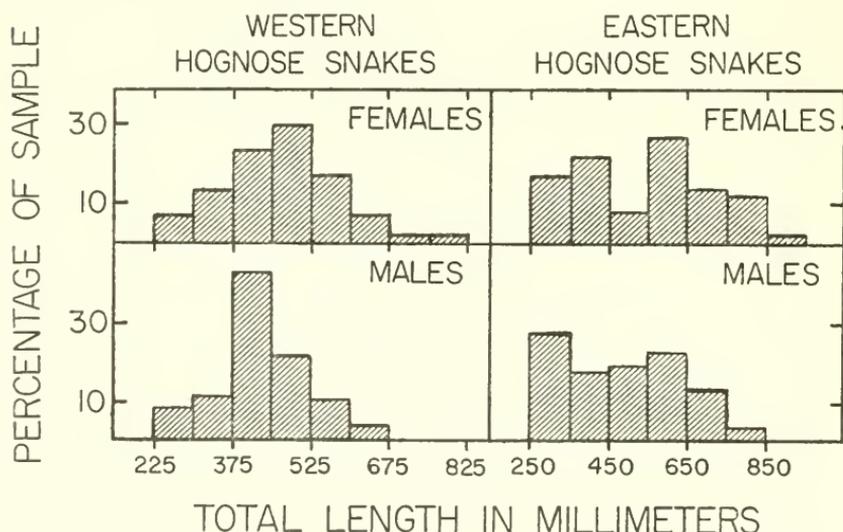


FIG. 9. Frequency distribution of measurements of total length in samples of 150 male and 130 female western hognose snakes and 95 male and 42 female eastern hognose snakes from Harvey County, Kansas.

The samples of the eastern species are bimodal, and the secondary sexual differences are less marked (Fig. 9). However, the larger size groups contain a smaller percentage of the sample of males than of the females. A test of homogeneity on the samples of male and female eastern hognose snakes from Harvey County did not indicate a significant difference (chi-square is 9.9 with five degrees of freedom), although the difference might have been significant if the sample of females had been larger. There is a significant difference between the two samples in Edgren's study (chi-square is 21.6 with seven degrees of

freedom). Klau and David (1952:364, 369) reported a similar pattern of sexual dimorphism in size in 441 specimens of the eastern species from various parts of its geographic range and in a sample of 89 specimens from Oklahoma. The larger size of females is due, at least in part, to a more rapid growth rate in females (Tables 31 and 33).

Coloration

Heterodon platyrhinos. The eastern hognose is variable in coloration. The background color on the dorsum varies in different individuals from yellow through various shades of brown, red, olive, and gray to black; yellowish-brown is most common. The dorsal and lateral blotches are usually dark brown or black, but they may be a darker shade of the background color or completely obscured.

Most specimens have distinct light and dark bands on the head and neck. A dark transverse band crosses the prefrontals and anterior edge of the frontal; another irregular and sometimes incomplete dark band with a pale area in its center crosses the parietals and the posterior supraoculars and frontal; and a dark stripe runs from the eye to the angle of the mouth. A pair of large, black, elongate blotches on the sides of the neck usually connect to the transverse band on the parietals and flank a smaller, elongate, middorsal nuchal blotch.

On the body a series of middorsal, transverse, dark blotches alternate with light crossbands of background color. Light and dark half-rings alternate on the dorsum of the tail. Laterally on the body two (one to three) longitudinal series of dark blotches alternate in position with the dorsal blotches. The dorsal series of lateral blotches are often darker and more distinct than the middorsal blotches. The ventral series consists of many small irregular spots on the first three or four scale rows. The background color is usually palest between the middorsal blotches. In some individuals the dorsal blotches merge with dark background color on the sides, and the snake appears to have a series of pale blotches on a dark background.

The venter is yellowish, gray, olive, or reddish, sometimes becoming darker (almost black) toward the vent. It may be immaculate or have irregular darker spots, especially on the sides. The undersurface of the tail is usually lighter than the belly.

Coloration varies within single populations of eastern hognose snakes, as well as geographically from one population to another. There are two common color phases with intermediates in Harvey County. Many snakes are yellow to yellowish-brown with distinct brown or black blotches. Others are varying shades of olive-brown to olive-gray with less distinct blotches of a darker olive or brown. King (1939:572) reported that in the Great Smoky Mountains National Park in Tennessee, most eastern hognose snakes have a gray background color with brown blotches, but some individuals have reddish-brown, orange, or yellow markings and some are melanistic. Individuals with reddish, pinkish, or orange background markings have also been reported from Pennsylvania (Netting, 1927:30-31), South Carolina (Malnate, 1944:730), Michigan (Edgren, 1952a:179), Illinois (Cagle, 1942:186), South Dakota (Over, 1923:28), Missouri (Anderson, 1942:210), northeast Texas (Strecker, 1926a:7), and southeast Texas (Brown, 1950:158).

Unpatterned eastern hognose snakes have been commonly reported. Uniform gray, olive, or brown snakes with only head patterns have been seen in

Massachusetts (Stull, 1926:130), New York (Engelhardt, *et al.*, 1915:3), Ontario (Milnes, 1946:2), Ohio (Conant, 1951:217), and Tennessee (Rhoads, 1895:393). Of 879 specimens examined by Edgren (1957), 82 or 9.33 per cent were melanistic. Some local populations have a high proportion of melanistic individuals. Melanism is most common in the southeastern part of the range of the species and is rare or absent in the northeastern and northwestern parts. No melanistic specimens have been collected in Kansas. Melanism is not correlated with habitat or sex. It may become more pronounced in older snakes. However, Evans (1947:20) collected an immature melanistic specimen and Clark (1949:248) found two black hatchlings. Albinism and erythrism are rare. Uniform reddish individuals have been found in Nebraska (Taylor, 1892:349) and "southeast of San Antonio, Texas" (Wright and Wright, 1957:307). Albino specimens have been seen in Autauga County, Alabama (Hensley, 1959:151), near Amherst, New Hampshire (Newton, 1940), and in Jefferson County, Texas (Van Devender, 1967:70).

Heterodon nasicus. Coloration varies less in the western hognose than in the eastern species. The dorsal background color is a shade of light brown, brownish-gray, buffish-brown, or reddish-brown. The dark blotches vary from a medium grayish-brown, buffish-brown or olive to deep cinnamon or chocolate brown.

The pattern on the head is similar to that of the eastern species. There is a dark band across the posterior azygous scales and the anterior edge of the supraoculars and frontals and a broad dark band from the eye to the angle of the mouth. The latter band extends along the posterior edge of the eye and across the posterior supraoculars to the frontal, but the bands from the two sides usually do not meet. Two lateral and one middorsal elongate nuchal blotches extend forward to the parietal scales and may or may not connect with one another.

On the body a series of dark, middorsal blotches alternate with interspaces of background color. The dark blotches may be outlined with black, especially on the anterior and posterior borders, and sometimes also with light lines; or they may merge into the background color. Laterally there are one to four alternating series of dark blotches. The dorsal most of the lateral series of blotches is most distinct and is always present. The ventral series are more obscure and may be absent. The venter is usually black with irregular white, yellow, or orange blotches, although sometimes it appears pale with large black blotches. The undersurface of the tail is always black with little light spotting. Most of the above-described variations in color were seen in individuals from Harvey County.

A small specimen from College Station, Texas, described by Peterson (1950:160) had an interrupted middorsal dark line and one dorsolateral series of blotches. No albinistic, melanistic, erythristic, or other unpatterned western hognose snakes have been found.

Lepidosis

The scutellation of hognose snakes is typical of colubrid snakes except for three specialized features: an enlarged projecting sharp-edged rostral scale, one or many azygous scales located dorsally between the paired internasal scales and between the paired prefrontal scales, and a complete ring of ocular scales surrounding the orbit.

Heterodon platyrhinos. The enlarged rostral scale has a sharp projecting anterior edge, a flat anteroventral surface, and usually a longitudinal keel on the dorsal surface. A single median azygous scale (sometimes divided transversely or missing) separates the internasals and the anterior parts of the prefrontals. The frontal is no longer than wide. Usually 10 or 11 small ocular scales (7 to 13) surround the orbit in addition to the large supraocular. The nostril is between a pair of nasals. A single loreal (rarely two or more) lies between the posterior nasal and the oculars. Three anterior temporals (two to five) and four posterior temporals (three to six) lie posterior to the ocular ring. Most individuals have eight supralabials (seven to nine). Infralabials are more variable in number, usually 10 or 11 (9 to 14). A pair of large anterior chin shields is followed by two pairs (median and lateral) of small posterior chin shields. An irregular series of gular scales separates the chin shields and infralabials from the ventrals. The anal plate and subcaudals are divided. There are 114 to 141 ventrals in males and 128 to 154 in females, and there are 42 to 57 subcaudals in males and 34 to 51 in females. Clines in numbers of ventrals extend from an area of high values in the west-central part of the range (Edgren, 1952a:83-84, 155). The dorsal body scales are keeled (except for the first one to three rows on each side) and bifossate. Most individuals have 25 scale rows anteriorly (22 to 27) and at mid-body (21 to 27) and 19 scale rows anterior to the anus (16 to 21).

Heterodon nasicus. The cephalic scales resemble those of the eastern species. The dorsal surface of the rostral scale is more concave, the projection up-curved, and its edge thinner and, in anterior view, more rounded. Two to 28 small irregular azygous scales may separate the prefrontals from the frontal and the internasals from the rostral, as well as separating the pairs of internasals and prefrontals. The frontal is short, as wide as long, or wider. Small ocular scales usually number 10 or 11 (9 to 13). Usually there are two or more loreals (single or absent in *H. n. kennerlyi*). There are usually four anterior temporals (two to five) and five posterior temporals (three to seven). Typically, there are 10, 11, or 12 infralabials (9 to 13). The anterior chin shields are large, but the posterior chin shields are reduced or absent. The anal plate and subcaudals are divided. There are 129 to 147 ventrals in males and 139 to 156 in females, and there are 35 to 50 subcaudals in males and 26 to 41 in females. Clines in numbers of ventrals extend in all directions from an area of high values in western Kansas (Edgren, 1952a:70, 155). Dorsal body scales resemble those of the eastern species but are in 23 rows anteriorly (21 to 26) and at mid-body (19 to 26) and 19 rows anterior to the anus (16 to 21).

Dentition and Jaw Structure

The palate and upper jaw are extremely loose and mobile in hognose snakes, because the quadrate is relatively longer than in most colubrids and the short maxilla has well-developed movable articulations. Edgren (1952a:6-9) and Weaver (1965:283-293) described the palatal structure of hognose snakes.

Anterior to the middle of the dorsomesial surface of the maxilla, a shallow depression receives the rounded end of a strong process of the prefrontal. The maxilla has two processes on its mesial surface. The anterior one forms the posterior border of the prefrontal articulation, receives the insertion of a strong ligament of this articulation, and underlies the short arm of the hook-shaped palatine bone to which it is attached by the palato-maxillary

ligament. A Y-shaped ectopterygoid movably articulates with the posterior mesial process of the maxilla. The lateral arm of the ectopterygoid articulates with the lateral face of the posterior end of the maxilla just dorsal to the socket of the lateral enlarged tooth. Anterior to this articulation, the postfrontal-maxillary ligament connects the ventral end of the postfrontal with the maxilla.

The maxillary teeth are diacranterian, with two large, laterally compressed fanglike teeth posterior to a diastema. Although Ditmars (1912:204) reported that these teeth have "faint traces of an anterior groove," other investigators, including myself, have found them to be ungrooved (Kapus, 1964:137; Weaver, 1965:284). The enlarged teeth are directed posteriorly, medially, and slightly ventrally from the posterior end of the maxilla. One enlarged tooth is attached anterior and slightly mesial to the other. Usually there are one or more replacement teeth beside each functional enlarged tooth.

The enlarged teeth lie parallel with the roof of the mouth and are enclosed in a fleshy sheath of buccal mucosa when the mouth is closed. The looseness of attachment of the maxilla allows lateral rotation, posterior movement, and a slight vertical rotation to erect the enlarged teeth and extend them from the sheath when the mouth is open. When erected, the enlarged teeth are oriented in a posteroventral direction.

Heterodon platyrhinos. The maxilla is relatively long and slender. The anterior mesial process extends straight mesially from the maxilla. There are 12 (11 to 13) teeth on the maxilla, 7 on the palatine, 12 on the pterygoid and probably 19 to 20 on the dentary (Edgren, 1952a:8-9).

Heterodon nasicus. The maxilla is shorter, deeper, and more massive, with longer and thicker teeth. The anterior mesial process of the maxilla curves posteriorly toward the posterior process. There are 10 teeth on the maxilla, 4 on the palatine, 9 on the pterygoid, and probably 14 on the dentary (Edgren, *loc. cit.*).

Hemipenis

The hemipenis of *Heterodon* is subcylindrical and bilobed distally. The sulcus spermaticus is bifurcate. The ornamentation is differentiated with calyculate, spinose, and nude portions.

The basal undivided portion of the hemipenis is spinose. On the side opposite the sulcus are two longitudinal rows of large spines with two or three spines in each row. Between each row of large spines and the sulcus there are medium-sized spines. The whole surface of the hemipenis between these spines is covered with spinules. Most of the anterior side of the hemipenis has only spinules. There is a narrow nude margin at the base of the hemipenis.

The distal lobes of the hemipenis are covered with papillate calyces. The calyces and papillae continue beyond the base of the lobe for a short distance along the sulcus. On the side opposite the sulcus, the proximal calyces tend to be more elongate and form a small papillate area between the distal ends of the rows of large spines. A narrow nude margin separates parts of the calyculate and spinose portions.

Edgren (1952a:11) reported that the hemipenis of the eastern species was longer and more slender than that of the western species. However, I found little difference for the *in situ* length of the hemipenes of the two species in Harvey County. The bilobed portion is almost one-third of the length of the hemipenis in the eastern species but less than one-fourth of the hemipenial length in the western species (Table 7).

TABLE 7. *In Situ* Position of Penial Structures With Reference to Subcaudal Plates of Hognose Snakes. Data Are From Eight Snakes Examined by Edgren (1952a:13) and From Ten Specimens Collected in Harvey County, Kansas.

	Western Hognose Snake		Eastern Hognose Snake	
	Mean subcaudal number		Mean subcaudal number	
	Edgren	Harvey county	Edgren	Harvey county
Insertion of large retractor muscle....	15.5 (15-16)	18.0 (14-21)	16.2 (15-18)	18.0 (16-19)
Bifurcation of hemipenis.....	12.3 (12-13)	14.3 (11-16)	12.0 (11-13)	12.7 (11-14)
Bifurcation of sulcus spermaticus.....	6.3 (6-7)	7 ^a	6.3 (6-7)	7 ^a

a. Based on only one measurement.

The hemipenis of the eastern hognose has fewer medium-sized spines, but the surface is more densely covered with spinules than that of the western species. One specimen of the eastern hognose had 10 medium-sized spines, whereas specimens of the western hognose had from 13 to more than 20.

Teratology

A number of dicephalic eastern hognose snakes have been observed (Cunningham, 1937:18, 29, 47-48, 56-58; Meyer, 1958:128). There are no records of this aberrancy for the western species, although some of the early records reported by Cunningham were accompanied by inadequate data concerning specific identification.

Minor aberrations of the scales were noted in some hognose snakes from Harvey County. Of the 124 eastern hognose snakes trapped, eight (six per cent) had one or more small ventral plates that extended less than two-thirds of the width of the belly, one had the ventral plate anterior to the anal plate divided, and two had a number of subcaudal plates undivided. Of the 241 western hognose snakes trapped, 32 (13 per cent) had one or more small ventral plates, five (two per cent) had one or more ventral plates divided, and 16 (seven per cent) had one or more subcaudal plates undivided.

TAXONOMIC STATUS

Taxonomic Position of *Heterodon*

Snakes of the genus *Heterodon* are primitive members of the family Colubridae. Dunn (1928:21) placed the genus *Heterodon* in the subfamily Ophiinae that included more than 50 other genera of snakes that have a forked sulcus spermaticus. Smith (1964) proposed a separate subfamily to include the North American genus *Heterodon*, the South American genera *Lystrophis* and *Xenodon*, and possibly the Malagasian genus *Lioheterodon*. He resurrected

the name *Heterodontinae*, but later concurred with Rossman and Wilson (1965:285) in using the name *Xenodontinae* for this group. Smith (1964:288) cited the following peculiarities of this subfamily, some of which are indicative of viperid relationship: adrenal gland enlarged; diet of toads; and epaxial trunk muscles and the posterior adductor externus superficialis mandibulae like those of viperids and different from those of colubrines. The maxillae of these xenodontine snakes are shortened and can be rotated to erect large posterior teeth (Anthony and Serra, 1951:46; Peters, 1953:330). *Lystrophis* has a pattern of defensive behavior similar to that of *Heterodon* (Schmidt and Inger, 1957:213).

Heterodon platyrhinos Latreille

Several variants of the eastern hognose that differ in coloration, degree of modification of the rostral scale, or absence of the azygous scale, have been named as subspecies or full species. However, the variation in this species, although notable, does not have a definable geographic pattern. Edgren (1952b:1-2), in the latest revision of the genus, concluded that no populations were sufficiently distinct to warrant subspecific designation.

Heterodon nasicus Baird and Girard

Edgren (1952b:2-4) recognized three subspecies, the plains hognose snake (*H. n. nasicus*), the Mexican hognose snake (*H. n. kenneryi*) and the dusty hognose snake (*H. n. gloydi*), and characterized them as follows:

Heterodon nasicus nasicus Baird and Girard

"*Diagnosis*. A series of 9-28 scales in the azygous area; dorsal blotches more than 35 in males and more than 40 in females. Generally two or more loreals on each side.

"*Range*. Texas panhandle and adjacent New Mexico north through western Oklahoma and Kansas to southwestern Manitoba and southeastern Saskatchewan in Canada; prairie portions of Minnesota, and prairie relicts in Illinois; eastward extension along the Prairie Peninsula in Missouri is to be expected" (pp. 2-3).

Heterodon nasicus gloydi Edgren

"*Diagnosis*. Generally similar to *Heterodon nasicus nasicus*; lepidosis identical. Color pattern and intensity differ somewhat from the typical subspecies. Dorsal blotches less than 32 (23-32) anterior to the vent in males; less than 37 (28-37) in females. The individual blotches tend to be obscured; they are generally a light grayish-brown and are not sharply defined by black borders, as is generally the case in *nasicus nasicus*. Ground color grayish-tan, not much differentiated from the color of the blotches. The coloration of the snake gives the appearance of being faded. . . .

"*Range*. Southeastern Kansas and southeastern Missouri, eastern Oklahoma, and all of Texas except for the panhandle, trans-Pecos Texas, and the extreme southern Rio Grande Valley" (p. 3).

Heterodon nasicus kenneryi Kennicott

"*Diagnosis*. Similar to *H. n. gloydi* in most respects but with only 2-6 azygous scales; loreals generally single (occasionally double or absent).

"*Range*. Mexico from Tamaulipas and central San Luis Potosi north and west along the Cordillera Occidental, invading the United States in extreme southern Rio Grande Valley, trans-Pecos Texas, southwestern New Mexico and southeastern Arizona" (p. 3).

Heterodon n. gloydi was described by Edgren (1952a:206, 212-213) on the basis of 36 specimens from Texas, Oklahoma, Kansas, and Missouri. I have

not reviewed all of this material, but, in an attempt to identify the population in Harvey County, Kansas, I examined 15 specimens (including nine that Edgren did not use) of *H. n. gloydi* from Texas and 28 specimens of *H. n. nasicus* from South Dakota, Colorado, North Dakota, Wyoming, and Nebraska. This study and the description (Ernest C. Tanzer, *in litt.*) of a live *H. n. gloydi* from Brazos County, Texas, have convinced me that the color differences between *H. n. nasicus* and *H. n. gloydi* reported by Edgren are not consistent (Plate 3).

The numbers of dorsal blotches differ in these two subspecies. Edgren (1952a:68) reported that "83.7% of the northern population complex is within the range of blotch variability defined above, and 88.0% of the southeastern complex of populations is within the limits described for it." All of the specimens that I examined from eastern Texas were within the limits of number of blotches defined for *H. n. gloydi*, whereas of the 28 specimens from populations north or west of Kansas, all except four were within the limits of *H. n. nasicus*. The lengths of dorsal blotches and interspaces were measured along the midline in numbers of dorsal scales. The two subspecies differ in both the size and spacing of blotches. The length of one dorsal blotch and one interspace taken together shows least variation within a population (Table 8).

TABLE 8. Size and Spacing of the Dorsal Blotches of *Heterodon nasicus nasicus* and *Heterodon nasicus gloydi* Measured in Numbers of Dorsal Scales.

	<i>H. n. gloydi</i> (11 specimens)	<i>H. n. nasicus</i> (9 specimens)
Mean length of blotches	2.6 (2.2-3.0)	2.0 (1.7-2.3)
Mean length of interspaces	2.0 (1.4-2.5)	1.5 (1.2-1.9)
Mean length of blotch and interspace	4.6 (4.2-5.0)	3.5 (3.2-3.7)

Figure 10 summarizes the distribution of specimens of *H. n. gloydi* and the relation of this subspecies to neighboring subspecies. In eastern Texas, where populations with low numbers of dorsal blotches are found, *H. nasicus* is rare (see p. 290), as the species has probably become less abundant in the eastern part of its range since the Xerothermic period (Smith, 1957:212). Most of the populations in the eastern part of Oklahoma are probably intermediate. In Kansas the specimens designated by Edgren (1952a:212-213) as *H. n. gloydi* are either from areas where populations are intermediate in number of dorsal blotches or from isolated populations. There is a broad area of intermediate populations and further investigations will probably indicate that a rather uniform cline exists. The cline runs from southeast to northwest. A similar cline in number of dorsal blotches is evident in the southern subspecies, *H. n. kennerlyi*, from east to west (Table 9).

Since, so far as is known at present, the only reliable difference between *H. n. nasicus* and *H. n. gloydi* is the number of dorsal blotches and this variation may constitute a cline and since nonconcordant clinal variation in the number of ventral plates has been demonstrated by Edgren (1952a:70) in *H. nasicus*,

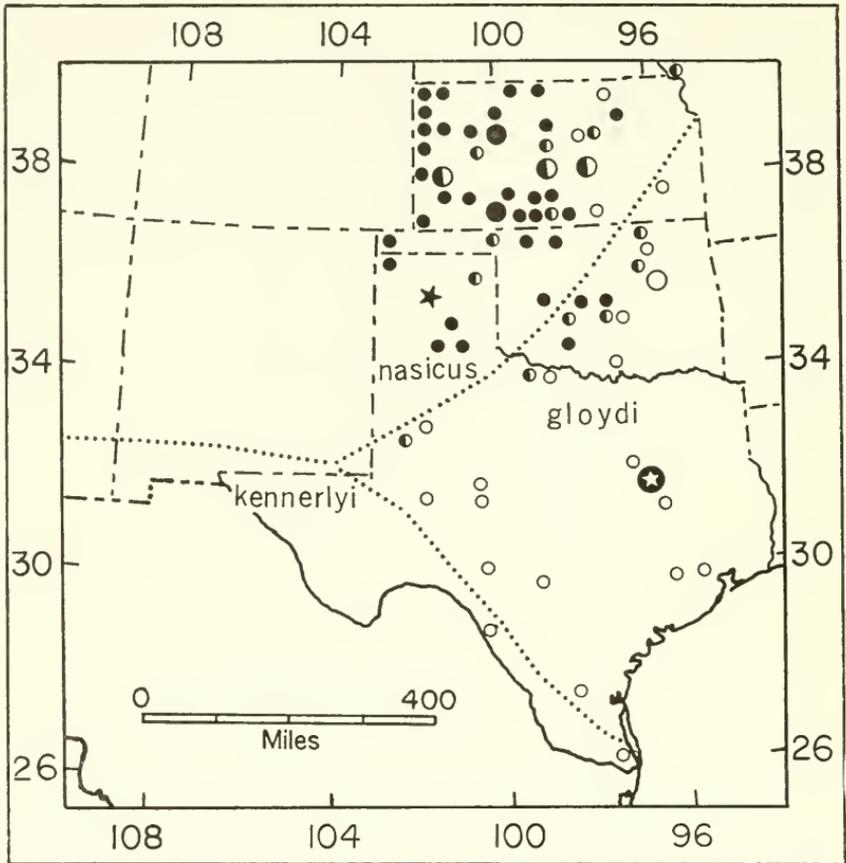


FIG. 10. The subspecies of the western hognose snake (*Heterodon nasicus*) in Kansas, Oklahoma, and Texas. Dotted lines mark the boundaries of the ranges of the three subspecies as mapped by Edgren (1952a:142). The symbols represent specimens from various counties that have been examined either by Edgren or myself. Dots represent counties from which at least 75 per cent of the specimens have numbers of dorsal blotches characteristic of *H. n. nasicus*, and circles represent counties from which 75 per cent of the specimens are typical of *H. n. gloydi*. Half circles represent counties with samples of specimens that are intermediate. Small symbols represent counties from which there are samples of only one to four specimens, and large symbols represent counties from which there are five or more specimens. The type locality of *H. n. nasicus* (Amarillo, Texas) is indicated by a black star and the type locality of *H. n. gloydi* (Wheelock, Texas) is indicated by a white star.

it is questionable whether the southeastern complex of populations is distinct enough to merit subspecific designation. More complete studies of variation in populations of this species are needed to determine the validity of the subspecies *gloydi*.

The population in western Harvey County, Kansas, is intermediate in number of dorsal blotches between *H. n. nasicus* and *H. n. gloydi*. Twenty-five per cent of 112 males from Harvey County were within the range of dorsal blotch counts of *H. n. gloydi*, 20 per cent were intermediate, and 55 per cent were within the

TABLE 9. Mean Number of Dorsal Blotches on Specimens of *Heterodon nasicus kennerlyi* Taken in Various Parts of Its Range (Data From Edgren, 1952a:64).

State	Male		Female	
	Number	Mean number dorsal blotches	Number	Mean number dorsal blotches
Texas.....	7	30.6 (23-36)	4	32.5 (30-33)
Coahuila.....	4	31.0 (29-34)	2	34.5 (34-35)
Chihuahua.....	2	33.0 (32-34)	2	38.5 (38-39)
Arizona.....	3	37.5 (35-39)	11	39.0 (35-42)

range of *H. n. nasicus*. For 124 female snakes, the respective percentages were 31 per cent, 21 per cent, and 48 per cent.

FOSSIL RECORD AND EVOLUTIONARY HISTORY

Fossil Record

The fossil record of hognose snakes rests, for the most part, on scattered vertebrae. The oldest fossils are three precaudal vertebrae from the Valentine formation (Upper Miocene to Lower Pliocene) of Brown County, Nebraska, *Paleoheterodon tiheni* Holman (1964b:633-634). He stated, "the holotype of *Paleoheterodon tiheni* more closely resembles Recent *H. nasicus* and *H. simus* than *H. platyrhinos* in having a flatter, less distinct hemal keel, and in the more rounded anterior borders of the prezygapophyseal faces."

The fossil species *Heterodon brevis* Auffenberg (1963:174) was described on the basis of a precaudal vertebra from the Alachua formation (Middle Pliocene) of Alachua County, Florida. Auffenberg stated that *H. brevis* "is closest to *platyrhinos* and direct phyletic relationship is hardly questionable."

Three maxillary bones and one palatine bone from the Rexroad formation (Upper Pliocene) of Meade County, Kansas, were basis for the name *Heterodon plionasicus* Peters (1953). Peters (1953:331) stated that the "new species is so much like the modern *nasicus* that a direct phylogenetic relationship is hardly questionable." Vertebrae and a quadrate bone from a Middle Pliocene deposit in Beaver County, Oklahoma, and two other Upper Pliocene deposits in Meade County, Kansas, have been assigned to *H. plionasicus* (Brattstrom, 1967:190-193).

Heterodon nasicus Baird and Girard is known from Pleistocene deposits of the Yarmouth and Sangamon interglacial periods in Kansas, of the Illinoian glacial period in Oklahoma, and of the Kansan and Wisconsin glacial periods and the Sangamon interglacial period in Texas (Holman, 1963:162, 1964a:81, 1965:104; Brattstrom, 1967:194). Transition from *H. plionasicus* to *H. nasicus* probably occurred "near the end of the Pliocene and beginning of the Pleistocene" (Brattstrom, 1967:196).

Heterodon platyrhinos Latreille is known from two Upper Pliocene deposits and from two Pleistocene deposits of the Yarmouth and Sangamon interglacial periods in Kansas, from one Pleistocene deposit of the Nebrascan glacial period in Nebraska, and from nine Middle Pleistocene to Recent localities in Florida (Holman, 1958:278, 1959:100; Auffenberg, 1963:173; Brattstrom, 1967:191-194).

Fossil vertebrae of *Heterodon simus* Linnaeus have been collected from five Middle to Late Pleistocene sites in Florida (Auffenberg, 1963:173; Holman, 1959:100).

Evolutionary History and Relationships

Snakes of the genus *Heterodon* are a specialized primitive group of colubrids, possibly closely related to the ancestral stock of the viperids (Smith, 1964:288). Weaver (1965:301) suggested that a xenodontine protoviper gave rise to *Heterodon*, *Xenodon*, and the solenoglyphous snakes. *Heterodon* retained a number of primitive viperlike characters, while *Xenodon* evolved certain myological characters resembling those in advanced colubrid snakes (Weaver, 1965:299-300).

From Eocene to Pliocene times, there was no land connection between South America and North America (Simpson, 1953:49). The ancestral xenodontine stock must have been in the New World prior to the Middle Eocene (South American faunal element of Dunn, 1931; Stuart, 1957:91). Part of this ancestral stock differentiated in South America into the genera *Lystrophis* and *Xenodon*, while part of this xenodontine stock in North America differentiated into the genus *Heterodon*.

Besides having some primitive colubrid and viperidlike characteristics, hog-nose snakes are specialized for fossorial habits and have a specialized palatal structure. Edgren (1952a:151) stated, "Unquestionably *nasicus* is the most bizarre of the three species, and, assuming a progressive evolution toward a more fossorial habitus, it is doubtless the most highly evolved." Weaver (1965:298) considered *H. platyrhinos* to be the most generalized species in the genus. Some characters of *H. platyrhinos* that more closely resemble those of a generalized colubrid snake include a longer maxilla with more teeth, a smaller rostral scale with less projection, a longer head, a somewhat longer tail, and fewer azygous scales. Such generalized characters are probably primitive in this genus. Large size is probably primitive, since *H. plionasicus* was larger than *H. nasicus* (Peters, 1953:328).

The fossil record indicates that the *platyrhinos*-line and the *nasicus*-line have had a long history of separate evolution. The similarity of the vertebrae of *Paleoheterodon tihenii* to those of *H. nasicus* indicates either that the *nasicus*-line and the *platyrhinos*-line were already separate in this pre-*Heterodon* stock of Miocene-Pliocene time or that *H. nasicus* has retained primitive vertebral characteristics that have been modified in *H. platyrhinos*. By Middle Pliocene there was a *platyrhinos*-like eastern form (in Florida) as well as the *nasicus*-like western form. By Upper Pliocene the maxillary bone of the western form (in Kansas) had become almost as specialized as that of modern *H. nasicus* (Peters, 1953). Both *H. plionasicus* and *H. platyrhinos* were present in Kansas at this time. All three modern species have existed since Pleistocene times.

Edgren (1952a:151-153) concluded that *H. nasicus* and *H. simus* are on separate evolutionary lines, each developing from a pre-*platyrhinos* stock, and

the similarities between them are due to parallel evolution. Edgren's conclusion is based upon the untenable assumption that either *H. nasicus* evolved from *H. simus*, or they both evolved in parallel fashion from *H. platyrhinos*. *Heterodon nasicus* and *H. simus* have many characteristics in which they resemble one another more than *H. platyrhinos*, including hemipenial characteristics, vertebral characteristics, size, cranial osteology, cranial myology, head proportions, maxillary size, azygous scales, and possibly defensive behavior (Edgren, 1952a; Auffenberg, 1963:172; Holman, 1965:104; Weaver, *loc. cit.*). Weaver (*loc. cit.*) considered *H. nasicus* and *H. simus* to be related. These two species are so similar that Cope (1875:43) and others considered *H. nasicus* to be a subspecies of *H. simus*. On the other hand, *H. simus* more closely resembles *H. platyrhinos* in number of dorsal scale rows, larger number of maxillary teeth, and a few osteological and myological characters (Edgren, 1952a; Weaver, *loc. cit.*).

The similarities between *H. nasicus* and *H. simus* are best explained by a common ancestry from a pre-*nasicus* line that was early separated from the pre-*platyrhinos* line. Modifications in numbers of scale rows and maxillary teeth have occurred since the pre-*nasicus* and pre-*simus* populations became separated. The fact that the two complete maxillary bones of *H. plionasicus* have nine (?) and ten teeth (Peters, 1953:328-329) indicates that this separation probably occurred prior to the Upper Pliocene (*H. nasicus* usually has ten maxillary teeth and *H. simus* has 11 or 12 maxillary teeth).

Heterodon simus today is confined to xeric habitats on the southeastern coastal plain (Weaver, 1965:277). The pre-*simus* population probably spread eastward along the Gulf Coastal Plain from the center of origin of the pre-*nasicus* line in the midwestern grasslands. At this time it was already reproductively isolated from the pre-*platyrhinos* population and had evolved many of the characters found in both *H. nasicus* and *H. simus*. The pre-*simus* population in the southeastern United States then became geographically isolated from the pre-*nasicus* population.

Other distributional data also support an eastward spread of western forms. Blair (1958:444-445) stated, "The Floridian fauna also includes a considerable element of species that belong to groups with centers of distribution in the Southwest, where they are generally adapted to more xeric conditions than exist today on the coastal plain. The presence of this western element in Florida suggests past climatic fluctuations on the coastal plain that favored eastern spread." There is fossil evidence that one early eastward migration to Florida occurred between the Lower Miocene and Middle Pliocene (Auffenberg, 1963:209).

GEOGRAPHIC RANGE AND HABITAT

Geographic Range

The limits of the geographic ranges of the eastern and western hognose snakes are difficult to delineate because both species exist in isolated populations beyond the limits of the continuous range. Also, they are not commonly collected and have probably been overlooked in some areas where they occur in small numbers. In the following discussion and on the distribution maps, the range of each species has been divided into a central continuous range from which there are many records of occurrence in varied habitats and a peripheral

range where the species is rare, where the species is locally common only in more favorable habitat, or where the records of occurrence are too few to determine the status of the species. The distribution and abundance of these two species has changed in some areas since settlement, and their present distribution in intensively cultivated or otherwise disturbed habitats in their continuous ranges may be greatly restricted.

The type of climax plant community and the type of soil are important direct and indirect factors affecting the distribution of hognose snakes, even though most plant communities are disturbed or changed at present. Names of plant communities used in the following discussion follow Küchler (1964) unless indicated otherwise. Soil types were determined from county soil survey maps for Kansas and from Gray and Galloway (1959), Ableiter, *et al.* (1960), Gould (1962), and collection data.

Heterodon nasicus (in Kansas). Many authorities (Smith, 1956:229; Conant, 1958:330; and others) have indicated that the range of the western hognose includes almost the entire state of Kansas. However, this species is commonly and continuously distributed only in the western half of the state (Fig. 11). I obtained locality data for specimens of the western hognose from Kansas in collections at the University of Kansas Museum of Natural History, Kansas State University, Fort Hays Kansas State College, Kansas State Teachers College at Emporia, University of Michigan Museum of Zoology, Chicago Natural History Museum, and Chicago Academy of Sciences. Of 128 specimens 121 were collected in the western region of Kansas shaded in Figure 11. Specimens

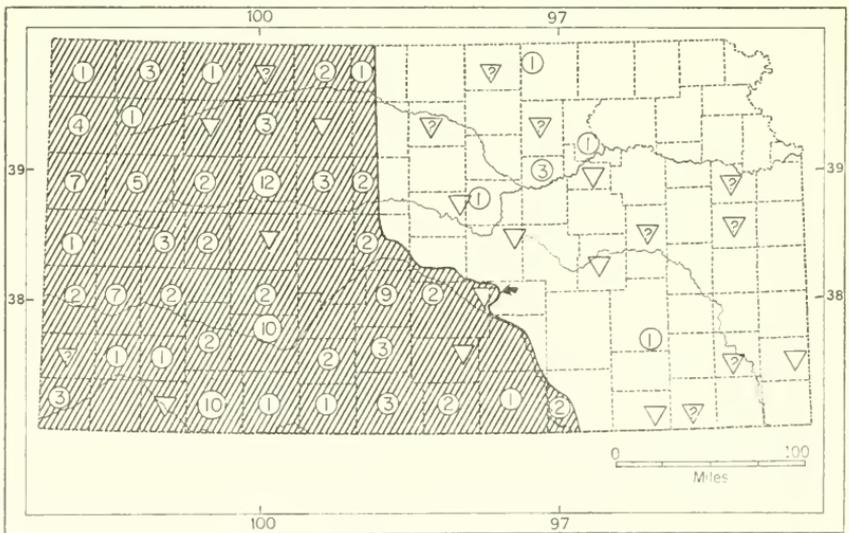


FIG. 11. The distribution of the western hognose snake in Kansas. The continuous range, where the species is widely and relatively commonly distributed, is shaded (see text). Circled numbers in counties indicate numbers of specimens in some university and museum collections (see text) or collected by me outside of Harvey County. Triangles denote counties from which there are reports of western hognose snakes but no existing specimens. Triangles with question marks denote records reported by Branson (1904:378). The arrow denotes the location of the study areas in Harvey County where many individuals were examined in my study.

have been collected from 38 of the 54 counties that are wholly or partially within this region. Western hognose snakes have been observed in at least eight of the remaining 16 counties.

There are a few substantiated records of the western hognose from outside this western region in Kansas, primarily in sandy habitats (Fig. 11). These include: "area of sand and rocks" in Washington County (UMMZ 67391; Burt and Burt, 1929b:456); sand dunes in Dickinson County (CNHM 18140-1; CA 5296; Burt and Hoyle, 1934:205); Bavaria, Saline County, and eastern Ellsworth County (CNHM 28458; Burt and Hoyle, *loc. cit.*); near Manhattan, Riley County (Cloyd, 1929:44; Burt and Burt, 1929a:10); Fort Riley, Geary County (Burt, 1933:196); and an area of "black jacks . . . in sand to sandy soil" in Greenwood County (KU20321; Dr. Claude W. Hibbard, *in litt.*).

There are other records of the western hognose from eastern Kansas that are questionable because there are no existing specimens to substantiate them: Roxbury, McPherson County (Munro, 1949a:133); Chase County (Breukelman and Clarke, 1951:544); Peru in Chautauqua County (Breukelman and Smith, 1946:107); and Crawford County (Hall and Smith, 1947:451). Mr. Robert J. Mangile of Pittsburg, Kansas, who has been collecting reptiles in Crawford County for a number of years, has not found any western hognose snakes, although he has visited the site of the previous collection.

Branson (1904:378), after examining collections at colleges, universities, and several high schools, recorded the western hognose from Clay, Republic, Mitchell, Lyon, Douglas, and Franklin counties in eastern and central Kansas. He reported sight records from Montgomery and Neosho counties. Cloyd (1928:121) concluded that Branson's record for Franklin County was probably in error. There are no existing specimens of the western hognose from Douglas County, although many herpetologists have collected there since 1904. Some of the other records listed by Branson for eastern Kansas probably were in error or were from local populations that have since become extinct.

In Kansas the western hognose is found primarily in short and mixed grass prairie and sand prairie. It is found commonly in the Grama-Buffer Grass steppe and the western two-thirds of the Bluestem-Grama prairie and is most abundant in the Sandsage-Bluestem Prairie. Western hognose snakes have been collected on many soil types in western Kansas, but they are most abundant on Tivoli dune sand. Most known collection sites are in the more widespread Keith-Colby and Hastings-Holdrege silt loam.

Abundant populations are found farther east in southern Kansas, where sandy land is prevalent. In northern Kansas the western hognose may be present as far east as the eastern edge of the Bluestem-Grama prairie, but is uncommon in north-central Kansas. Local populations exist in sandy habitats along the Kansas River and its tributaries, at least as far east as Riley County. It is also found, at least in local populations, in the Cross Timbers community on sandy soils in southeastern Kansas.

There may be other local populations in eastern Kansas, particularly on sandy soils along rivers, but the western hognose is certainly absent from most of the Bluestem Prairie and Oak-Hickory Forest. Some relict populations may have become extinct since settlement.

Heterodon nasicus (total range). Edgren (1952a:140) stated, "Generally speaking the range of *Heterodon nasicus* is closely correlated with the grassland

areas of the west-central portion of the United States." Analysis of the records of occurrence indicates that it is further limited largely to the short grass and mixed grass prairie. The eastern limits of its continuous range north of Kansas are within or at the eastern edge of the mixed grass prairie and in the south at the eastern edge of savanna communities (Fig. 12).

In its range north of Kansas the western hognose snake is primarily found in the Grama-Buffalo Grass, Wheatgrass-Needlegrass, and Nebraska Sandhills Prairie major community types and its found less commonly in the Grama-Needlegrass-Wheatgrass and Wheatgrass-Bluestem-Needlegrass communities. It was probably found only in local colonies on disturbed or sandy sites in the Bluestem Prairie before settlement.

In Nebraska, south of the Platte River, six specimens have been collected in Thayer, Clay, Adams, and Webster counties (Hudson, 1942:52) in what is termed Bluestem Prairie by Kuchler (1964). However, the grassland in most of these counties is transitional to mixed grass prairie (Weaver and Bruner, 1954:117; Weaver, 1960:83-85). North of the Platte River, the eastern limits of the continuous range are probably within the Wheatgrass-Bluestem-Needlegrass prairie, although one specimen has been collected from Wayne County in eastern Nebraska, probably from a sandy area in the western part of the county (Hudson, *loc. cit.*).

There are relatively few records of the western hognose from South Dakota and North Dakota. They are found locally in northwestern South Dakota and southwestern North Dakota, especially in the Badlands and near the Missouri River valley. They are also found in sandy and gravelly habitats in southeastern North Dakota, northeastern South Dakota, and western Minnesota (Breckenridge, 1944:112; Dr. George C. Wheeler, *in litt.*). They are found in north-central North Dakota, especially in sandy habitats of glacial Lake Souris. Stanley (1941:267) stated that the species was common and not limited to sandy areas near Minot.

The western hognose is relatively common in western Texas and Oklahoma in the short grass, mixed grass, and savanna communities. It is not found in the Bluestem Prairie, Oak-Hickory Forest, or Oak-Hickory-Pine Forest of eastern Oklahoma; but it is common in the savanna type Cross Timbers community with sandy soil that lies east of the mixed grass prairie in Oklahoma. In Texas the western hognose snake is found on the High Plains, Rolling Plains, Trans-Pecos, and South Texas Plains of Gould (1962:10-14). The species is probably absent from the Edwards Plateau "except for local areas where the ecology is favorable" (Dr. Gerald G. Raun, *in litt.*).

In eastern Texas the western hognose is rare (Dr. John W. Forsyth, *in litt.*; Dr. Bryce C. Brown, *in litt.*; Dr. Richard J. Baldauf, *in litt.*). Nine specimens have been collected in Brazos, Robertson, and Colorado counties, and the species has been reported from Waller County (Sabath and Worthington, 1959:32). They were probably from the Post Oak Savanna with sandy soils (described by Gould, 1962:9-10; termed Oak-Hickory Forest by Kuchler, 1964). The western hognose is found on the Southern Cordgrass Prairie (Gulf Prairies and Marshes of Gould, 1962:8-9), at least near Galveston, Texas. It is not found in the Oak-Hickory-Pine Forest (Pineywoods of Gould, 1962:8) of eastern Texas and has not been collected in the Blackland Prairie, Fayette Prairie, or the Cross Timbers (except one specimen from Waco, McLennon County, that came from either the Cross Timbers or the prairie).

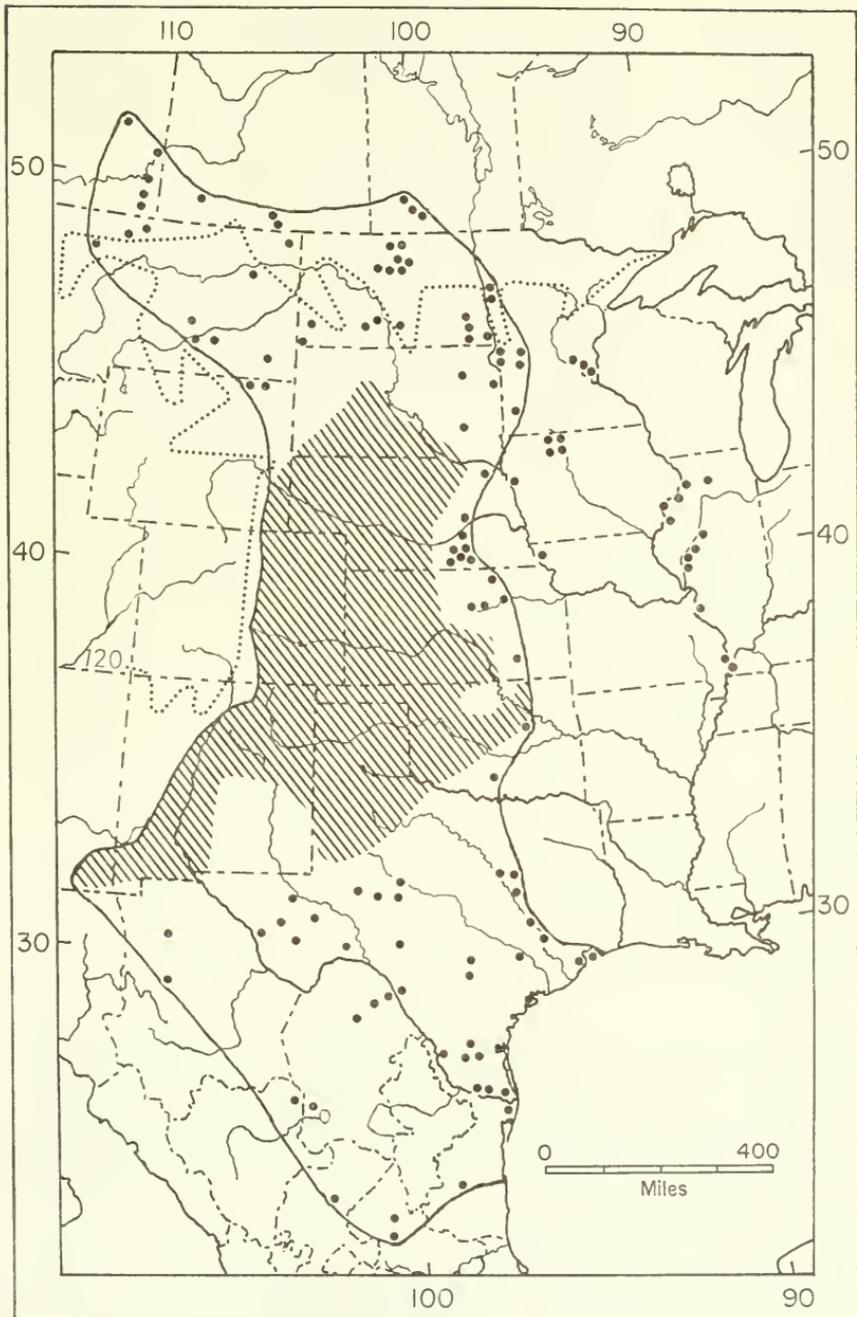


FIG. 12. The geographic range of the western hognose snake. The shaded area is the continuous range of the species (see text). In the peripheral range, where the species is rare or only locally common in semi-isolated populations, or where the records of occurrence are too few to determine the status of the species, localities of apparently valid records in the literature or of specimens are denoted by dots. Isolated relict colonies outside the main range are indicated by dots in Minnesota, Iowa, Missouri, and Illinois. The dotted line connects localities having an average frost-free growing season of 120 days (Espenshade, 1964:53).

A number of isolated relict colonies are probably remnants of an eastward extension of the range of the western hognose snake in the Prairie Peninsula during the postglacial Xerothermic period (Smith, 1957:211-212). Colonies have been found along the Missouri River in Holt County, Missouri (Anderson, 1945:274); near Blue Lake in Monona County, Iowa (Ruthven, 1919:2); in northwest Iowa in Emmett, Dickinson, Palo Alto, and Clay counties (Guthrie, 1926:175; Ruthven, 1910:198); along the Mississippi River in Anoka, Sherburne, and Ramsey counties, Minnesota (Breckenridge, 1944:110), in Whiteside, Rock Island, Mercer, Henderson, and Monroe counties, Illinois (Moll, 1962:207-208), and in Scott and Mississippi counties, Missouri (Evans, 1940:53); along the Illinois River in Tazewell, Mason, Cass, and Morgan counties, Illinois; and in Lee County, Illinois (Moll, *loc. cit.*). The specimen from Monroe County, Illinois, was collected in a hill prairie with soil derived from loess (Dr. Philip W. Smith, *in litt.*). The other colonies along the Mississippi and Illinois rivers are in sand prairies, similar in many respects to the sand prairies in Harvey County, Kansas (Table 10; also see Vestal, 1913). The area around Blue Lake in Monona County, Iowa, is sandy flood plain forest and sand prairie. The colony in northwestern Iowa is in a mixed grass prairie (Dr. Kenneth D.

TABLE 10. Mechanical Analyses of Surface Soil From the Study Areas in Harvey County, Kansas, and From Areas Where Relict Colonies of Western Hognose Snakes Are Found.

Locality	Per cent soil particles in each size fraction		
	More than .90 mm.	.90 to .16 mm.	Less than .16 mm.
Harvey county, Kansas	trace	93.3	6.7
Monona county, Iowa	trace	95.0	5.0
Mason county, Illinois	trace	86.7	13.3
Henderson county, Illinois	trace	84.4	15.6

Carlander, *in litt.*; Ruthven, 1910:198). The specimens from northwestern Missouri were collected on silt loam soil near the flood plain of the Missouri River (Anderson, 1965:187; and *in litt.*).

There is no reliable evidence of relict colonies of the western hognose east of Illinois. Smith and Mittleman (1947:78) noted that a specimen in the University of Michigan Museum of Zoology supposedly had been collected along Wolf Creek in Bartholomew County, Indiana, by Harry T. Folger in 1925. Although there is sandy soil in this vicinity, the area was originally in heavy timber. Dr. Folger cannot remember collecting the snake, and it is probable that locality data from a collection of fish were transposed to a snake from another locality (Dr. Harry T. Folger, *in litt.*; Dr. Sherman A. Minton, Jr., *in litt.*).

The Rocky Mountains are a barrier limiting the westward distribution of the western hognose. It probably occurs throughout the Great Plains of eastern Montana, Wyoming, and Colorado to the foothills of the Rockies (below 6,000

feet in Colorado, Maslin, 1959:54). Few specimens have been collected in northern Wyoming and Montana, and it may only be present in local semi-isolated populations.

The southern mountains are not a barrier to dispersal, and the western hognose is found throughout the short grass and shrubsteppe communities of eastern and southern New Mexico and into southeastern Arizona. In Arizona it is not found outside the plains area in the southeastern corner (Gloyd, 1937:99). Its range extends as far northwest in New Mexico as Albuquerque and northern Santa Fe County and to elevations of at least 5,000 feet (Gehlbach, 1956:369).

The southern limits of the range of the western hognose are poorly known because it is rarely collected in Mexico. It is probably found in many parts of the xeric shrub grassland of northern Mexico. It extends south at least as far as southern San Luis Potosi on the east and Durango and Zacatecas on the west. It has not been collected in Nuevo León and only one specimen, without precise locality, is known from Sonora.

The range of the western hognose extends into southern Canada. The species is present, but rare and perhaps restricted to semi-isolated populations in favorable habitat, in much of the Grama-Needlegrass-Wheatgrass prairie of southern Alberta and Saskatchewan (Moore, 1953:173; Lewin, 1963:212). The species has not been collected in the Wheatgrass-Needlegrass prairie in eastern Saskatchewan but is present in western Manitoba on sandy soil in the mixed forest and prairie of the Oak Lake-Brandon-Spruce Woods Forest Reserve area (Logier and Toner, 1961:72-73; Mr. Francis R. Cook, *in litt.*).

Heterodon platyrhinos (in Kansas). The eastern hognose is most abundant

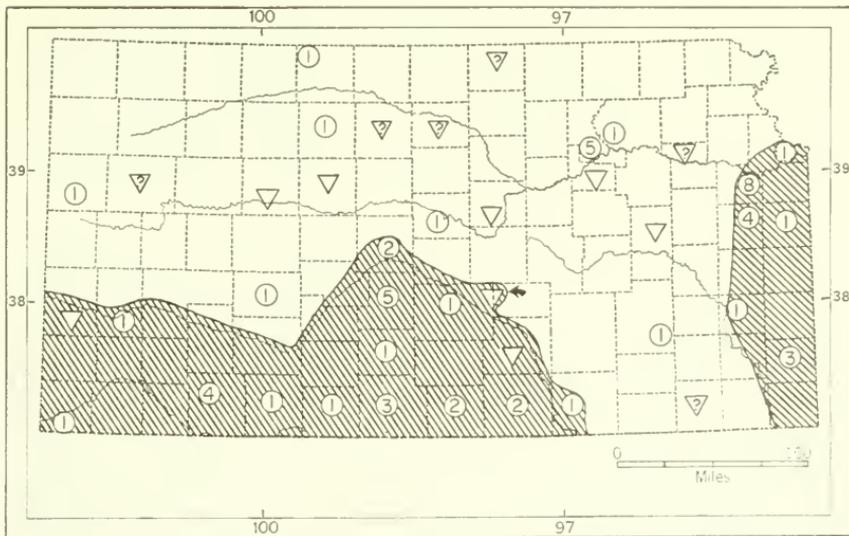


FIG. 13. The distribution of the eastern hognose snake in Kansas. Most specimens have been collected in the shaded areas. Circled numbers indicate the number of specimens from a county. Triangles denote counties from which there are reports of eastern hognose snakes but no existing specimens. Triangles with question marks denote records reported by Branson (1904:376). The arrow denotes the location of the study areas in Harvey County where many individuals were examined in my study.

in Kansas in the Great Bend Prairie Physiographic Province, in the eastern two tiers of counties, and along some of the larger river valleys (Fig. 13). It has been collected most often on sandy soil. In the Great Bend Prairie it is most abundant in the Sandsage-Bluestem prairie, although it is also found less commonly on the Bluestem-Grama prairie. The eastern hognose is less common than the western species in both communities. The eastern species is found in sandy areas along the Arkansas and Cimarron rivers to the western border of the state.

In Kansas, north of the sandy areas along the Arkansas River and west of the 97th meridian, only five specimens have been collected, and four of these are more than forty years old. Eastern hognose snakes are not common in northwestern Kansas and are probably restricted to more moist or loose-soiled habitats.

The eastern hognose is absent from most of the Bluestem Prairie except along rivers or possibly in a few sandy areas. The single record from Lyon County (no specimen is in existence) is from a sandy area (Clarke, Breukelman and Andrews, 1958:173), but further collecting in this area has produced no more specimens (Dr. Robert F. Clarke, *in litt.*). Other specimens are from along the Kansas River in Riley and Pottawatomie counties.

One specimen of the eastern hognose is from Greenwood County in the Cross Timbers, and other specimens have been collected in extreme eastern Kansas from the Kansas River valley south. The species is probably found in the Oak-Hickory Forest in the latter area in limited numbers, although it may be less abundant now than at the time of settlement.

Heterodon platyrhinos (total range). The eastern hognose is most abundant and widespread in the deciduous forest communities of eastern North America from the southern portions of New York, Pennsylvania, Ohio, Indiana, Illinois, and Missouri south to the Gulf Coast (Fig. 14). Although it is abundant in sandy regions on the Coastal Plain, such as the pine barrens of New Jersey, it has also been reported as common on clay, loam, and rocky soils. It is widely distributed in the Southern Mixed Forest, Oak-Hickory-Pine Forest, Oak-Hickory Forest, Mixed Mesophytic Forest and in parts of the Appalachian Oak Forest. It is found in the Appalachian Mountains on the lower hills and in the valleys (below 2,500 feet in Tennessee, King, 1939:572).

The northern limit of the range of the eastern hognose snake in New England lies in the transition between the Appalachian Oak Forest and the Northern Hardwoods Forest (mixed deciduous and conifer). The eastern hognose is found in the lower Hudson Valley in New York north to the sandy pine barrens west of Albany. It has been able to disperse into southwestern Pennsylvania along the Ohio-Allegheny valleys; but it is more common in the larger river valleys and the intermountain valleys of the Ridge and Valley Section east of the Allegheny Front. "The northern limit of the range of *Heterodon* in eastern Pennsylvania is generally the edge of the glaciated section of the Appalachian Plateau, but this boundary may be penetrated along river flood plains" (McCoy and Bianculli, 1966:153-155). It has not been reported from northeastern Ohio, and it is not common in the central glaciated part of the state; but it is common in the southern forested parts (Conant, 1951:270). On the south shore of Lake Erie the eastern hognose is found in colonies on sandy fossil beaches in northwest Ohio and on Presque Isle in Erie County, Pennsylvania. Whitcher (1942:62) suggested that it probably occurs in western New York near Lake Erie, but there is no evidence of such occurrence.

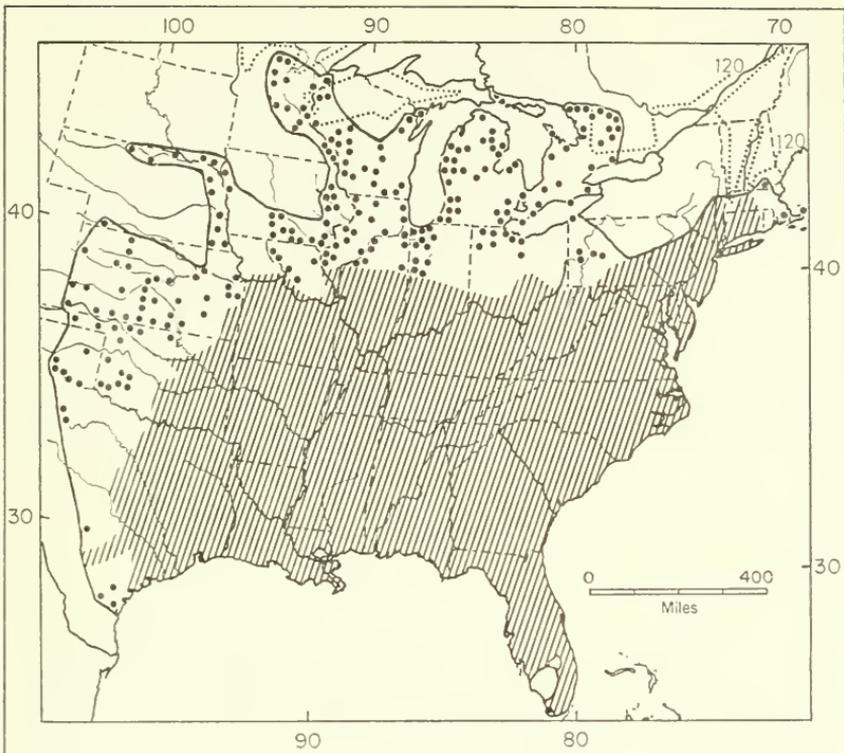


FIG. 14. The geographic range of the eastern hognose snake. The shaded area is the continuous range of the species (see text). In the peripheral range where the species is rare or only locally common in semi-isolated populations, or where the records of occurrence are too few to determine the status of the species, localities of apparently valid records in the literature or of specimens are denoted by dots. The dotted line connects localities having an average frost-free growing season of 120 days (Espenshade, 1964:53).

The eastern hognose is found on the peninsula of southern Ontario, the southern peninsula of Michigan, and in Wisconsin. It is present in the Oak-Hickory Forest, Oak Savanna, and Beach-Maple Forest, and it extends north into the Northern Hardwoods Forest and the Great Lakes Pine Forest. However, it is uncommon except in dry sandy areas, particularly along both coasts of Michigan, in western Wisconsin, and along the north shore of Lake Erie. Populations in parts of Michigan and Ontario have probably decreased in recent years (Creaser, 1944:239; Mr. Francis R. Cook, *in litt.*).

The western limit of the continuous range of the eastern hognose in the north is at the forest-prairie border. In Minnesota the species is restricted to "fluvial sands and sand dune areas" along the Mississippi, Minnesota, and St. Croix rivers. It has not been found on the sandy fossil beaches of glacial Lake Agassiz in the prairie region of Minnesota (Breckenridge, 1944:108; Hedrick and Holmes, 1956:125).

In Illinois the eastern hognose is abundant in the Oak-Hickory Forest south of the Shelbyville Moraine but is rare in much of the north on loam prairies. It is locally abundant on sand prairies in northern Illinois (Smith, 1961:191).

The eastern hognose has been collected in Missouri mainly from the forested

region south of the Missouri River. Most of the specimens collected north of the river are from counties along major river valleys. Only a few specimens have been collected from prairie regions.

In Iowa most specimens of this snake have been collected in southern and eastern parts that were primitively a mosaic of Oak-Hickory Forest and Bluestem Prairie. The eastern hognose is the third most abundant snake on the Eldon Research Area in Davis County, Iowa, that includes much shrubby and timbered land (Klimstra, 1950:430). It has spread northwest, probably up river valleys, as far as Polk, Madison, and Dallas counties.

The eastern hognose has spread north along the Missouri River and its tributaries and is found in extreme eastern Nebraska and western Iowa in forest regions and the edge of the prairie. It has been collected in the southeast corner of South Dakota near the Missouri River (Fishbeck and Underhill, 1959:111), and along the Niobrara River as far west as Valentine in Cherry County, Nebraska, but there is no evidence that it has spread into other parts of the Nebraska Sandhills Prairie. All reports of the eastern hognose snake from North Dakota and Montana are based on two old specimens for which the locality data are probably in error (Wheeler and Wheeler, 1966:16-17).

The eastern hognose has spread farther into the prairie region in the south. It is found throughout most of Oklahoma. It has been collected in the Oak-Hickory Forest, Oak-Hickory-Pine Forest, and Cross Timbers in the eastern part, and in the short grass steppe of western Oklahoma and the Texas panhandle. In northwest Texas it is restricted to the valleys of the major river systems or to deep sands (Fouquette and Lindsay, 1955:411; Dr. Donald W. Tinkle, *in litt.*). In western Oklahoma the eastern hognose occurs mainly in sandy areas, often along floodplains of rivers and streams (Dr. Robert G. Webb, *in litt.*).

The eastern hognose is more common in eastern Texas than the western species, being found in the Bluestem-Sacahuista Prairie and the Southern Cordgrass Prairie of the Gulf Coast, the Oak-Hickory-Pine Forest of northeast Texas, and west through the Cross Timbers and prairie regions. It is probably more abundant on sandy or timbered tracts than on the Blackland or Fayette Prairie. Curtis (1949:7) reported that the eastern hognose was found in the timbered lowlands and upland dry cedar brakes of the southern half of Dallas County, especially in sandy fields, but had not been collected in the prairie region of the northern half. Dr. John W. Forsyth (*in litt.*) stated that the eastern hognose "was at one time reasonably common in those parts of the Fort Worth prairie region of Texas adjacent to or including sandy soils. It has become scarce in recent years." The eastern hognose reaches the southwestern limits of its distribution in the Mesquite-Acacia Savanna of the South Texas Plains. It is found on the Edwards Plateau only in local favorable areas (Dr. Gerald G. Raun, *in litt.*).

Habitat

Heterodon nasicus. Published statements concerning the habitat preferences of western hognose snakes include:

"Largely in the Upper Sonoran Life-zone. Principally in sandy or gravelly areas with low-growing plants such as grasses and bushes" (Stebbins, 1954: 364, in western North America); "in sandy or gravelly areas . . . in the open sand blowouts, where almost no cover is available . . . sparse scrub oak" (Breckenridge, 1944:112, in Minnesota); "fairly dry, usually

sand areas with little vegetation . . . dune areas" (Webb, 1952:159, in Oklahoma); "relatively dry areas, and is especially abundant in sand dunes" (Smith, 1956:231, in Kansas); "usually found in more open situations than the eastern species. It is especially common in the sandhills" (Hudson, 1942:51, in Nebraska); "gravelly or sandy soil covered with grass or low bushes. Old dry stream bottoms are likely spots . . ." (Davis and Weeks, 1963:6, in Montana); "preference for sandy locations and also damp lowlands" (Moore, 1953:173, in Alberta, Canada); "characteristic of the grasslands, inhabiting dry areas, especially sand dunes" (Wheeler and Wheeler, 1966:74, in North Dakota).

Heterodon platyrhinos. Published statements concerning the habitat preferences of eastern hognose snakes include:

South: "High pine and upland hammock" (Carr, 1940:79, in Florida); "open sandy soil with scattered pines" (Duellman and Schwartz, 1958:293, in southern Florida); "common around the Lee's sandy clearing and in all dry parts of the swamp" (Wright and Bishop, 1915:156, in Okefinokee Swamp, Georgia); "mainly in deciduous woods" (Corrington, 1929:70, in South Carolina); "in the drier upland regions" (Lynn, 1936:170, in Stafford County, Virginia); "on the mountain sides . . . in open fields, and on sandy beaches . . . always alike in being dry" (McCauley, 1945:64-65, in Maryland); "diverse habitats . . . the Ohio River floodplain, creek bottomlands, and both wooded and open uplands" (Craddock and Minckley, 1964:388, in Meade County, Kentucky); "uplands and lowlands . . . in forests and thinly-wooded tracts, but favors the more open hillsides and even the borders of cultivated fields" (Parker, 1948:26, in western Tennessee); "diverse habitats varying from wooded swamps to cultivated fields" (Clark, 1949:248, in northern Louisiana); "all habitats, especially dry, sand uplands" (Fitch, 1949a:89, in western Louisiana).

Northeast: "dry open fields" (Fowler, 1907:187, in New Jersey); "dry fields and woodlands" (Street, 1914:2, near Beverly, New Jersey); "dry woods and sandy hillsides" (Surface, 1906:183, in Pennsylvania); "dry sandy soils . . . also in low and wet meadows" (DeKay, 1842:52, in New York); "sandy pine barrens" (Bishop, 1923:117, in Albany County, New York); "Dry, usually sand areas" (Lamson, 1935:18, in Connecticut).

Great Lakes Region: "the sandy-soiled, sparsely timbered areas" (Patch, 1919:60, near Point Pelee, Ontario, Canada); "dry open woods of either pine or deciduous dominance . . . fossil and modern beaches" (Conant, 1951:43, in Ohio); "dry situations such as cultivated fields, old fence-rows, open pastures and roadsides; also dry hillsides and the banks of streams. At times it may be seen along water-courses and the shores of ponds and lakes. We have rarely observed it in meadows or on wet or marshy ground" (Evermann and Clark, 1915:346, in Indiana); "partial to dry woodland or to open country along streams" (Minton, 1944:455, in Indiana); "prefers dry woods and occurs particularly in sandy regions" (Ruthven, Thompson and Thompson, 1912:89, in Michigan); "correlated with sandy areas, although I have collected it in the rich Beech-Maple forests" (Edgren, 1952a:136, in west-central Michigan, western Illinois, and northern Indiana); "on floodplains, in forest-edge habitats, and in dry, open woods where the soil is clay or sandy loam" (Smith, 1961:191, in southern Illinois); "sandy or dry localities" (Higley, 1889:165, in Wisconsin).

Prairie and deciduous forest border: "sand areas" (Smith, *loc. cit.*, in northern Illinois); "There may be some association with sandy soil in our area, but it is not at all exclusively confined to sand areas in its total range" (Schmidt and Necker, 1935:68, near Chicago, Illinois); "open fields and rolling hills . . . dry sandy areas . . . rocky timbered terrain" (Anderson, 1965:184, in Missouri); "in dry woods, on sandy shores of rivers, in sand dunes, but seldom in moist or heavily wooded areas" (Smith, 1956:227, in Kansas); "sparsely vegetated areas or in wooded regions with a sandy soil" (Webb, 1952:157, in Oklahoma).

Harvey County, Kansas. Harvey County is on the eastern edge of the mixed grass prairie. It is therefore at the eastern boundary of the continuous range of the western hognose and in a peripheral part of the range of the eastern species. Both species are now common only in the sand prairies in the western part of the county. No specimens have been collected in the eastern part of the county on loam soils. It is probable that before the land was intensively cultivated there were small localized populations of hognose snakes in suitable disturbed habitats in eastern Harvey County.

In the summers of 1960 to 1963, fewer trap stations were operated in Graber Pasture than in Harvey County Park. However in Graber Pasture 85 eastern and 199 western hognose snakes were caught, while in Harvey County Park only 39 and 90 respectively were captured. Both species prefer the more disturbed habitat of the Graber Pasture with short sparse vegetation and more open sandy areas. These snakes can burrow more easily in this substrate than in a more dense sod interlaced with the roots of grass. Also, lizards and toads burrow more readily in open situations, and these are dug out for food by hognose snakes. The short ground cover allows full sunlight to maintain body temperature during the morning and evening when these snakes are most active.

There was a wide variation in the success of various trap stations in catching eastern hognose snakes. Trap stations in Graber Pasture caught from 17 to zero individuals, while those in Harvey County Park caught from five to zero in four summers. There was a disproportionately large number of trap stations where either a large number of snakes or none at all were captured. Of trap stations in apparently similar situations, some were unsuccessful and others notably successful. However, all trap stations where large numbers of eastern hognose snakes were captured were either near ponds or on sites with sparse ground cover near or within groves of trees.

Trap stations in Harvey County Park caught from 12 to zero, and those in Graber Pasture caught from 22 to zero western hognose snakes. Those that caught large numbers were near water, in shrubby upland grass, or in areas of sparse grass near groves of trees.

Limiting Factors

Heterodon nasicus. The studies summarized above indicate certain features of optimum habitat for the western hognose. Some of these features may indirectly affect the snake by affecting other organisms. The optimum physical environment for the western hognose includes: 1) a well-drained soil, 2) a loose silty or sandy surface soil, 3) sparse vegetative cover, especially short grass prairie or disturbed sites, 4) proximity to water—probably of less importance than to the eastern species, and 5) climatic conditions typical of the grassland biome.

The western hognose is characteristic of the short grass or mixed grass prairie of the High Plains. It is most abundant in disturbed sandy habitats but is common in less-than-optimum habitats in this area.

The limitation of the geographic range of an animal is due to a combination of many factors, although one or a few factors that exceed the limits of tolerance may be the most obvious. Because experimental data are lacking, any discussion of the factors limiting the geographic distribution of hognose snakes must be speculative. However, on the east the distribution of the western species seems to be limited by increasing density of vegetation or compactness of soil

associated with the true prairie and the deciduous forest. These factors may affect ease of burrowing, presence of burrowing prey, light and heat relations, and possibly other factors. On sandy soil, the western hognose may live in rather dense tall grassland or in tall grass savanna.

To the west the range of the western hognose is limited by the Rocky Mountains, and to the southwest probably by the increasingly xeric conditions of the desert. Important factors affecting the northern limits of the range of the western hognose are probably summer temperatures and the length of the summer season. The known distribution tends to parallel summer isotherms and to extend to areas having a frost-free season of 100 to 120 days (Fig. 12).

Heterodon platyrhinus. The physical features of optimum habitat for the eastern hognose include: 1) a well-drained soil, 2) a loose or sandy surface soil, 3) open vegetative cover such as open woods, brushland, forest edge, or disturbed sites, 4) proximity to water (or abundance of amphibians), and 5) climatic conditions typical of the eastern deciduous forest biome.

The eastern hognose is characteristic of dry deciduous or pine forest and forest edge, and is more abundant in open woods than in dense moist woods. Although it is not usually found within swamps or other poorly-drained habitats, it is typically found in greatest abundance on well-drained sites near lakes, rivers, or swamps where the amphibians on which it feeds are abundant. Its optimum habitat is on disturbed sandy sites where it can burrow with ease.

The northern limits of the eastern hognose are probably importantly affected by summer temperatures or the length of the summer season (Fig. 14). This snake seems to be limited by less adverse temperature conditions than the western species and is most common in regions having a frost-free season of 160 days or more. On loose sandy soils and in areas with abundant amphibians, it is able to live farther north (growing season of 120 days) than it can under less favorable edaphic or biotic conditions.

A factor that has a limiting effect on the westward dispersal of the eastern hognose may be the dense surface vegetation in the tall Bluestem Prairie. However, it has been able to spread into the prairie along river valleys and to disperse into favorable habitats on the prairie, particularly sandy or disturbed sites. It has also been able to spread into moist savanna habitats that have features similar to the forest edge.

In the South, with higher temperatures and a longer active season, it has been able to spread farther west into the grassland. Its presence on the Gulf Coast prairies is probably favored by optimum conditions of temperature and water. The southern and western limits of the range of the eastern hognose in the grasslands and savanna are controlled by increasing desiccation of the environment. However, it exists on the High Plains of Texas, Oklahoma, and Kansas, where large river valleys or deep sand provide a favorable edaphic and biotic habitat.

TEMPERATURE

Cloacal temperatures of hognose snakes were measured with a Schultheis quick-reading thermometer under three different conditions: (1) immediately after capture in the field by hand (termed normally active snakes in the following discussion); (2) in live-traps; (3) in an outdoor pen in which both shade and full sunlight were available. The ground surface temperature was measured with the thermometer shaded at the place where the snake was

captured. Terminology follows that of Cowles and Bogert (1944:277) and Brattstrom (1965:377) unless otherwise indicated.

Heterodon nasicus. Cloacal temperatures of western hognose snakes are summarized in Figure 15. Cloacal temperatures of normally active snakes were between 21.4°C and 36.2°C (ground surface temperatures of 17.6°C to 36°C). This is the normal activity range as defined by Brattstrom (*loc. cit.*). The mode was between 31°C and 32°C and the mean was 30.2°C. A usual activity range may be defined as that restricted range of cloacal temperatures

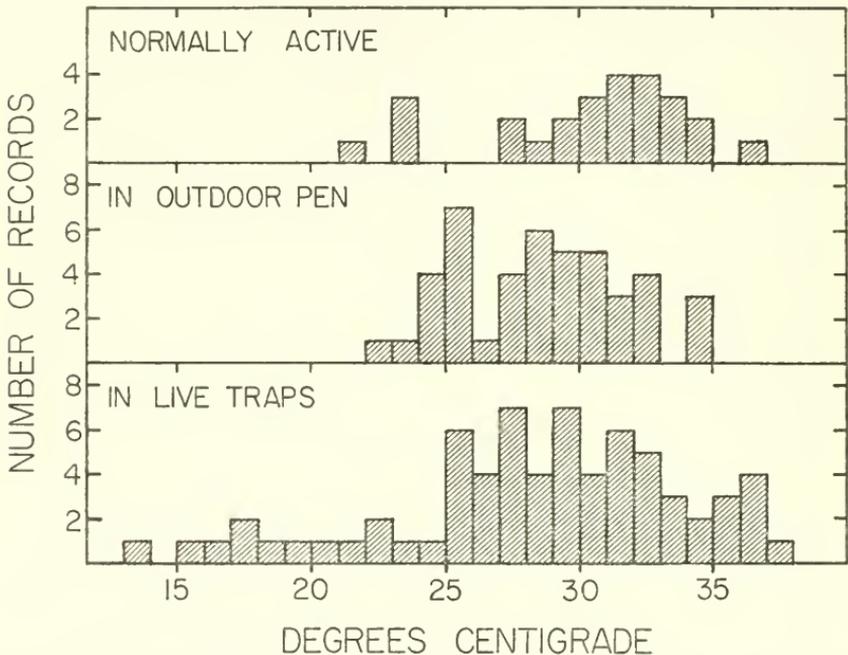


FIG. 15. Cloacal temperatures of western hognose snakes in Harvey County, Kansas, including 26 records from snakes caught by hand while they were normally active in the field, 44 records from snakes in an outdoor pen, and 69 records from snakes in live traps.

grouped about the mode that includes more than 75 per cent of the measurements. The usual activity range of normally active western hognose snakes was between 27°C and 35°C (includes more than 80 per cent of the cloacal temperatures).

Heath (1964) criticized this method of determining the normal activity range of a reptile from field data, because it does not demonstrate thermoregulation. He pointed out that a temperature distribution much like those in Figure 15 can be obtained by measuring, at intervals throughout the day, the temperature of cans of water placed in the sun. However, the activity ranges of a reptile are of biological interest in indicating the body temperatures of normally active animals, whether thermoregulation is effective or not. The body temperature of a snake is the result of the potential for exchange of heat between the animal and its environment, modified by any thermoregulatory or thermal-adjusting ability the animal possesses. Field data can

be used to demonstrate the ability to make thermal adjustments, although further experimental studies are necessary to determine the nature of adjustment mechanisms. Table 11 summarizes the mean deviations of the cloacal temperatures of western hognose snakes from ground surface temperatures at various ground temperatures. Even snakes in live-traps have some ability to regulate temperature as can be seen by the significant changes in mean deviation at higher temperatures. Temperature regulation probably involves changing position in the trap to minimize absorption of solar radiation or increasing evaporative heat loss. The data also indicate that 35°C is a biologically significant temperature at which mean deviation changes from a positive to a negative number. This temperature is close to the voluntary maximum temperature (36.2°C) as determined from the data on normally active snakes. The sample of normally active snakes is too small to show significant differences in temperature relationships at different ground temperatures, but the data are suggestive of some regulation at lower temperatures, as well as at higher temperatures.

The temperatures of the cans used in Heath's (*loc. cit.*) experiments had a skewed distribution with a maximum of 35°C. The air temperature (maximum 30°C) and the solar radiation probably reached similar peaks each day, and, under these conditions, the physical properties of the cans allowed sufficient heat absorption to balance heat loss by evaporation at 35°C. However, a passive exchange would not produce a similar temperature curve for snakes on the study areas in Harvey County. The shaded air temperature reached 38°C to 40°C for at least three or four hours during many days of the summer. The ground surface temperature in habitats where hognose snakes were seen in the morning or evening often rose to 45°C or 50°C during the middle of the day. The cloacal temperature of snakes placed in the direct sunlight at this time rose above 40°C in a few minutes. A few snakes died in live traps from excessive heat, even though the traps were shaded. Therefore, since no normally active snakes were found with cloacal temperatures much above 36°C, the western hognose snake must have a means of avoiding such potential excessive body temperatures. The snake probably moves to a protected micro-environment, or it burrows if it can no longer maintain a favorable body temperature on the surface. The temperature within a burrow may be more than 10°C cooler than the ground surface temperature during the middle of the day (Table 12).

The voluntary minimum temperature of a reptile can only be demonstrated from field data on the basis of negative evidence. Seven cloacal temperatures of western hognose snakes in traps were below 20°C, indicating that such potentialities for body temperatures were present. No normally active snakes were captured with cloacal temperatures below 20°C. The normally active snakes with cloacal temperatures below 25°C were captured in early morning. The temperature of a reptile immediately after emergence from its burrow in early morning may be lower than the temperature at which it would seek protection at another period in the day (Heath, 1962:891). The latter temperature would be a more significant measurement of voluntary minimum temperature. The lowest temperature at which a normally active snake was captured after 8:00 a. m. was 27.2°C. However, in an outdoor pen in late morning, two western hognose snakes in the sunlight had cloacal temperatures of 24.6°C and 25.8°C, and one snake in the shade had a temperature of

TABLE 11. Mean Deviations of Cloacal Temperatures of Western Hognose Snakes From Temperatures of the Ground Surface at Various Ground Temperatures in Three Samples of Snakes From Harvey County, Kansas.

Ground surface temperatures	Normally active			In live traps			In pen		
	Number of snakes	Mean deviation	t	Number of snakes	Mean deviation	t	Number of snakes	Mean deviation	t
Less than 20°C.	2	+5.5	0.4	6	+2.8	0	7	+2.6	0.1
20°-25°C.	7	+7.1	1.9	24	+2.8	0.5	27	+2.7	0.3
25°-30°C.	8	+3.1	1.9	23	+2.3	2.8**	19	+2.9	1.7
30°-35°C.	6	+1.0	3.4*	30	+ .4	3.3**	4	+ .6	
More than 35°C.	1	-4.0		15	-2.2		0		

TABLE 12. Comparison Between Temperatures at Ground Surface and in Burrows of Hognose Snakes, 120 to 170 Millimeters Deep, in an Outdoor Pen in the Summer of 1961.

Date	Time	Ground surface temperature	Temperature in burrow
July 3	1:15 p.m.	42.6°C	26.5°C
July 3	5:45 p.m.	36.0°C	29.0°C
July 25.....	1:35 p.m.	35.2°C	26.8°C
July 28.....	2:00 p.m.	41.0°C	28.8°C
July 29.....	2:00 p.m.	45.4°C	31.5°C
July 30.....	2:00 p.m.	43.5°C	28.7°C

18.2°C. Cloacal temperatures of 21.9°C at 9:30 a. m., 23.8°C at 11:00 a. m., and 24.9°C at 4:00 p. m. were measured for western hognose snakes in the pen on cool or cloudy days. These data indicate that the temperatures of normally active snakes captured early in the morning were at or above the temperature at which they would seek shelter later in the day. Therefore, the voluntary minimum temperature can be assumed to be approximately 20°C.

Only one western hognose snake that appeared to be basking was captured in the field. Its cloacal temperature was 21.4°C. Three cloacal temperatures were measured for snakes that were basking in the outdoor pen, and these varied from 19.5°C to 30.8°C. All basking was observed in the morning. The basking range is probably from 20°C to 30°C, although many snakes were active and not basking at these temperatures.

When the ground temperature was within the normal activity range of the western hognose, the cloacal temperatures of snakes in the shade in live-traps average 2°C to 3°C above that of the ground (Table 11). Normally active snakes maintain greater disparities at low temperatures, probably by absorption of solar radiation. When the body temperature of a snake is maintained within the normal activity range by a passive heat exchange with the environment, the snake probably does little to modify this balance, except at the upper and lower ends of the range. Therefore, the usual range of temperatures within the normal activity range is probably determined by the temperature characteristics of its environment, as well as by the responses of the snake. Both direct sunlight and shade were available to western hognose snakes in the outdoor pen when the cloacal temperatures summarized in Figure 15 were measured. However, less than one-third of the pen was in full sunlight. Most of the normally active snakes captured in the field were in relatively open situations in direct sunlight. The lower trend of cloacal temperatures of the snakes in the pen reflect the lower average temperatures and lower solar radiation in the shady environment (Fig 15).

The critical maximum temperature and the lethal maximum temperature were not determined. The critical maximum temperature is above 40.5°C. Two western hognose snakes were released in full sun and lay still for 5½

minutes before they slowly crawled into the shade of some shrubs. As they started to crawl away, their cloacal temperatures were between 40°C and 41°C.

A western hognose snake having a cloacal temperature of 13.7°C was sluggish when taken from a trap. Two snakes with cloacal temperatures of 15.4°C and 16.3°C were able to writhe and feign death, and two others with cloacal temperatures of 15.4°C and 17.4°C could crawl normally.

Six tests to determine the critical minimum temperature were made by placing western hognose snakes in a refrigerator for a number of hours and then in the freezing compartment for 30 to 40 minutes. The cloacal temperatures of the snakes when they were removed from the refrigerator were from 1°C to 4.4°C. These snakes made only generalized muscular contractions on stimulation. They were first able to make avoidance movements in response to stimulation at cloacal temperatures of 4°C to 8°C. They were first able to turn over at 5.6°C to 9.4°C. Tongue flicking began at 7.0°C to 13.5°C, and locomotor ability returned at 7.0°C to 13.5°C. The lower temperatures in these series of readings are more meaningful. It is difficult to determine the threshold for any given response, because the snakes may be unresponsive to stimulation even at normal temperatures. A western hognose snake was cooled to 7.6°C in the refrigerator and then removed. It could turn over, slowly extend its tongue, and crawl in response to stimulation. A snake that probably acclimated during a period of three months at low temperatures in a cage in a refrigerator was able to crawl slowly at 6.7°C. These measurements indicate that the critical minimum temperature is approximately 7°C.

Western hognose snakes burrow in response to low temperatures. A number of individuals becoming responsive after a period of cold narcosis began to press their snouts against the substrate in what appeared to be a burrowing movement. Six snakes were kept for three months in a cage with deep sand in a refrigerator at 10°C or below. Soon after being placed in the refrigerator, they all burrowed into the sand.

Heterodon platyrhinos. For the eastern hognose the normal activity range seems to be similar to that of the western species, with a voluntary minimum of approximately 22°C and a voluntary maximum of approximately 34°C (mean is 29.4°C; Fig. 16). Two snakes removed from traps when their cloacal temperatures were 8.9°C and 10.4°C were sluggish. However, a snake with a cloacal temperature of 9.4°C was active. A snake with a cloacal temperature of 11.4°C was able to writhe and feign death. Four tests to determine the critical minimum temperature of the eastern hognose indicated that it was similar to that of the western species, approximately 7°C. Five eastern hognose snakes were placed in a cage with deep sand in a refrigerator for three months and probably acclimated to some extent. When the temperature of the cage was maintained at 10°C, the snakes remained on the surface of the sand. At 5.6°C they could still crawl slowly, spread their necks, and hiss. At 3.3°C, after 1½ months in the refrigerator, three snakes had burrowed, and the two snakes on the surface could only spread their necks but did not hiss.

These experiments indicate that the critical minimum temperatures of the two species are much alike, but that the eastern species may remain active on the surface at lower temperatures than the western species. This is consistent with seasonal differences in activity (see p. 314).

Compared with other snakes, hognose snakes have a high normal activity

range and a high mean cloacal temperature. The temperature range of hog-nose snakes is similar to that reported for the diurnal racer, *Coluber constrictor* (Fitch, 1956; Brattstrom, 1965).

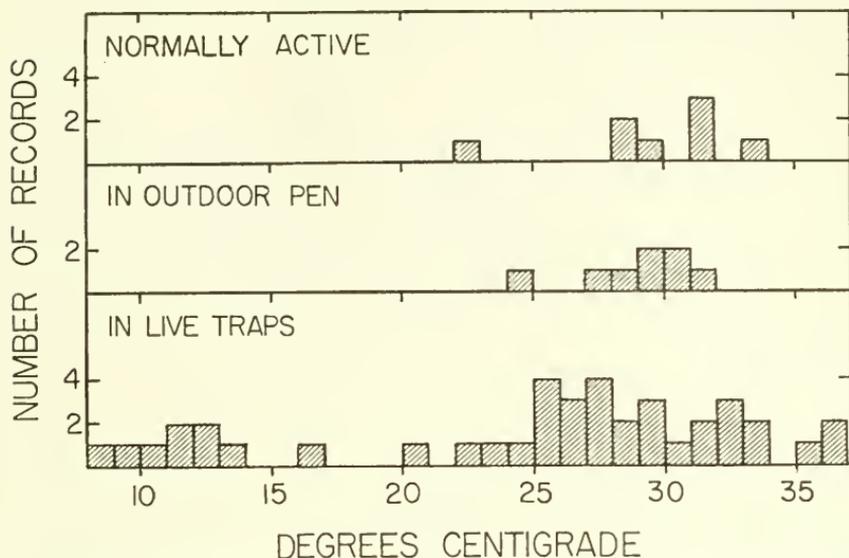


FIG. 16. Cloacal temperatures of eastern hognose snakes in Harvey County, Kansas, including eight records from snakes caught by hand while they were normally active in the field, eight records from snakes in an outdoor pen, and 40 records from snakes in live traps.

PERIODICITY

Seasonal Patterns of Activity

Heterodon platyrhinos. Winter dormancy of eastern hognose snakes in Harvey County lasts approximately six months. In the years 1959 to 1963 they were first captured after emergence from hibernation in the period from April 17 to May 23 (average date May 2). The latest dates on which live eastern hognose snakes were captured in autumn were in the period from October 12 to 25 (average date October 20).

The microclimate of the hibernaculum is an important factor affecting dormancy. The only soil temperatures available were measured at a depth of four inches in loam soil on the Hutchinson Experimental Field in Reno County, Kansas, approximately 30 miles west of my study areas (Robb, 1959 to 1963). Temperatures in the loose sandy soil on the study areas were probably warmer in the spring than those at the Hutchinson Experimental Field. However, temperatures at the greater depth of the hibernacula used by hognose snakes would have been cooler than temperatures recorded at a depth of four inches.

Comparisons of daily median soil temperatures and the dates of first capture and last capture of eastern hognose snakes are shown in Figure 17. In spring the first snakes were captured on the study areas after a period in which the soil temperature had increased and finally exceeded 60°F (15.5°C). The last

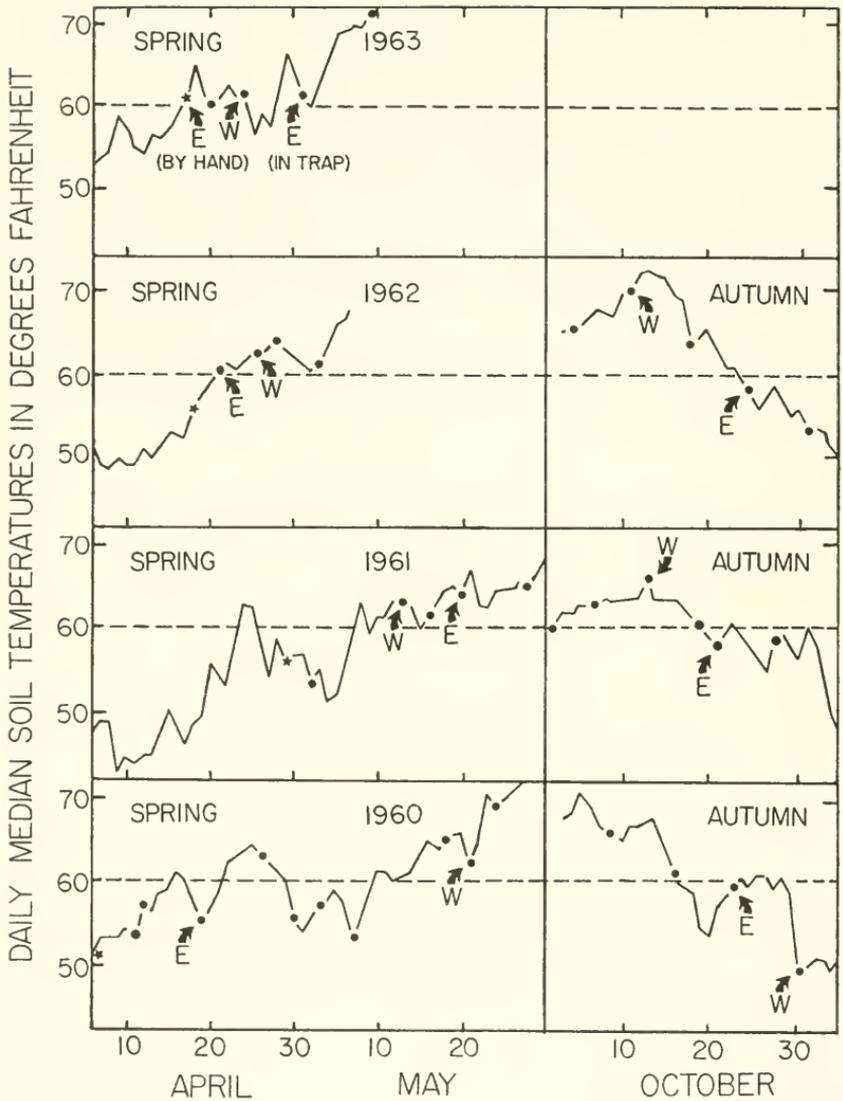


FIG. 17. Dates of first and last capture of hognose snakes in the years 1960 to 1963 in Harvey County, Kansas, compared to median daily ground temperatures. The ground temperature are from U. S. Weather Bureau records measured at a depth of four inches at a locality 30 miles west of the study areas (see text). The dates on which the trap stations were put in operation each spring are denoted by stars, and the dates on which the traps were checked are indicated by dots. Arrows indicate the dates on which the first eastern hognose snakes (E) and the first western hognose snakes (W) were captured in the spring and the dates on which the last snakes were captured in the autumn. The snakes entered the traps between the day indicated and the last previous day on which the traps were checked.

snakes were trapped each autumn in periods when soil temperatures were decreasing and were near 60°F. Soil temperature is probably an important factor in determining the period of dormancy for this species.

An eastern hognose snake may become active during warm periods in winter, probably when the temperature in the hibernaculum increases above a threshold. Snakes of this species have been collected on December 2, 1926, in Union County, Pennsylvania (Netting, 1927:30), in February in snow in West Virginia (Strader, 1935:34), and on January 24, 1933, in Clermont County, Ohio (Conant, 1951:44).

A number of authors have stated that, of the various species of snakes occurring in an area, the eastern hognose appears earliest in spring and disappears latest in autumn (Abbott, 1885:290; Neill, 1948:110; Guidry, 1953:51). In Harvey County, however, both racers (*Coluber constrictor*) and garter snakes (*Thamnophis* sp.) were active earlier in spring and later in autumn.

Eastern hognose snakes were collected in Lucas County, Ohio (Conant, 1938:138), and on the Eldon Research Area, Davis County, Iowa (Klimstra, 1958:233), from April to October. During the periods when these snakes were entering and leaving hibernation in Ohio, mean air temperatures were from 50°F to 60°F (Conant, 1938:138-139). Klimstra (1958:235) reported that initial activity of snakes occurred at mean air temperatures of 40°F and peak activity at 58°F. Brimley (1925:102) collected eastern hognose snakes near Raleigh, North Carolina, in all months except February and December.

Little information is available concerning the hibernacula of eastern hognose snakes. They have not been found in dens where aggregations of other species of snakes hibernate. Abbott's (*loc. cit.*) statement that aggregations of eastern hognose snakes (occasionally including other species) coiled together in a globular mass during hibernation is probably in error. Neill (*loc. cit.*) reported that they hibernate singly in Richmond County, Georgia, "beneath rocks, stumps, or rubbish piles, in burrows in hard red clay soil, or even beneath slabs of tin on the open ground." Anderson (1965:184) stated that the eastern hognose "usually hibernates in rodent burrows in open fields and is conspicuously absent from the limestone ledge areas that most snakes select for hibernating." He related (*in litt.*) instances in which an eastern hognose emerged from the burrow of a thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) on April 8, and in which a torpid eastern hognose snake was found in a mole tunnel at a depth of approximately three feet in mid-November.

In areas where the soil is suitable, eastern hognose snakes probably dig burrows in which to hibernate. However, it is not known whether they deepen burrows that have been used for shelter in summer or dig special hibernacula. On November 25, 1963, a large eastern hognose was released on the Harvey County Park study area with a trailer attached to trace its movements. On December 5 it was found in the opening of a burrow that had probably been dug by a hognose snake. The snake was held by tangled thread in the trailer. The trailer was removed, and the snake immediately entered the burrow. Later in December the burrow was excavated, but it could not be followed and the snake was not found.

Eastern hognose snakes are inactive for periods of a few weeks in summer. Three snakes kept in an outdoor pen from early July to September were inactive for one or two periods of from one to three weeks each. All three snakes stayed in burrows for a period in August or early September when they moulted.

On the study areas in Harvey County, the numbers of eastern hognose snakes caught in ten-day periods throughout the season in the years 1959 through 1962 indicate variability in activity in different parts of the season (Fig. 18A). There were two peaks in activity, in mid-May and mid-October, and a low point in early September. Under quite different environmental conditions near Raleigh, North Carolina, Brimley (1925:101-102) found maximum activity in May, a low point in September, and a secondary rise in October. A similar activity pattern was reported for eastern hognose snakes on the Eldon Research Area in Iowa, with minimum activity in August (Klimstra, 1958:233). Conant (1938:138, 140) reported little seasonal fluctuation in numbers caught in Lucas County, Ohio, but they were caught in largest numbers in July, May, and September, in that order.

First-year snakes left hibernation later than adults in Harvey County. Maximum activity of first-year snakes was later in the spring, and they re-

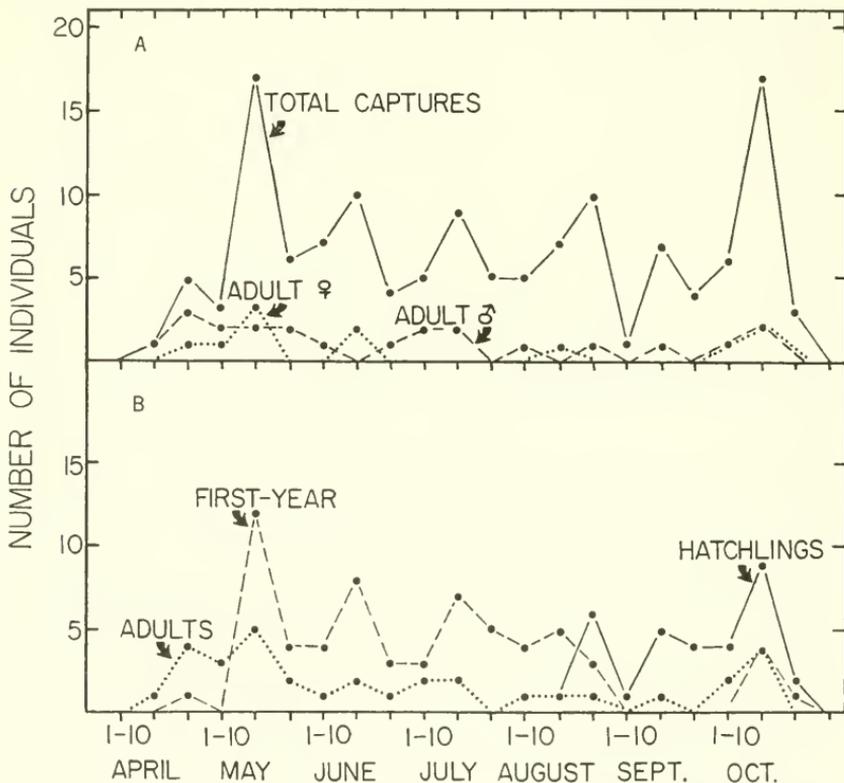


FIG. 18. Numbers of eastern hognose snakes captured on the study areas in Harvey County, Kansas, in approximately ten-day periods throughout the season of activity in the years 1959 through 1962. A. The seasonal distribution of total captures and captures of adult males and females. B. The seasonal distribution of captures of individuals in various age groups in the population.

mained more active in the middle of summer than adults. The large sample of snakes caught in mid-May were mostly first-year snakes (Fig. 18B). There was some resurgence in activity of both first-year and adult snakes in autumn, primarily a few weeks before entering hibernation. However, in a number of studies, most of the snakes caught in autumn were hatchlings (Fig. 18B; Conant, 1951:44; Klau and David, 1952:366-367). Hatchlings and first-year snakes remained active later in autumn than adult snakes (Fig. 18B; Neill, *loc. cit.*).

Males and females have different periods of activity. The first snakes to emerge in spring in Harvey County were adult males, and the peak of activity for adult males in spring was in late April and May. Females had a later period of maximum activity. Few adult females were caught after they had laid eggs in late June (Fig. 18A). At all ages more male eastern hognose snakes were caught than females, probably because of greater activity of males.

Factors that may cause variations in the number of snakes caught at different seasons, as suggested by various investigators (Brimley, 1925:102; Conant, 1938:140; Oliver, 1947:9-11; Klimstra, 1958:233-235), are in four categories: (1) differences in effectiveness or intensity of collecting; (2) differences in size of the population; (3) differences in physiological state or needs of the snake; and (4) environmental differences. The first category of factors can be ignored in my study, because the methods and intensity of trapping were similar throughout the season. Factors in the other three categories interacted to produce seasonal fluctuations in activity of eastern hognose snakes. The major seasonal fluctuations in numbers caught on the study areas were primarily caused by physiological and population factors. Large numbers of snakes were caught in autumn because of an increase in population size with the influx of hatchlings; the high activity level of hatchlings in search of food during a period of rapid growth; and some increase in activity of older snakes, possibly caused by search for hibernation sites and fall mating activity. Large numbers of snakes were caught in mid-May, because of the large population of first-year snakes with high nutritional needs for rapid growth. Later in the season mortality had reduced the number of first-year snakes, and their growth was slower. The maximum activity of adult males was probably associated with mating activity in late April and early May.

A number of authors have pointed out that the maximum activity of snakes in spring and in autumn occur at similar mean air temperatures (Conant, 1938:142; Oliver, 1947:10; Klimstra, 1958:235). This was also true for eastern hognose snakes in Harvey County (mean air temperatures of 60°F to 65°F). Although temperatures certainly did affect these periods of maximum activity, the population and physiological factors discussed above were most important as direct factors causing this pattern of activity for eastern hognose snakes in Harvey County. Temperature was important as one of the primary factors determining the time of winter dormancy and thereby secondarily affecting these periods of activity before and after dormancy.

Climatic features operate as indirect factors that have caused the evolution of certain inherent patterns of activity or as direct factors causing fluctuations in activity. Inherent rhythms are usually adaptively related to periods of optimum or adverse environmental factors. The decrease in activity of both sexes in August and early September was caused primarily by an inherent rhythm, probably related to moulting, and was less directly related to the more

adverse environmental conditions of late summer. Decreased activity and moulting was noted in snakes in cages in the laboratory in late August or September.

Climatic factors are probably of direct importance in contributing to the changes in timing of activity periods that occur from one year to the next. In 1960 and 1961 only one or two eastern hognose snakes were captured on the study areas in the last half of May, but, in 1962, 11 snakes were caught in this period. The mean air temperature for May, 1962, was 74.9°F, ten degrees above the normal mean temperature, whereas the mean temperatures in May, 1960 and 1961 (64.1°F and 60.7°F, respectively), were below normal. No eastern hognose snakes were captured in the last half of June in 1960 and 1961, while in 1962 this was a major period of activity. The weather was exceptionally cool in early June, 1962, but became warmer in the last half of the month (Robb, 1960 to 1963). Changes in population size and structure were probably also important in causing these differences in activity from year to year. The relatively large population of first-year snakes in 1962 was an important factor in causing differences in the pattern of activity on the Graber Pasture study area.

The number of snakes caught on the study areas varied from one trapping period to the next. Some of this variation was chance fluctuation, but weather conditions also probably affected activity. Fewer snakes were caught in cool, rainy periods. In June and July those trapping periods in which eastern hognose snakes were captured had a mean maximum air temperature of 90.2°F, while those in which no captures occurred had a mean maximum temperature of 86.2°F. Tests of association (using graphs and 2×2 contingency tables) of captures of eastern hognose snakes in June and July with high temperatures, increasing temperatures, rainfall, and percentage of daylight hours that were predominantly sunny indicated no significant association with any of these factors. With the data available, the degree of fluctuation caused by population and physiological factors made it impossible to detect fluctuations caused by climatic factors. Also, climatic factors interact in a complex manner, making analysis of association more difficult. For instance, rainfall may stimulate or decrease activity, depending upon other conditions (Oliver, 1947:10-11).

Klimstra (1958:234) suggested that greater activity might occur during a period of food scarcity because of more intensive searching for food. On the other hand, maximum nutritional needs and maximum feeding may be related adaptively by evolution to times of maximum availability of food. There was no obvious response in activity by eastern hognose snakes to maximum activity of frogs, their principal prey, in mid-July (Fig. 19).

Heterodon nasicus. In the years 1959 to 1963 western hognose snakes were first captured after emergence from winter dormancy in the period from April 24 to May 23 (average date May 9). The latest dates on which they were captured in autumn were in the period from October 11 to 31 (average date October 18). In spring they were not caught until the temperature of the soil had remained above 60°F (15.5°C) for a few days. The last captures in autumn were usually immediately before the temperature of the soil dropped below 60°F (Fig. 17). No hibernaculum has been described, but each individual probably hibernates solitarily after digging a burrow below frost level.

Most activity of the western hognose on the study areas was in the period

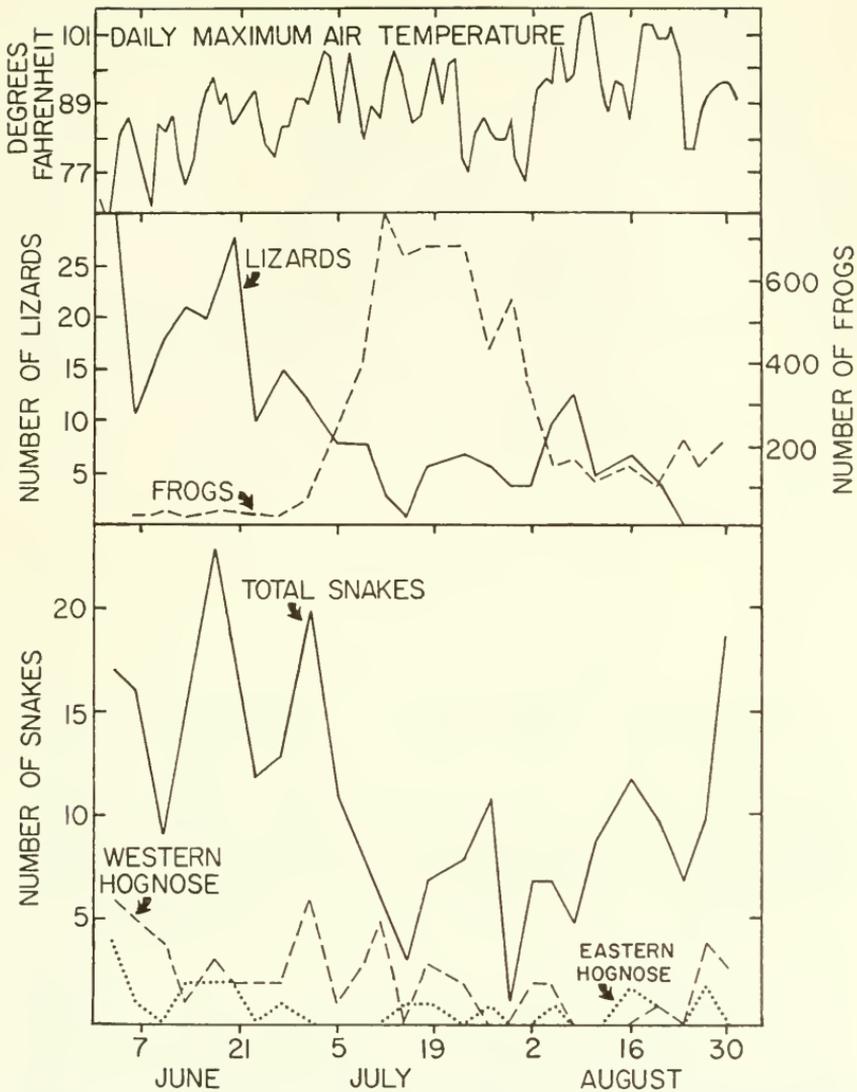


FIG. 19. Total captures of certain vertebrates in live-traps on the study areas in Harvey County, Kansas, in each trapping period in June, July, and August, 1962.

from May to early August. The latter part of August was a period of inactivity and moulting, and there was only a limited resumption of activity in autumn (Fig. 20). This annual cycle of activity was probably caused by inherent factors, as it recurred from year to year despite changing weather conditions (Fig. 20A).

Adult males were active earlier than females, and maximum activity occurred earlier. The peak of activity in mid-May coincided with the usual mating season. The decrease in activity that followed was probably a period of moulting. When activity of females decreased in the last part of June,

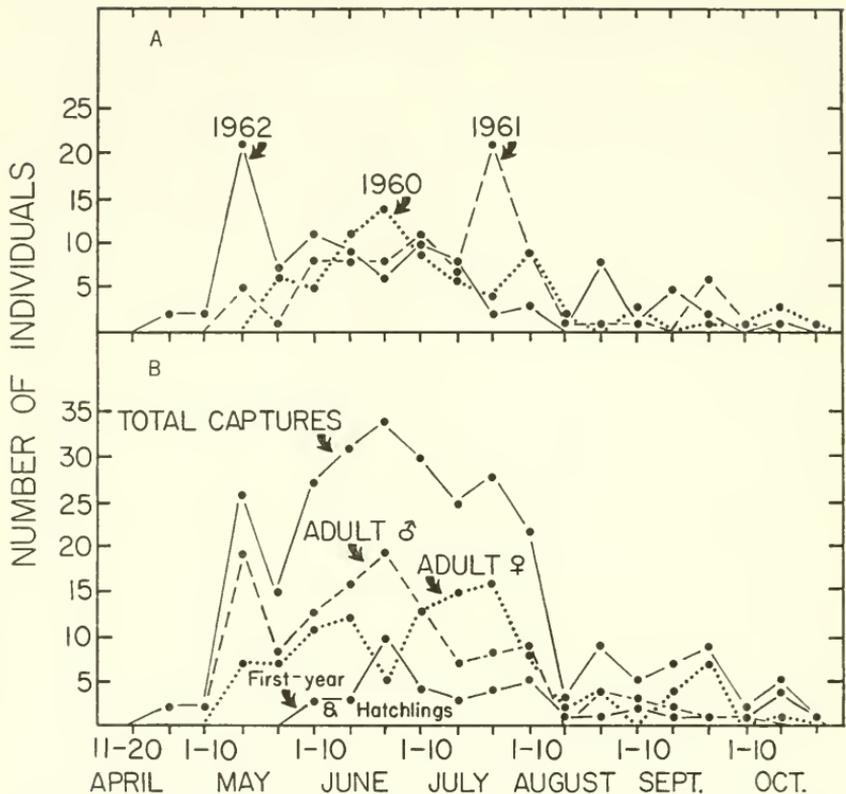


FIG. 20. Numbers of western hognose snakes captured on the study areas in Harvey County, Kansas, in approximately ten-day periods throughout the season of activity in the years 1959 through 1962. A. The seasonal distribution of captures in three different years. B. The seasonal distribution of total captures and captures of individuals in various sex and age groups.

most were probably moulting (see p. 360). Maximum activity of females occurred during and after egg-laying in middle and late July. Most of the females that were trapped in this period had either laid eggs or were not breeding. Females were more active than males in late summer and autumn (Fig. 20B). Total activity throughout the year was equal in the two sexes.

The activity of six western hognose snakes in an outdoor pen was studied in 1960 and 1961. The periods during which they were not observed above ground are listed in Table 13. The male snakes were less active than females in July and August. Each snake that was in the pen for two months had at least two periods of inactivity, one of which was in August when at least five of them moulted. Periods of inactivity in late summer were not obviously related to weather changes but seemed to be inherently determined, at least in part.

The distribution of activity throughout the period from May to August varied from year to year (Fig. 20A). The effect of climatic factors on fluctuations in activity of western hognose snakes was studied in the major period of activity after June 1 in three years, namely June 1 to August 6, 1960, June 1

TABLE 13. Periods of Inactivity That Lasted More Than One Week for Western Hognose Snakes in an Outdoor Pen in Harvey County, Kansas.

Sex	Period snake was observed in pen	Periods of inactivity
Male.....	Aug. 6 to Sept. 5, 1960	Aug. 16 to 31 ^a
Male.....	June 22 to Sept. 8, 1961	July 4 to 17 July 18 to 24 July 25 to Aug. 16 Aug. 17 to Sept. 5 ^a
Female.....	July 13 to Sept. 5, 1960	July 24 to Aug. 7 Aug. 20 to 29 ^a
Female.....	June 22 to Sept. 8, 1961	July 13 to 21 July 24 to Sept. 2 ^a
Female.....	June 22 to Sept. 8, 1961	July 26 to Aug. 4 Aug. 11 to Sept. 5 ^a
Female.....	July 1 to Sept. 8, 1961	July 29 to Aug. 17 Aug. 26 to ?

a. Moulting was observed to have occurred in this period of inactivity.

to August 9, 1961, and June 1 to July 25, 1962. These data lend themselves to detection of climatic effects on activity because no important seasonal changes in population size that significantly affected the number of snakes caught were evident. For each trapping period, the number of snakes caught per day was utilized as a measure of activity. For contingency tests, trapping periods with catches of one or more snakes per day were designated as periods with high activity and those with catches of less than one snake per day were periods with low activity.

Western hognose snakes were most active during trapping periods with mean maximum temperatures between 86°F (30°C) and 97°F (36°C), but low activity was found at a wide range of temperatures. Tests using a 2 × 2 contingency table did not show any significant association between high levels of activity and high temperatures (chi-square was 1.6). A significant association was found between increasing temperatures and high levels of activity. Trapping periods that had mean maximum temperatures at least four degrees Fahrenheit higher than the immediately preceding periods were predominantly periods of high activity, while those periods that had mean maximum temperatures lower or the same were predominantly periods of low activity (periods with increasing temperature: 15 periods with high activity and 4 with low activity; periods with same or decreasing temperature: 5 with high activity and 19 with low activity). A contingency test indicated an association that was significant at the one per cent level (chi-square was 12.2).

Large numbers of captures of western hognose snakes were usually restricted to relatively sunny periods. Sunny trapping periods (with more than 60 per cent of the daylight hours sunny) were more often periods of high activity, while periods with 60 per cent sunshine or less were predominantly periods of low activity (more than 60 per cent sunshine: 18 periods with high

activity and 12 with low activity; less than 60 per cent sunshine: 6 periods with high activity and 15 with low activity). However, a contingency test indicated an association between sunny periods and high activity that only bordered on significance at the five per cent level (chi-square was 3.7). Periods in which rain occurred showed no significant association with low or high numbers of captures (chi-square was 1.6).

Although the associations may be fortuitous, the above tests suggest the hypothesis that in June and July, western hognose snakes are most active in sunny periods of rising temperature.

Figure 19 shows the number of hognose snakes and other animals caught in traps on the study areas in the summer of 1962. The periods of maximum numbers of captures of lizards and of frogs complemented one another, so abundant food was available during the entire period of activity of western hognose snakes. The pattern of activity of the western hognose seems to parallel that of other kinds of snakes. It was more similar to the pattern of activity of lizards than to the pattern of activity of frogs on the uplands. This similarity in activity may have been caused by similarities in response to climatic factors and/or similarities in physiological rhythms.

Comparison of seasonal activity in the two species. Eastern hognose snakes usually become active earlier and enter dormancy later than snakes of the western species, but in some years western hognose snakes were captured earlier in spring (Fig. 17). Maximum activity of the eastern species in spring also comes earlier than that of the western species (Figs. 18A and 20B).

The seasonal distribution of all captures of eastern hognose snakes has a different pattern from that for captures of the western species (Figs. 18A and 20B). The exaggerated double peaks in the distribution of eastern hognose snakes represent primarily hatchlings and first-year young, but in the western species these young snakes were not commonly caught. The graphs for adult snakes are more alike, with definite peaks of activity in spring. Activity in the eastern species is more evenly distributed throughout the year. That of the western species is concentrated in late spring and summer, with relatively little resurgence of activity in autumn. Both species have a definite period of minimum activity in late summer, in mid-August for the western hognose and in early September for the eastern species.

Males of both species are active early in the season. Female western hognose snakes are most active after egg-laying, while female eastern hognose snakes are rarely captured after egg-laying. Females of the eastern species are much less active than males, whereas male and female western hognose snakes are equally active.

Diel Patterns of Activity

Heterodon nasicus. Western hognose snakes are reported to be diurnal (Smith, 1956:231). Although they were sometimes seen at dusk, I found none active after dark either in the field or in an outdoor pen. Those kept in the outdoor pen were in burrows at night. In June and July they were found most commonly in the field in morning or late afternoon. Ten individuals captured by hand were all found before 9:30 a. m. or after 5:30 p. m., but snakes were not sought so intensively during the midday hours.

TABLE 14. Diel Activity of Western Hognose Snakes in an Outdoor Pen in the Summers of 1960 and 1961.

Time	Days with maximum temperatures lower than 90°F		Days with maximum temperatures of 90°F or higher	
	Number of observations of pen	Number of snakes seen per observation	Number of observations of pen	Number of snakes seen per observation
	6:00 to 9:00 a.m.....	22	.09	30
9:01 to 12:00 a.m.....	11	.91	4	.50
12:01 to 3:00 p.m.....	20	.35	19	.37
3:01 to 6:00 p.m.....	18	.39	24	.71
6:01 to 9:00 p.m.....	12	.25	11	.73

Individuals observed in the outdoor pen in 1960 and 1961 were in burrows during part of each day. The pen was observed at various times in the day, and the numbers of active snakes were recorded (Table 14). On days when the maximum air temperature was below 90°F (32.2°C), their activity cycle was monophasic with maximum activity in late morning. On days with maximum temperatures of 90°F or above, the cycle was diphasic with maximum activity in early morning and late afternoon. This change in diel pattern of activity may be a response to change in general temperature level or may be a direct response to optimum temperature in a changed temperature rhythm. Heckrotte (1962:206) studied the patterns of activity of plains garter snakes (*Thamnophis radix*) under constant conditions of temperature and light, and found that changes in diel activity cycles were related to the temperature level and not to changes in temperature rhythm.

Heterodon platyrhinos. Most investigators have reported that this snake is diurnal or crepuscular (Carr, 1940:79; McCauley, 1945:65; Smith, 1956:228). Gaines (1894:959) and Newton (1940:1) stated that captives were active only by day. Stallcup (1959:80) reported that three captives were inactive during the day and active at night. Snakes that I observed in the field or in an outdoor pen were active only in the day, mostly in the morning and the late afternoon.

The two species have similar diel cycles in Harvey County.

SHELTERS AND BURROWING

Shelters

When released in the field, an eastern or western hognose snake usually crawls to the nearest shrub or clump of grass and conceals itself under the surface litter. The paths of a few snakes after release were traced by means of a thread unwinding from a trailer taped to the tail of the snake. These snakes crawled through relatively dense vegetation mainly between the surface of the sand and the surface litter, although they emerged on the surface of the litter for short distances.

During part of the day and most of the night, hognose snakes are in burrows. They are often plowed up by farmers (Lœnberg, 1894:328; Force, 1930:30; Harper, 1930:154). I have collected hognose snakes in late afternoon that had just emerged from burrows.

I have not found hognose snakes under rocks, logs, or other objects in the field, although individuals of both species occasionally found shelter under a board lying on the ground in an outdoor pen. Minton (1944:455) and Edgren (1955:112) stated that hognose snakes are seldom found under objects. Eastern hognose snakes have been found occasionally under logs, boards, rocks, and debris (McCauley, 1945:65; Webb, 1952:157; Edgren, *loc. cit.*; Adams and Clark, 1958:9). The western hognose is also found infrequently beneath objects (Gloyd, 1937:116; Webb, 1952:159 and *in litt.*).

Burrows and Burrowing

Hognose snakes utilize the following types of burrows: temporary shallow burrows, shelter burrows, nests (see pp. 333-334, 338), and hibernacula (see p. 307). They also burrow to capture prey (see pp. 361-362).

Hognose snakes were observed to bury themselves in sand to a depth of a few centimeters in a temporary shallow burrow. A shallow burrow dug by an eastern hognose snake carrying a trailer was parallel to the surface of the sand. It was approximately 60 centimeters long and had a maximum depth of five centimeters. The snake burrowed in from one end and left through an opening at the other end. Some temporary burrows are shallower and cave in when the snake leaves. Edgren (1952a:119) reported that a western hognose had apparently been burrowed for the night in surface sand below a prostrate plant. Breckenridge (1944:113) described an instance in which a western hognose attempted to escape capture by shallow burrowing.

Shelter burrows are somewhat deeper and may be used by the same snake for weeks or months. A burrow (in loam soil in an outdoor pen) that had been habitually used by a small eastern hognose for a few weeks had a single irregularly oval opening, approximately 30 mm. by 24 mm. The burrow was vertical to a depth of five centimeters and then sloped at an angle to a maximum depth of 11 centimeters. There was a small chamber (10 centimeters by 7.5 centimeters) at the end, in which the snake was coiled. When burrows were first made, the openings were much narrower (diameter 16 mm.). Burrows used by western hognose snakes were similar. Burrows in sand in cages often had two or more openings and were up to 20 centimeters deep. In a sandy orchard Burt and Hoyle (1934:205) excavated an eastern hognose snake's burrow that was three feet (91.5 centimeters) long and eight inches (20.3 centimeters) deep. The hole averaged three inches (7.5 centimeters) in diameter. Hognose snakes sometimes escape into shelter burrows when pursued in the field (Evermann and Clark, 1915:346; Dr. W. J. Breckenridge, *in litt.*).

One eastern and four western hognose snakes in an outdoor pen during the summer used from three to six burrows for daily shelter. Three burrows were used for one month, after which three others were dug in another part of the pen. The new burrows were then used more commonly, although all six were used. Each individual utilized from two to four of the six burrows, and each burrow was utilized by from one snake to five different snakes. Seemingly the snakes located the burrows by olfaction. Hognose snakes remained in burrows for periods of two weeks or more, but it was not determined whether the burrows used during such dormant periods were the same as those used for daily shelter.

The burrowing movements of a western hognose were observed in a glass-walled cage, 40 mm. wide, that was filled with damp sand. The upturned rostral region of a western hognose snake is an effective scoop for loosening sand. In starting a burrow, the neck of the western hognose snake was bent in a U-shaped curve and the head was held at a 90° angle to the surface of the sand. With a series of small dorsal and lateral thrusts, the head was pushed into the sand and the sand was pushed to the side. The snake continued to burrow underground by scoop-like dorsal or lateral thrusts of its head. Each thrust involved an extension of the anterior body and bending of the neck. During a lateral thrust, the head was sometimes rotated to face obliquely the side to which it moved. During each thrust the sharp edge of the rostral scale cut into and loosened sand. This loosened sand was then pushed dorsally, laterally, or posteriorly by the dorsal surface or sides of the head.

The snake dug within an enlarged excavation chamber that had been formed by movements of the head. In the moist sand of the observation cage, this chamber was approximately 30 mm. wide. Movements within this chamber were visible when the scooping movements of the snake's head cleared sand from the glass on one side of the cage. The thrusting movements of the snake's head were for a time directed to the right side of the excavation chamber and then to the left side. The snake paused periodically for a minute or more. Most of the loosened sand moved by each thrust of the head was pushed or fell to the back of the excavation chamber, where movements of the body pressed it to form the compact walls of the burrow. The completed section of the burrow was only slightly wider than the diameter of the body of the snake.

While the snake's head was loosening and moving sand in the excavation chamber, the posterior part of its body on the surface was thrown into loops that pressed against ridges of sand or other irregularities. Part of the body probably pressed against the walls of the completed burrow and thus provided a firm support from which the head and anterior body could thrust. Waves of muscular movement passed along the body of the snake as it burrowed.

In making a shallow, horizontal burrow, the upward thrusts of the snake's head push up a low ridge of sand over the burrow. Although a western hognose snake may bury itself in a shallow burrow within two minutes, digging a deeper burrow by a large snake may require from five minutes to more than half an hour.

Davis (1946:75-78) described similar burrowing movements of the eastern hognose snake. The orientation of the head in initiating burrowing in dry sand was at a smaller angle (30 degrees) to the surface. The head was moved in lateral thrusts alternately to either side.

"The position into which the head is drawn at the beginning of each thrust brings the sharp lateral edge of the rostral scute into direct contact with the substratum. During subsequent movements of the head, the wedge-shaped rostral region functions as a double-shared ridging plow, forcing its way through the substratum and pushing the sand to the side. The power for these vigorous movements is derived solely from the anterior dorsal axial musculature, which is enormously hypertrophied in the members of this genus." (p. 76.)

Eastern hognose snakes may utilize burrows of other animals, especially in regions where soils are less suitable for burrowing (see p. 307).

To determine whether hognose snakes have a preference for certain substrates in which to burrow, test cages were prepared, each having the right half filled with one type of soil and the left half with another (Pl. 5, Fig. 1). The soils used were a garden loam, coarse sand from a creek channel, and fine sand from the study areas (Table 15). One hognose snake was placed in each cage. Each day the number of new burrow openings was recorded for each substrate. The snake was changed to a new cage after three weeks to one month. The results of these tests with western hognose snakes are shown in Table 16. Assuming that the number of burrow openings is related to the total amount of burrowing that occurred in a substrate, the results indicate that fine sand is definitely preferred.

Although the western hognose can burrow easily in moist loam, burrowing in wet loam is difficult. The coarse sand is probably less favorable for burrowing because the variable large particles provide more resistance to the shearing

TABLE 15. Mechanical Analyses of Soils Used in Burrowing Experiments With Caged Hognose Snakes.

Soil	Per cent soil particles in each size fraction				
	Greater than 0.90 mm.	0.90 to 0.375 mm.	0.375 to 0.185 mm.	0.185 to 0.16 mm.	Less than 0.16 mm.
Coarse sand.....	35.7	56.4	5.5	1.6	.8
Fine sand.....	tracc	45.7	37.8	9.8	6.7
Garden loam.....	3.2	7.5	6.5	10.2	72.6

TABLE 16. Number of Burrows Opened by Western Hognose Snakes in Different Substrates in Test Cages.

Test	Loam	Coarse sand	Fine sand	Chi square
Fine sand vs. loam....	3	32	22.4**
Fine sand vs. coarse sand.....	7	19	10.9**
Loam vs. coarse sand..	29	17	3.1

action of the rostral projection, and coarse sand forms less stable burrow walls. Few tests were made with eastern hognose snakes, but preferences for substrate are probably similar.

Mr. W. Charles Kerfoot (*in litt.*) collected a small western hognose with its head in a hole in the side of an ant hill on the upper slope of a chalk bluff in Wyoming. Dr. Monroe H. Bartel told me that he had seen these snakes burrowing in ant hills a number of times in the silt loam soil of Kearny County, Kansas. This behavior was never observed on the sandy study areas. When fine-textured surface soils are too dry to permit easy digging, western hognose snakes may dig in the looser soil of ant mounds to reach moist deep layers.

The skull of hognose snakes is modified for their mode of burrowing by: 1) shortening posterior to the postfrontals, providing an increased mechanical advantage for burrowing movements; 2) antero-posterior flattening of the premaxillary bone and development of a projecting dorso-anterior vertical bar and a dorso-lateral expansion that provide the skeletal framework for the rostral projection; 3) elongation of the nasals which are fused and expanded anteriorly and posteriorly to provide support for the premaxillary and to prevent rotation at the naso-frontal articulation; 4) widening of the frontals and parietals to provide stronger support (Weaver, 1965:282-283; 296-297).

Other features that are adaptive for the method used by hognose snakes in excavating a burrow are: 1) a short thick body allowing the snake to bury itself in a shorter burrow; 2) a short tail; 3) keeled scales providing more friction with the burrow wall, thereby giving firmer support to the head in

digging movements. These features are quite different from those of burrowing snakes such as *Arizona* or *Chionactis* that push the body through loose sand with "swimming" movements (Norris and Kavanau, 1966:660). The latter snakes have smooth scales and are more narrow and elongate, causing less displacement of substrate, since the burrow is not actually excavated.

All of the skull adaptations are more highly developed, the body is shorter and thicker, and the tail is shorter in the western hognose than in the eastern species. The rostral projection of the western species is more upcurved and longer, forming a better scooping surface. The dorsal "cutting" edge is rounded, giving a broad edge for dorsal thrusts as well as lateral thrusts. In the eastern hognose the projection is pointed dorsally. The rostral projection is thinner in the western species, with a more acute wedge-shaped cutting angle that could probably be forced through compact soil more easily.

The rostral projection can be used for prying as well as burrowing. A small hognose snake held in the clenched hand will sometimes insert the rostral projection between fingers and attempt to pry. Hognose snakes have been observed to insert the rostral projection in the mesh of a wire fence of an outdoor pen and twist to attempt to enlarge the opening.

LOCOMOTION AND PROWLING BEHAVIOR

Hognose snakes use horizontal undulatory, rectilinear, sidewinding, and concertina modes of locomotion. Most prowling and escape involves horizontal undulatory locomotion. On open sand a hognose snake makes a track consisting of small longitudinal piles of sand that are used as pivots against which to press the side of its body (Pl. 5, Fig. 2).

When a snake is slowly prowling, the horizontal undulatory loops of the body are shallow and few. Movements of rectilinear type are often important. While prowling, the snake tests its surroundings by flicking the tongue. Although a hognose snake probably cannot identify motionless objects by sight, it responds to movements at distances of at least ten feet.

When a hognose snake attempts to crawl swiftly, as in escape from a person, the loops of the body become wider and more numerous. The snake rarely flicks its tongue as it attempts to escape.

When it senses the presence of a person, a hognose snake sometimes "freezes." When starting to move after such a period of inactivity, it begins a series of jerky movements that involve the whole body. The snake progresses one or two inches at each movement. Each movement is followed by a pause, during which the snake flicks its tongue. The movements gradually last longer with shorter pauses, becoming finally swift, smooth, horizontal undulatory locomotion. If the person makes a motion during the period when the snake is moving jerkily, the snake will usually "freeze" again. If the person moves after the snake has begun to move more rapidly, the snake will attempt to move faster.

Sidewinding by hognose snakes has not been observed in the field, but does occur on a smooth surface, such as a wooden floor. Western hognose snakes sidewind more readily than eastern. The locomotion pattern is well developed, indicating that sidewinding is probably sometimes used in the field. Schmidt and Necker (1935:68) found tracks of hognose snakes that were similar to those made by a sidewinding snake. Concertina locomotion by hognose snakes has rarely been observed.

Hognose snakes are slow-moving. Locomotion was timed for intervals varying from 6.5 seconds to 122.5 seconds to determine the speed of uninterrupted locomotion for short distances. The maximum speed recorded for the western species was .53 miles per hour compared to maximum speeds from .224 to 3.60 miles per hour for the various species of snakes tested by Mosauer (1935:7).

Five measurements of the speed of western hognose snakes using horizontal undulatory locomotion to escape in the field or in an outdoor pen averaged .37 (.25 to .53) miles per hour. Five measurements of the sidewinding speed on a wooden floor averaged .34 (.17 to .51) miles per hour. Three measurements of the speed of prowling, including few pauses, averaged .17 (.15 to .19) miles per hour.

Six measurements of the speed of eastern hognose snakes using horizontal undulatory locomotion to escape on a wooden floor averaged .30 (.12 to .44) miles per hour. Two measurements of the speed of sidewinding on a wooden floor averaged .23 (.11 to .35) miles per hour. One eastern hognose snake prowling on a mowed lawn moved at the rate of .18 miles per hour.

The eastern hognose occasionally swims. They have been observed in both sea water and fresh water (Linsley, 1844:43; LaVie, 1920:39; Myers, 1929: 101-102; Allen, 1932:13; Breckenridge, 1944:108). A large eastern hognose captured on the bank of the lake in Harvey County Park voluntarily entered the water and swam across the lake when it was released.

Western hognose snakes have never been observed to swim voluntarily. I threw one into a pond approximately ten feet from shore. It swam to shore with rapid undulations of the body, holding its head approximately 1½ inches above the water with its snout pointed vertically.

Hognose snakes do not ordinarily climb and were never found above the surface of the ground in the field. A number of eastern and western hognose snakes were kept in a cage with a vertical tree branch approximately three feet long in the center. The snakes were able to climb this branch to gain the warmth of the electric light at the top of the cage.

HOME RANGE AND MOVEMENTS

Dice (1952:231) defined home range as an ". . . area over which an individual animal habitually travels while engaged in his usual daily activities." The term implies a restriction of activities to a familiar area. Restriction in movement can be caused by restricted locomotor ability or restricted habitat. However, many animals limit their movements to part of the habitat that can be traversed in a few days or less.

Hognose snakes could move freely to and from the study areas in Harvey County, since the study areas were located within more extensive similar habitat. The ungrazed grassland of the Harvey County Park study area was not as favorable for hognose snakes as the grazed pastures that adjoined it on the west and south. Ungrazed grassland was present north of the study area, although movements to the north were partially obstructed by a lake. To the east was the picnic area of the park and the Little Arkansas River that restricted long distance movements. A road on the south side of the study area was probably no barrier to movement by these snakes. The Graber Pasture study area was surrounded by similar grazed grassland.

The mean distance from the original point of capture for animals that wander without attachment to a home range will increase with time. However, for hognose snakes on the study areas, there was no evidence of increasing distances, except possibly in the first one or two months for the western species (Table 17). All mean distances of movement were shorter than the mean distance between trap stations (calculated from the measurements of distances between each trap station and every trap station on the study area, including zero distances between a trap station and itself). In all cases the mean distance of

TABLE 17. Distances of Movement Between Captures of Hognose Snakes on the Two Study Areas in Harvey County, Kansas. Time Between Captures Includes Only Days Within Season of Activity.

	Number of measurements	Distance (feet)
Mean distance between trap stations (Harvey County Park).....	378	1,131
Mean distance between trap stations (Graber Pasture).....	253	1,048
WESTERN HOGNOSE SNAKE		
Recaptured after 5 to 30 days.....	12	387
Recaptured after 15 to 30 days.....	8	418
Recaptured after 31 to 50 days.....	9	661
Recaptured after 51 to 100 days.....	13	598
Recaptured after 101 to 200 days.....	16	586
Recaptured after more than 200 days.....	5	290
EASTERN HOGNOSE SNAKE		
Recaptured after 5 to 50 days.....	8	811
Recaptured after 15 to 50 days.....	4	538
Recaptured after 51 to 200 days.....	10	723

movement could be travelled by a hognose snake moving at prowling speed in less than one hour. This evidence is consistent with the hypothesis that hognose snakes are restricted in their daily activities to a home range.

Numbers of recaptures for individual hognose snakes were insufficient for a reliable estimate of size of the home range by the minimum polygon or the density probability function methods. Estimates of the size of an animal's home range calculated by the method of Fitch (1958:73) are affected by the spacing between traps unless there are many traps in each home range. Also, an estimate by this method will be biased if many home ranges are not circular. In my study, I have calculated the mean distance of movement as an index of

the extent of movement and the size of the home range. Indices calculated for different species of snakes caught in the same trap stations or in trap stations with similar spacing can be compared.

Some of the longer movements made by hognose snakes were made by individuals outside their home ranges or shifting home ranges (see p. 324). Some of the shorter movements may have been made by individuals that had not yet dispersed from the point of release. The upper ten per cent and the lower ten per cent of the records were arbitrarily eliminated from the calculations of mean distance.

Heterodon nasicus. The mean distance between points of capture of individual males in the Graber Pasture study area was 259 feet and for females, 307 feet. The difference between sexes is not statistically significant, and the measurements for males and females were combined to give a mean distance between successive captures of 277 ± 47 feet (N is 32).

In Harvey County Park the mean distance between successive captures for males was 678 feet, and for females, 838 feet. The combined data give a mean distance between successive captures in Harvey County Park of 785 ± 72 feet (N is 26).

The mean distance of movement in the Harvey County Park study area is substantially greater than in the Graber Pasture study area. If this difference were the result of a scarcity of resident individuals and a large proportion of "wanderers" at Harvey County Park, few snakes would remain in the study area for long periods of time. The mean period between first and last captures of recaptured western hognose snakes was 134 days in Graber Pasture and 98 days in Harvey County Park (counting only days during season of activity). This difference is not statistically significant, but it does indicate a tendency for greater wandering in those individuals captured in Harvey County Park. Also, a smaller proportion of first recaptures occurred after the lapse of a winter season in Harvey County Park. However, the proportion of snakes that were recaptured was slightly higher in Harvey County Park (23.5 per cent) than in Graber Pasture (18.1 per cent). Some snakes remained in the Harvey County Park study area for long intervals or else returned there after periods of wandering. One male snake was captured four times in the central part of the study area between July 2, 1960, and August 31, 1962.

There is no evidence of a contrast between wandering individuals and a small sedentary population in Harvey County Park. The measurements of movement are rather evenly distributed in the interval from 0 to 950 feet in Graber Pasture and from 0 to 1,475 feet in Harvey County Park, with the general trend of measurements higher in the Harvey County Park series.

A plausible explanation of the increased distance between captures on the study area at Harvey County Park is that most individuals in this population move over larger areas in finding food and shelter and performing other daily activities. Within each home range an individual hognose snake must have available food and one or more burrows. The restriction of activities to a home range may be caused partly by the tendency to return to a familiar burrow, although there is evidence that an individual hognose snake uses more than one burrow (see p. 317). In Harvey County Park, shelter burrows are probably located on the higher grassland, the weedy areas, or in small groves of trees, because the low grassland with its thick vegetation and interlaced mat of roots is less suitable for burrowing. The ponds and flooded areas, with high popula-

tions of frogs, that are important as prey, are localized and surrounded by lowland grass. For lizards, also important prey animals, suitable habitat is restricted to the higher, more open uplands. Therefore, within a day and within a season, a hognose snake must cover a relatively large area to obtain the essentials for survival. In Graber Pasture, areas of flooded lowland were scattered throughout the entire study area. Open sandy areas bordered ponds, so that the habitats suitable for lizards and for frogs were in places contiguous, and a hognose snake could satisfy its needs in a relatively small area (Fig. 2; Pl. 2, Fig. 1).

The home range of an individual western hognose snake is determined by a balance between the relative "inertia" of the snake and the favorableness of the habitat. As long as the snake can satisfy its needs within a restricted area, it continues to confine its activities to a small home range. When some of its needs are not met, it must enlarge its home range or shift to a new location of restricted activity. Stickel and Cope (1947:129-130) also suggested that the size and shape of a home range are affected by habitat.

Movements outside the usual home range may occur, and may involve: (1) Searching movements made by male snakes motivated by the sexual drive in the breeding period. (2) Shifts of home range or enlargements of home range when changes in the habitat necessitate such movements to satisfy requirements of the snake. (3) Movements by "wanderers" that temporarily or permanently have the "wanderlust."

A movement of 1,340 feet between April 26 and May 12 and one of 1,240 feet between August 2 and October 2 were recorded for male western hognose snakes in Graber Pasture in spring and autumn breeding seasons. Males that moved 2,550 feet between June 18 and July 20 and 1,975 feet between October 17, 1959, and June 28, 1960, in the Harvey County Park study area probably shifted their home ranges.

The record movement of approximately one mile is that of a female that moved from the Graber Pasture study area to the Harvey County Park study area between August 9, 1961, and June 12, 1962. This snake continued to "wander." From June 15, when she was released, to June 17, she moved 1,875 feet. Although she remained active and was caught three more times in the summer of 1962, her movements were subsequently restricted to the eastern part of the Harvey County Park study area, and involved distances of 600, 825, and 1,240 feet. The records for this individual indicate that a snake may become a "wanderer," at least for a period of time.

Hognose snakes probably hibernate in or near their home ranges. There is no evidence of large-scale movement to hibernation sites in the autumn.

Homing ability was not demonstrated by snakes in my study. Two individuals caught approximately one mile from the Harvey County Park study area, were released in the park, and both were recaptured in the autumn, three to four months later, still within the park. One was recaptured near the point of release, and the other had moved in a direction away from the area of its original capture.

Heterodon platyrhinos. The mean distance between successive captures in the Graber Pasture study area was 682 ± 100 feet (N is ten). The mean distance between captures in Harvey County Park was 952 ± 326 feet (N is seven). The mean distance of movement of eastern hognose snakes in the Graber Pasture study area was more than twice that of the western species,

indicating that the eastern species has a larger home range. The mean distance of movement of eastern hognose snakes in Harvey County Park was somewhat larger than that of the western species, but both distances were similar in magnitude to the mean distance between trap stations.

Two records of movement of 2,570 feet and 2,815 feet by males in Harvey County Park between April 26 and early May were within the breeding season.

REPRODUCTION

Spermatogenetic Cycle

I obtained cloacal smears from a sample of male hognose snakes from Harvey County after palpating the abdominal area to force semen from the ductus deferens. Motile spermatozoa were found in the smears from three of seven male western hognose snakes (43 per cent) with snout-vent lengths less than 300 mm., from 13 of 23 snakes (57 per cent) with snout-vent lengths of 300 to 349 mm., and from 43 of 48 snakes (90 per cent) with snout-vent lengths of 350 mm. or more. Samples of active spermatozoa were not obtained from males of the eastern species with snout-vent lengths of 450 mm. or less but were obtained from 15 of 17 snakes (88 per cent) with snout-vent lengths of 451 mm. or more. Most of the negative tests on larger snakes were made in July when there were few spermatozoa in the ductus deferens of mature snakes.

Most male eastern and western hognose snakes initiate spermatogenesis in their first spring, when they are approximately nine months old, and they have mature spermatozoa when they are one year old. Some individuals, particularly those that have grown slowly or have been injured, may not become mature until the second year (see p. 354).

The cytologic details of spermatogenesis in hognose snakes are similar to those described for garter snakes by Cieslak (1945:303-306) and Fox (1952) and for the European viper (*Vipera berus*) by Volsøe (1944:81-89, pls. 8-10). The histology of the testes and accessory reproductive organs of nine mature male western hognose snakes collected in May (one), June (one), July (three), September (three), and October (one) was studied. Five first-year males collected in June (one), July (three), and September (one) were also studied. Four mature male eastern hognose snakes collected in May (one), June (one), August (one), and October (one), and four first-year males collected in June (one), July (two), and August (one) were studied. The most common stages in the prophase of primary spermatocytes were leptotene, synizesis, and pachytene. Secondary spermatocytes were relatively rare at all times, indicating that the second meiotic division occurs quickly. Eight stages of spermiogenesis, similar to those described by Fox (1952:499-500), could be distinguished. Stages I, II, and VII were most common.

Hognose snakes have postnuptial spermatogenesis completed before winter dormancy, and spermatozoa are stored in the ductus deferens during dormancy (Pl. 4, Fig. 4). This is similar to the spermatogenesis of the few other colubrid snakes that have been studied (Cieslak, *loc. cit.*; Fox, 1952; Fitch, 1963: 415-416).

The testes of both eastern and western hognose snakes increase in size during spermatogenesis. The diameters of seminiferous tubules in sections from testes collected in July and early August, when spermatogenetic activity was at a

peak, were approximately twice the diameters of tubules in early spring (Pl. 4). However, the actual increase in size was smaller, since the empty tubules shrink more during preservation than those with large numbers of germinal cells.

Heterodon nasicus. The seminiferous tubules of the testes of mature male western hognose snakes when they leave winter dormancy in Harvey County are partially occluded with Sertoli syncytium, and the Sertoli nuclei are plump and located away from the basement membrane of the tubule. During active spermatogenesis most Sertoli nuclei are flattened against the basement membrane. In sections from a testes taken in May, spermatogonia were the only common germinal elements, although some primary spermatocytes were present. The germinal elements formed an irregular layer around the tubule (Pl. 4, Fig. 1). In early June the tubules had broad open lumina, and the germinal epithelium was still dominated by spermatogonia. Primary spermatocytes were more numerous. Germinal elements had increased in number in the tubules of testes taken in late June and July, and the germinal epithelium was at least ten cells thick. Primary spermatocytes and early spermatids were common in early July, but by late July, spermatids of all stages had become the dominant cells (Pl. 4, Fig. 2). Some spermatozoa were present in the tubules of a testes taken in early July. No specimens were collected in August. In early September the dominant cells were spermatozoa and spermatids of all stages. The germinal epithelium was thinner (five to eight cells thick, excluding the clusters of spermatozoa in the lumen), as the tubules had become partially emptied (Pl. 4, Fig. 3). In the specimen preserved on October 20, most of the spermatozoa had left the tubules, and the tubules appeared shrunken. There was a single scattered layer of spermatogonia just inside the basement membrane and some spermatozoa in the lumen or caught in the Sertoli syncytium that partially occluded the lumen (Pl. 4, Fig. 4).

In first-year males the tubules were smaller and appeared more shrunken than in older individuals. The spermatogenesis was similar but appeared to be later and more irregular.

The efferent ductules and the epididymis contained spermatozoa from mid-July through autumn. During this time the epithelial lining was thicker and glandular and secretions were evident in the lumen.

The ductus deferens was enlarged, convoluted, and filled with spermatozoa from at least early September (probably mid-August) to early June. Sections of the ductus deferens of specimens taken in July had few or no spermatozoa. Although cloacal smears obtained from live males showed that spermatozoa were present in the ductus deferens of some males at all seasons, the percentage of cloacal smears that showed spermatazoa was lower in June and July. There are probably insufficient spermatozoa in the ductus deferens for insemination to occur during June, July, and early August. The epithelium of the ductus deferens does not appear to be glandular. The mean thickness of the epithelium when the ductus deferens was enlarged and convoluted was 11.9 microns, but it was thicker (18.6 microns) when the duct was empty and smaller.

The pre-terminal or "sexual segment" of the renal tubules is enlarged and glandular in the kidneys of male snakes. In male western hognose snakes collected between the middle of May and the end of July, the epithelium lining these tubules consisted of a single layer of tall columnar cells containing round eosinophilic secretory granules (Pl. 4, Fig. 5). The tubules were minimal in

size (105 microns in diameter) in May but increased to 135 microns in diameter in July. The epithelium increased in height from 40 microns in May to 60 microns in July. In three of four specimens collected in September, the cytoplasm of the epithelial cells of the pre-terminal renal tubules was either vacuolate or homogeneous, the secretory granules were reduced or absent, and a homogeneous eosinophilic secretion filled the lumina of the tubules (Pl. 4, Fig. 6). In the specimen collected in October secretory granules were present in the cytoplasm, and the tubules were 112 microns in diameter. Although some secretion was present in the lumina of the tubules at other seasons, particularly in May and October, the period of maximum secretion was in September (and possibly in August) when spermatozoa were collecting in the ductus deferens.

The pre-terminal segments of renal tubules of first-year males were enlarged and contained secretory granules by mid-June. Although the diameter of the tubules was less than that in mature males (77 to 87 microns in July), the histological characteristics were similar.

Volsøe (1944:143) suggested three possible functions for the secretions of the pre-terminal segment of the renal tubules of snakes: 1) the secretion may block the renal tubules or ureter during copulation, thereby separating semen from urine; 2) the secretion may be expelled after the semen, thereby resulting in complete emptying of the urogenital ampulla or possibly serving as a vaginal plug; or 3) the secretion may give scent to the urine during the mating season. However, maximum secretion by the renal tubules of western hognose snakes does not occur during the mating season. The suggestion by Moore (1939:392), that the albuminoid secretion of the renal tubules contributes to the semen, is more plausible. This is possible because the ductus deferens and the ureter join at the urogenital ampulla before opening into the cloaca. In the western hognose snake most of this secretion is added to the semen while spermatozoa are collecting in the ductus deferens, although some secretion may be added during the whole period that the spermatozoa are stored.

Heterodon platyrhinos. The spermatogenic cycle of the eastern hognose is similar to that of the western species. By the end of August spermatozoa were common in the testes of a mature male, and few primary spermatocytes were present. By the middle of October the germinal epithelium had been reduced to a single layer of spermatogonia near the basement membrane and some late spermatids and spermatozoa in the lumen.

The ductus deferens of eastern hognose snakes was filled with spermatozoa from August to early June. Cloacal smears indicated that spermatozoa were present in the ductus deferens of some snakes throughout the year, but a number of smears from mature males did not have spermatozoa in July.

The pre-terminal segments of the renal tubules of first-year males were undeveloped from June to early August during their initial spermatogenesis. The renal tubules of mature males resembled those of male western hognose snakes collected in a comparable season. No kidney sections from mature specimens were available for July, August, and September; and no specimens showed maximum secretory activity. In the specimen collected in October, the basal cytoplasm of epithelial cells had few secretory granules and was somewhat vacuolate, while dense secretory granules were present at the apex of the cells. There was little secretion in the lumina of the tubules.

Mating

Heterodon nasicus. Behavior of the western hognose in courtship and copulation has never been described nor was it observed at any time during my study. The principal mating period is in the spring, although some mating may also occur in the autumn. Cloacal smears from females captured on May 13 (three), May 15 (one), and May 29 (one) in Harvey County contained spermatozoa. Males were more active than females in early spring (see p. 311). Since hognose snakes do not hibernate in aggregations, male snakes probably wander widely and seek out the more sedentary females in the first few weeks after they leave hibernation. One female had abundant cloacal sperm on August 28. She may have mated in captivity, since she had been in a cage with a male snake for one day before she was tested. Western hognose snakes are relatively inactive in autumn, and mating at this time is probably not common.

Social attraction between individuals is evident during the mating season and at other times. At each trapping station on the study areas there were two traps, one at either end of a drift fence. Of 23 instances in which two western hognose snakes were caught at one trapping station in one trapping period, 19 pairs were caught in the same trap and only four pairs were in separate traps. This is significantly different from equality (chi-square is 8.5). Many factors could cause this tendency to aggregate, including a greater probability of snakes entering one of the traps at many of the stations. However, this tendency of western hognose snakes to be caught together was probably the result of a second snake following the odor trail of a snake that had already entered a trap. Social attraction was not limited to heterosexual pairs. Of 17 pairs of definitely known sex caught in the same trap, seven pairs each had snakes of the same sex, but these were either immature snakes or adult males. The two pairs of adult females caught at the same trapping station were caught in separate traps. Of the ten heterosexual pairs, eight consisted of two adults, and five of these were captured in May. Although the sample is too small for reliable conclusions, the data are suggestive of a strong attraction between adult males and females in May, and also possibly some social attraction between male snakes and between male and female snakes at other seasons.

Heterodon platyrhinos. The precopulatory behavior of the eastern hognose snake has never been described, although a number have been observed in copulation. The female part in courtship behavior is probably passive and permissive. Medsger (1927:180) reported that two males were found *in copula* with one dead female. The males had not been present when the female was killed earlier in the day. Hay (1892a:117) described an instance in which a second male was entwined about a pair *in copula*. Edgren (1953:162-163) dissected a pair that had been preserved *in copula*. The spines of the inserted hemipenis were buried deeply in indentations of the female cloacal wall. The penis filled only the posterior three-fourths of the cloaca, while the anterior one-fourth was filled with clotted semen.

Most of the dates on which mating of eastern hognose snakes have been observed are in April (Table 18). In my study, no females with cloacal sperm were captured in the spring. Mating apparently takes place soon after the snakes leave hibernation. A female captured on October 9 had spermatozoa in her cloaca, indicating that mating may sometimes occur in the autumn.

TABLE 18. Dates of Observed Matings of Eastern Hognose Snakes in Nature.

Date	Locality	Authority
March 28.....	Southeast Texas	Guidry (1953:51)
April 11.....	Weyanokie, New Jersey	Medsker (1927:180)
April 13.....	Vigo County, Indiana	Blatchley (1891:33)
April 16.....	Louisiana	Clark (1949:249)
"sometime in May"....	Mankato, Minnesota	Hay (1892a:117)

Ovarian Cycle

Heterodon nasicus. In my study the smallest female that was undoubtedly gravid was 366 mm. in snout-vent length. Another female, that was 312 mm. in snout-vent length, appeared to be gravid when first captured on June 14, but later in captivity the eggs were resorbed.

A thick-walled cloacal capsule is evidence of sexual maturity in female hognose snakes (Fitch, 1960a:50). In my study 22 female western hognose snakes with snout-vent lengths greater than 375 mm. had well-developed cloacal capsules. Of eight females with snout-vent lengths between 335 and 375 mm., four had well-developed and four had poorly-developed cloacal capsules. Five females less than 335 mm. in snout-vent length had no detectable cloacal capsules.

In a sample of 22 females caught in south-central Kansas and dissected, all those with snout-vent lengths less than 360 mm. were judged immature from the condition of the oviduct and ovary (Pl. 6). Seventy-five per cent of the females with snout-vent lengths of 360 to 400 mm. were immature. Of those snakes that were 400 to 500 mm. in snout-vent length, one (17 per cent) was obviously immature and one other was possibly immature. All of the snakes more than 500 mm. in snout-vent length were reproductively mature (Table 19).

The above data indicate that most female western hognose snakes mature at a snout-vent length between 350 and 400 mm. Some individuals produce their first clutch of eggs at 20 to 22 months of age, but some do not mature until the following season or even later.

In spring immature female specimens of the western hognose had an average of 11 ova (7 to 15) that were one to three mm. in length in both ovaries combined. In the late summer preceding sexual maturity some of these ova (mean of 9.5 ova in four individuals) had enlarged to three to five mm. in length. Approximately half of these enlarged ova would have matured the following spring. In mature females that had recently laid eggs, 8 to 25 ova that were four mm. long and numerous smaller ova remained in the ovary.

The maturing ova enlarge rapidly in the spring and can be detected by external palpation of the abdomen more than one month before they are laid. Gravid females become heavier in the spring. A standard or normal weight for a female of a specific length can be calculated from the regression coefficient of weight on total length (Fig. 4). In the sample of dissected females, those that were gravid were 14 to 98 grams overweight, whereas those that were parturient were normal in weight or slightly underweight (Table 19).

TABLE 19. Reproductive Conditions of 22 Female Western Hognose Snakes Collected in South-Central Kansas.

Date killed	Snout-vent length (mm.)	Maximum diameter of ova (mm.)	State of oviduct	Deviation from normal weight (gm.)	Remarks
July 6...	267	3	immature	+4	
July 1...	277	3	immature	
July 6...	277	3	immature	0	
Aug. 15..	278	3	immature	+3	
June 27..	322	3	immature	-2	
July 19..	351	3	immature	
July 1...	358	3	immature	
July 10..	361	4	immature	+3	
Sept. 8..	363	5	immature	-3	
July 7...	366	32	mature	+14	gravid
Aug. 9...	389	4	immature	-5	
July 29..	409	4	mature	+8	parturient
July 13..	429	15	mature	-7	injured; ova being re-sorbed
July 6...	436	4	immature?	-2	
June 12..	477	3.5	immature	+1	
July 4...	482	4	mature	parturient
July 30..	492	4	mature	+10	
July 8...	505	4	mature	-14	parturient?
July 1...	575	..	mature	+98	gravid
June 15..	610	26	mature	+89	gravid
May 10..	632	4	mature	-19	
June 15..	648	19	mature	+26	gravid

Of 12 female western hognose snakes that were more than 350 mm. in snout-vent length and were captured in May on the study areas, all except one were underweight (mean deviation from normal weight of -20 grams). Two females that were captured 36 days before they laid eggs had palpable eggs and were overweight 20 to 35 grams. The earliest date on which eggs were

laid by captive western hognose snakes in my study was July 2. Therefore, in the period from June 2 to July 1, most breeding females would be overweight and have palpable eggs, and few would have laid eggs. Data from 29 females caught in this period that were more than 350 mm. in snout-vent length are summarized in Table 20.

TABLE 20. Reproductive Condition of 29 Female Western Hognose Snakes That Were Live-trapped in Harvey County, Kansas, Between June 2 and July 1 inclusive, in the Years 1959 to 1963.

	351-400 mm. snout-vent length (13 snakes)	401-450 mm. snout-vent length (9 snakes)	Over 450 mm. snout-vent length (7 snakes)	Total (29 snakes)
With palpable eggs, per cent..	15	22	43	24
Mean deviation from normal weight at capture.....	+17 (+14 to +20)	+21 (+17 to +25)	+31 (+28 to +35)	+24
With palpable eggs? ^a per cent		33		10
Mean deviation from normal weight at capture.....		0 (-4 to +5)		0
No palpable eggs, per cent.....	85	45	57	66
Mean deviation from normal weight at capture.....	-2 (-9 to +5)	-7 (-9 to -3)	-17 (-70 to +9)	-6

a. These snakes had palpable eggs when captured but later resorbed them (in captivity).

Most of the snakes that had snout-vent lengths of 351 to 400 mm. and were not gravid were probably immature. One female in the largest size class had recently been injured and was 70 grams underweight. Among snakes of intermediate size there were three of approximately normal weight that had palpable eggs when captured, but resorbed the eggs after a period in captivity. Whether this would have occurred in nature is not known, but resorption of eggs does occur in nature (Table 19). Although this sample is small, it indicates that possibly up to one-half of the mature female western hognose snakes are not gravid in any one season in Harvey County (Table 20). If non-breeding females are more active than those that are gravid, my sample may be biased in favor of non-breeding snakes.

Seventeen females, each with a snout-vent length of 451 mm. or more, were collected in July on the study areas. One was gravid and weighed 30 grams more than normal. Five appeared parturient and had a mean deviation from normal weight of -14 grams. Eleven were not gravid, did not appear parturient, and had a mean deviation from normal weight of -3 grams. Some of the latter were probably parturient, but possibly one-half of this sample of large females were non-breeders.

Some individual histories provide evidence of breeding in alternate years. Female 5L 2R (537 mm. snout-vent length) weighed 18 grams less than normal and was probably parturient when captured on July 5, 1960. On July 25, 1961, she was 34 grams overweight and obviously not gravid nor parturient. Female 13L 6R (383 mm. snout-vent length) was two grams overweight and appeared parturient on July 20, 1962. On June 8, 1963, she was not gravid and was nine grams underweight. No records were obtained of a female that produced eggs in two consecutive years.

Females that mate in May do not always produce a clutch of eggs. Female 6L 16R (408 mm. snout-vent length) had cloacal sperm when she was captured on May 13, 1961. On June 24, 1961, she was recaptured and was not gravid. Female 7L 2R (484 mm. snout-vent length) had cloacal sperm when she was captured on May 29, 1963. She was not gravid on June 24, 1963.

These data indicate that some female western hognose snakes, if not most, have a biennial ovulation. Biennial reproductive cycles have been previously reported in some ovoviviparous snakes (Klauber, 1956:687; Fitch, 1960b:162-164; Tinkle, 1962; Volsøe, 1944:18). Fitch (1963:421-422) found that a minority of large female racers fail to breed in any one season. Oliver (1955:244) stated that some reptiles from the northern extremes of their ranges breed only in alternate years. However, Harvey County is in the central part of the range of the western hognose snake. Biennial reproduction may be a general reproductive pattern in the western hognose.

Heterodon platyrhinos. The smallest female recorded to have produced a clutch of eggs was 584 mm. total length (corresponding to a snout-vent length of approximately 500 mm.; Meyer, 1958:128). In my study the smallest female that had a well-developed cloacal capsule was 500 mm. in snout-vent length. Seven of nine females that had snout-vent lengths greater than 500 mm. had cloacal capsules. Female eastern hognose snakes that are most typical in their development probably mature when they are 20 to 22 months of age and approximately 560 mm. in snout-vent length (Table 31).

The sample of female snakes caught in the spring on the study areas was too small to determine the proportion of mature females that breed each year. The earliest date on which a clutch of eggs was laid in the laboratory was June 27. In the period between May 27 and June 26, only four females of mature size were caught, two of which were gravid; whereas the other two, recorded on June 18 and June 19, appeared to be parturient.

Female 6L 4R was 11 grams overweight when she was caught on May 19, 1962, but other females caught on April 26, May 3, and May 19 were underweight. On June 4, 1963, female 6L 4R was gravid (54 grams overweight) with 14 eggs. Hence she may have produced clutches in two consecutive seasons.

Although these data are meager, they are consistent with the conclusion that most of the female eastern hognose snakes of more than 560 mm. snout-vent length lay eggs each season.

Oviposition and the Clutch of Eggs

Oviposition by snakes in nature is not usually observable. Observations of oviposition of captive snakes must be interpreted with caution, because captivity may delay egg-laying, cause the resorption of some eggs or the whole clutch, and modify behavior.

Heterodon nasicus. Eight females from Harvey County laid clutches of eggs on dates from July 2 to July 23 inclusive, after being in captivity from 4 to 36 days. One snake laid a clutch on July 22, after being in captivity only four days. The earliest date on which a parturient female was caught on the study areas was July 3. Most eggs are laid during the first three weeks of July by western hognose snakes in Harvey County. Munro (1949a, b:133) reported that a western hognose from McPherson County, Kansas, laid eggs on the nights of July 5 and 6 after being in captivity for 33 days.

In Texas some western hognose snakes lay eggs earlier. Records include: clutches of eggs were laid on June 3 (Werler, 1951:41) and July 17 (Sabath, 1960:72); a snake that died in captivity on June 17 contained large eggs almost ready to be laid (Anderson, 1965:190); a clutch of two eggs was laid by a female from Waller County on August 24 (Sabath and Worthington, 1959:32), but both the small size of the clutch and the late date indicate that this was an abnormal instance, possibly due to the effects of captivity.

Egg-laying dates in the northern part of the range are from the middle of June to early August. Records include: a snake from Manitoba, Canada, laid a clutch of eggs between June 12 and 17 (Mr. I. L. Traill, *in litt.*); a snake from Alberta, Canada, laid eggs between July 19 and 23 (Moore, 1953:173); a snake containing eggs was captured on July 13 in Minnesota (Breckenridge, 1944:113); a snake with eggs of "laying size" was collected in Montana on July 20 (Mosimann and Rabb, 1952:25); and a snake from Iowa laid eggs on August 4 (Ruthven, 1910:208). Davis and Weeks (1963:6) stated that the western hognose lays eggs in Montana in late July and August.

The elliptical white eggs have smooth, thin, papery shells. The eggs may adhere, although they usually do not. The mean length of 45 normal eggs from eight clutches was 32.5 (26 to 38) mm. and the mean width was 18.1 (14 to 23) mm. The mean weight of 38 normal newly-laid eggs from six clutches was 5.8 (4.1 to 8.7) grams. The variation in dimensions of eggs from a single clutch was less than the variation between clutches (Table 21).

The total weights of the eggs in each of four clutches laid by snakes from Harvey County were 83 per cent, 70 per cent, 68 per cent, and 42 per cent of the weight of the respective female snakes immediately after oviposition. The total weight of a clutch of eggs laid by a western hognose snake from McPherson County, Kansas, was 70 per cent of the weight of the snake (data from Munro, 1949b:134).

Natural nests of the western hognose have not been described. The late Mr. Ralph M. Woods, who lived near my study areas, plowed up a nest of eggs of the western hognose in August in sandy soil three to four inches deep. The descriptions of two nests made in cages in captivity are quoted from my notes:

"Digging in the sand, I found a nest of seven eggs. They were not in a burrow but were completely covered with sand. They were resting on the bottom, 90 mm. deep. Some eggs were touching and some were separated by sand.

"Five eggs were laid along a tunnel in the sand at the bottom of the cage. They were strung out instead of being laid in one cavity."

TABLE 21. Size of Eggs in Clutches Laid by Western Hognose Snakes.

Size of clutch	Length (mm.)	Widths (mm.)	Weights (grams)	Authority
11.....	33.5 (31.5-35.5)	19.5 (18.5-20.0)	6.5 (6.1-6.8)	Munro, 1949b: 134
7.....	32.1 (30.0-35.0)	19.4 (18.0-23.0)	6.5 (5.8-8.7)	Platt
6.....	30.8 (27.0-32.5)	15.8 (15.0-17.0)	4.9 (4.5-5.3)	Platt
5.....	32.6 (30.0-34.0)	19.6 (19.0-20.0)		Sabath, 1960:72
5.....	35.6 (34.0-37.0)	17.0 (16.0-18.0)	6.1 (5.5-6.6)	Platt
5.....	29.0 (26.0-32.0)	17.5 (17.0-18.0)	5.2 (4.7-5.7)	Platt
4.....	31.8 (31.0-38.0)	14.2 (14.0-15.0)	4.5 (4.1-5.2)	Platt
2.....	32.0 (31.0-33.0)	20 (20)		Sabath and Worthington, 1959:32

Reliable published records of the numbers of eggs in clutches of the western hognose snake (determined after oviposition or by dissection) have been reported by Breckenridge (1944:113), Marr (1944:484), Munro (1949b:133), Mosimann and Rabb (*loc. cit.*), Moore (1953:173), Stebbins (1954:366), Sabath (1960:72), and Anderson (1965:190). Unpublished records include a clutch of five eggs from Logan County, Kansas (Mr. John S. Applegarth, *in litt.*), a clutch of 12 from Shilo, Manitoba, Canada (Mr. I. L. Traill, *in litt.*), and clutches of 16, 15, 14, 6, two clutches of 7, four clutches of 5, and three clutches of 4 from south-central Kansas in my study. The mean size of 31 clutches was 9.4 (4 to 23) eggs. Thirteen of these clutches were from south-central Kansas and had a mean size of 7.5 (4 to 16) eggs. The size of the clutch of eggs increases with increase in size of the snake. Females with snout-vent lengths greater than 489 mm. laid nine clutches with a mean size of 14.0 eggs; snakes with snout-vent lengths between 440 and 489 mm. laid eight clutches with a mean size of 6.8 eggs; and snakes with snout-vent lengths less than 440 mm. laid seven clutches with a mean size of 5.1 eggs. The differ-

ence between the sizes of clutches laid by large and medium-sized snakes is statistically significant at the one-tenth per cent level (t is 5.6), but the difference between clutches laid by medium-sized and small snakes is not significant (t is 1.4).

Since 23 of the 31 clutches were from Kansas, there is little data bearing on geographic variation in clutch size. The 23 clutches from Kansas averaged 9.5 eggs per clutch. Two clutches from Texas averaged 10.5 eggs per clutch. Six clutches from Minnesota, Montana, and Canada averaged 8.8 eggs per clutch.

Heterodon platyrhinos. Dates on which captive eastern hognose snakes from known localities laid eggs are listed in Table 22. Some of the records

TABLE 22. Dates of Oviposition Reported for Captive Female Eastern Hognose Snakes From Known Localities.

Locality	Date	Authority
IN CAPTIVITY LESS THAN 45 DAYS		
Harris Co., Texas	May 27, 28, and June 1 (4 clutches)	Kennedy, 1961:418
Gayle, Louisiana	June 3	Strecker, 1926b:6
Woods Co., Oklahoma	June 24-30	Platt
Miami Co., Kansas	June 23-26	Gloyd, 1932:402
Harvey Co., Kansas	June 27 and July 2 (2 clutches)	Platt
Pike Co., Ohio	June 19	Conant, 1951:44
Hocking Co., Ohio	June 25 or 26	<i>Ibid.</i> :217
Lucas Co., Ohio	July 1	<i>Ibid.</i> :44
Anoka Co., Minnesota	July 7	Breckenridge, 1944:109
Elgin Co., Ontario, Canada	June 28-29	Mr. H. T. Hiemstra, <i>in litt.</i>
IN CAPTIVITY AN UNKNOWN TIME		
Polk Co., Florida	July 5 and 9 (3 clutches)	Telford, 1952:179
Harris Co., Texas	June 29	Kennedy, 1964:212
Marshall Co., Oklahoma	July 19-23	Webb, 1952:157
Southern Oklahoma	August 16-17	Carpenter, 1958:114
Maryland	July 20, 21, 25 (3 clutches)	McCauley, 1945:65
Carbondale, Illinois	June 6-7	Clark, 1952a:28
Illinois	June 21	Smith, 1961:190
Illinois	June 26	Cagle, 1942:187
Illinois	August 28	Smith, <i>loc. cit.</i>
Ashford, Connecticut	June 18	Clark, <i>loc. cit.</i>
IN CAPTIVITY MORE THAN 45 DAYS		
Southeast Texas	June 1	Guidry, 1953:51
Dallas Co., Texas	June 13	Raun, 1962:3
Ross Co., Ohio	July 11	Conant, 1951:217
Nashville, Indiana	July 14	Meyer, 1958:128
Oxford Co., Ontario	July 12	Logier, 1939:22; Milnes, 1946:2
South Kent, Connecticut	August 8-11	Clark, <i>loc. cit.</i>

from snakes in captivity for long periods may be abnormal. In the southern United States, oviposition occurs as early as the last week in May but may continue until the middle of July. Wright and Bishop (1915:156) reported that in the Okefinokee Swamp region of Georgia, female eastern hognose snakes came to cultivated fields to lay eggs throughout the month of June. In northern Louisiana Clark (1949:249) collected gravid females in the period from June 7 to July 15 inclusive.

In northern Oklahoma and Kansas most eggs are laid in the last half of June and early July (Table 22). A DOR specimen with large eggs in the oviducts almost ready for laying was collected on June 9 in Harvey County. The first parturient females were trapped on the study areas on June 18.

Most of the records of egg-laying from the northern part of the range of the eastern hognose are in the last half of June or the first half of July (Table 22). Minton (1944:456) reported that captive snakes from Indiana laid eggs from June 16 to August 1 inclusive. Gravid females were collected in early July in Iowa (Guthrie, 1926:173) and Minnesota (Breckenridge, 1942:128).

Abbott (1885:289), who lived in New Jersey, stated, concerning the eastern hognose, "In the month of May I have frequently found their eggs in considerable numbers a few inches below the surface." This date is early, and the report may be in error. However, some eggs may be laid early along the Atlantic Seaboard, as hatchlings have also been found early (see p. 343).

Most of the records of oviposition from middle and late August (Table 22) are probably the result of "captive-induced delay in oviposition" as suggested by Smith (1961:190) for the record that he reported. A gravid specimen collected in August, 1927, in Adams County, Ohio (Conant, 1951:44), must have been an abnormally late breeder.

Oviposition in the eastern hognose snake has been described by Kennedy (1961:417-418), Clark (1952a:28), and Cloyd (1932:402). Kennedy observed a female that laid eggs on the floor of her cage in the morning:

"The body of the snake was in an acute U form. The tail was extended anterior to the head with the base of the tail almost touching the head. Slow contractions were discernible from anterior to posterior as the eggs passed through the oviducts. Just before the egg was to be expelled, the tail was slowly elevated and the cloacal region was greatly distended. The posterior wall of the cloaca was visible as it circumscribed the egg . . . After most of the eggs had been laid the tail of the snake was drawn posteriorly so that the body was roughly J-shaped. None of the eggs were deposited on top of each other."

Sixteen eggs were laid in six hours and ten minutes, an average of 23.1 minutes per egg (the interval varied from 15 to 47 minutes for the last seven eggs).

The female snake described by Clark (*loc. cit.*) was placed in a cage filled almost to the top with moist sand. Construction of a wide U-shaped burrow required $3\frac{1}{2}$ hours. The snake buried itself in the burrow with head and tail protruding and gradually inched forward as the eggs were laid. The time required for passing each egg varied from 12 to 30 seconds, the longest time being required for the first egg. Oviposition began at 5:30 p. m. on August 10 and was completed by 7:30 a. m. on August 11. An average of 30 minutes elapsed between eggs prior to 9:45 p. m. and 38 minutes during the rest of the night. Cloyd (1932:402) observed a female lay six eggs between 8:30 a. m. and 1:00 p. m., with intervals between eggs ranging from 10 to 60 minutes.

The elliptical eggs of the eastern hognose are white or cream in color. Gloyd (*loc. cit.*) reported that newly laid eggs were soft, moist, and almost transparent but became opaque and cream-white after ten minutes of exposure. The shell is smooth, thin, and papery (Wright and Bishop, *loc. cit.*; Brimley, 1941:23; McCauley, 1945:66; Edgren, 1955:105; Kennedy, 1961:419). The eggs may adhere together but usually do not. The egg at the time of oviposition contains a small embryo (Brimley, 1903:262-263).

Thirty-nine normal eggs laid by three females in my study had a mean length of 34.6 (29.0 to 42.0) mm. and a mean width of 22.6 (18.0 to 25.0) mm. In addition to the records from Harvey County, Kansas, data on dimensions of eggs of the eastern hognose have been reported by Milnes (1946:2), Conant (*loc. cit.*), Clark (1925b:29), Telford (1952:179), Webb (1952:157), Carpenter (1958:114), Edgren (1955:106), Smith (*loc. cit.*), and Kennedy (*loc. cit.*, 1964:212). The 421 eggs from 21 clutches had a mean length of 31.9 mm. and a mean width of 20.0 mm. In individual clutches the mean lengths of eggs varied from 21.8 to 38.7 mm. and the mean widths varied from 14.6 to 24.5 mm. The variation in dimensions of eggs within clutches was less than the variation between clutches. Larger snakes produced eggs of larger mean dimensions. Female snakes with snout-vent lengths more than 724 mm. laid 84 eggs (four clutches) with a mean length of 35.1 mm. and a mean width of 21.8 mm.; snakes with snout-vent lengths between 610 and 724 mm. laid 101 eggs (five clutches) with a mean length of 33.3 mm. and a mean width of 21.1 mm.; and snakes with snout-vent lengths less than 610 mm. laid 64 eggs (4 clutches) with a mean length of 29.0 mm. and a mean width of 18.2 mm. Clark (1952b:29) measured by water displacement the volume of 41 eggs of two clutches and reported mean values of 2.6 (2.0 to 3.0) and 4.25 (3.5 to 5.0) cubic centimeters for the two clutches.

Weights of the eggs of the eastern hognose snake are variable (Table 23). The mean weight of 193 eggs from ten clutches was 8.4 grams. The mean weight of 39 eggs from three clutches laid in my study was 10.0 grams. The

TABLE 23. Weights of Eggs of the Eastern Hognose Snake at the Time of Oviposition.

Number of clutches	Number of eggs	Mean weight (grams)	Range of weights (grams)	Authority
4.....	99	9.5	7.2-11.7	Kennedy, 1961:419
1.....	14	11.1	8.8-12.4	Platt
1.....	12	10.1	8.5-10.7	Platt
1.....	13	8.6	6.7-10.0	Platt
1.....	17	6.3	5.5- 7.1	Kennedy, 1964:212
1.....	23	4.77		Webb, 1952:157
1.....	15	4.9	2.7- 6.2	Edgren, 1955:106

total weights of eggs laid by each of four snakes from Texas were 147 per cent, 139 per cent, 91 per cent, and 78 per cent of the weight of the female snake after oviposition (data from Kennedy, 1961:418-419). The eggs of the eastern hognose are relatively broader and heavier than those of the western species.

There was no significant correlation between length and width of 39 eggs from three clutches laid in my study (r was -0.21). No significant correlation in these dimensions was shown by the eggs in each clutch (r values were $+0.33$, -0.33 , and -0.36). Clark (1952b:30-31) reported a high positive correlation between length and width in the eggs from three clutches laid by eastern hognose snakes (r was $+0.81 \pm .04$), but the correlation in individual clutches was much lower (r was $+0.46 \pm .15$, $+0.30 \pm .15$, and $+0.08 \pm .22$). He contrasted the positive correlation between length and width in eggs of the eastern hognose snake with the negative correlation in these dimensions that had been reported for some other snakes. The high positive correlation found by Clark was due largely to the variation between clutches, for larger snakes lay larger eggs in both length and width. The lack of correlation within clutches makes spurious the conclusion reached by Clark (1952b:30) that there is "no limitation of egg size by lateral distensibility of oviduct, nor by the length of the oviduct . . ." and "therefore that *Heterodon* has achieved a more advantageous relationship between ovarian and oviducal capacity, which might indeed be a quality of some survival value."

Natural nests of the eastern hognose snake have been briefly described. They have been found: in cultivated fields in sandy soil, four to five inches below the surface in the Okefinokee Swamp area of Georgia (Wright and Bishop, 1915:156); "in a patch of hot sand at the base of a cactus plant in a vacant lot" in Georgia (Neill, 1950:116); "under a rock" in southern Illinois (Cagle, 1942:187); "near an old stump in the edge of a cornfield" in northern Louisiana (Clark, 1949:248); and in "a gravel deposit at a depth of about six inches" in Minnesota (Breckenridge, 1944:109). Logier (1939:22) reported that eggs of the eastern hognose snake "are deposited in dampish situations such as decaying logs." Milnes (*in litt.*) found a shallow nest on September 11 with 12 empty egg shells on the surface of loose sand, 8 empty shells and a hatchling half out of the egg at a depth of one inch, and 20 eggs (that hatched three to six days later) at a depth of two inches. Kennedy (1961:417) collected two female eastern hognose snakes together in a depression four or five inches deep in loose soil in a recently spaded strawberry patch. Since the two snakes were gravid, Kennedy suggested that this depression was probably a nest. However, it is more likely that this depression was a shelter burrow since it contained excreta. The nest is probably dug immediately before oviposition.

Hahn (1908:564) found a female eastern hognose "buried in the soft earth of a cornfield apparently guarding her eggs, among which she was coiled." Hay (*loc. cit.*) reported a second-hand description of a female that defended her eggs when they were plowed up. Strecker (1926b:6) reported that a female in captivity coiled twice around her clutch of eggs in the first three days after the eggs were laid. Other investigators, including myself, have found that female eastern hognose snakes pay no further attention to their clutches after they are laid.

Reliable published records of the numbers of eggs in clutches of the eastern hognose snake (determined after oviposition or by dissection) have been reported by Cragin (1879:710), Hay (1892a:115-116), Brimley (1903:262),

Dunn (1915:37), Wright and Bishop (1915:156), Guthrie (*loc. cit.*), Strecker (*loc. cit.*), Gloyd (*loc. cit.*), Boyer and Heinze (1934:195), Breckenridge (1942:128, 1944:109-110), Cagle (1942:186-187), Hudson (1942:50), Malnate (1944:729), Minton (*loc. cit.*), McCauley (1945:65), Milnes (1946:2), Clark (1949:248-249), Conant (1951:44, 217), Clark (1952b:29), Telford (1952:179), Webb (*loc. cit.*), Guidry (1953:51), Edgren (1955:106), Myers (1957:291), Meyer (1958:128), Smith (*loc. cit.*), Kennedy (1961:417-418, 1964:212), Raun (1962:3), and Conant (1966:54). Unpublished records include a clutch of 48 eggs from Elgin County, Ontario, Canada (Mr. H. T. Hiemstra, *in litt.*), a clutch of 20 from Shannon County, Missouri (Mr. Paul Anderson, *in litt.*), a clutch of 32 from Woods County, Oklahoma, a clutch of 27 from western Kansas, and clutches of 14 and 12 from Harvey County, Kansas, in my study. The mean number of eggs per clutch in 59 clutches was 22.3 (4 to 61). The mean number of eggs in two clutches from Harvey County was 13. Welter and Carr (1939:129), working in Kentucky, reported that eggs laid in the laboratory on a number of occasions averaged 15 eggs per clutch.

Large eastern hognose snakes produce larger clutches of eggs. Snakes having snout-vent lengths more than 724 mm. laid nine clutches with a mean size of 37.9 (14 to 61) eggs; snakes having snout-vent lengths between 610 and 724 mm. laid 11 clutches with a mean size of 22.2 (12 to 31) eggs; and snakes having snout-vent lengths less than 610 mm. laid nine clutches with a mean size of 17.1 (9 to 28) eggs. The difference between the size of clutches laid by the large snakes and the medium-sized snakes is statistically significant at the one per cent level (t is 3.1), but the difference between clutches laid by the medium-sized and small snakes is not significant (t is 1.9).

The mean number of eggs per clutch is much larger for the eastern hognose than it is for the western species. This difference is correlated with the difference in size of the two species. The mean number of eggs per clutch for the largest western hognose snakes (14.0 eggs) is similar to the mean for the smallest eastern hognose snakes (17.1 eggs) that are nearly the same length. The difference between these two means is not statistically significant (t is 1.5).

To investigate geographic variation in clutch size in the eastern species, the range was divided into three north-to-south areas. Twenty clutches from a northern area, including Nebraska, Iowa, Minnesota, Wisconsin, Illinois, Indiana, Ohio, Ontario, New York, and Connecticut, had a mean size of 25.1 eggs. Seventeen clutches from an intermediate area, including Kansas, Oklahoma, Missouri, Maryland, Virginia, and South Carolina, had a mean size of 19.1 eggs. Eighteen clutches from a southern area, including Texas, Louisiana, Georgia, and Florida, had a mean size of 22.1 eggs. The differences in mean sizes of clutches for adjacent areas are not statistically significant (t values are 1.2 and 1.5).

There is little variation in clutch size from west to east. The western area included 25 records from west of the Mississippi River, with a mean of 21.4 eggs per clutch. The intermediate area included 14 records from Illinois, Indiana, Ohio, Wisconsin, and Ontario, with a mean of 23.8 eggs per clutch. The eastern area included 16 records from Florida, Georgia, South Carolina, Virginia, Maryland, New York, and Connecticut, with a mean of 22.3 eggs per clutch. The differences in mean sizes of clutches for adjacent areas are not statistically significant (t values are 0.6 and 0.4).

Incubation Period

Heterodon nasicus. In my study eggs of the western hognose were incubated in moist sand in cans. Nine eggs that were kept in a laboratory at normal summer temperatures had a mean incubation period of 57 (52 to 64) days. In the summer of 1961 three clutches of eggs were divided for incubation. Some eggs from each clutch (six eggs) that were incubated in a laboratory where the temperature varied each day from approximately 88°F to 72°F (mean daily temperature was approximately 80°F) had a mean incubation period of 56 (52 to 61) days. Eight eggs that were kept in a basement at a relatively constant temperature of 74°F had a mean incubation period of 81 (70 to 89) days, 25 days longer than those in the laboratory. Those eggs that were incubated in the laboratory hatched between August 27 and September 21 inclusive, while those that were incubated in the basement hatched between September 29 and October 16 inclusive. The effect of constant and variable temperatures upon the development of the eggs is not known. However, disregarding this factor, the incubation period was shortened approximately four days for each increase of one degree Fahrenheit in mean daily temperature. Blanchard and Blanchard (1941:172) found that an increase of one degree Fahrenheit in average temperature shortened the gestation period of the ovoviviparous eastern garter snake (*Thamnophis sirtalis*) by 4½ days.

A clutch of eggs incubated in a room with a maximum temperature of 90°F hatched between September 1 and 4, after an incubation period of 58 to 61 days (Munro, 1949b, c:133-134). One young snake hatched from a clutch of eggs from Texas on September 10, after an incubation period of 56 days (Sabath, 1960:72). Eggs laid by a female from Shilo, Manitoba, Canada, between June 12 and 17 hatched on August 2, after an incubation period of between 47 and 52 days (Mr. I. L. Traill, *in litt.*).

There is little information relative to the incubation period and hatching dates of western hognose snakes in nature in Harvey County. Few hatchlings were trapped in the autumn; two that had recently hatched were caught on September 3 and 7. The late Mr. Ralph M. Woods plowed up a clutch of eggs in early August, but he returned them to moist earth and they hatched between August 9 and 15. This record indicates that some eggs laid near the surface of the soil where summer temperatures are high may require only 40 to 50 days to develop. However, most hatching probably occurs in the latter part of August and early September after an incubation period of 50 to 60 days.

During incubation, eggs increase appreciably in width and weight but only slightly in length. Measurements were made only during the early part of the incubation period for two clutches in my study, because the shells became thinner as development proceeded and were easily ruptured when the egg was handled. Five eggs from one clutch had increased an average of 5 per cent in length, 15 per cent in width, and 29 per cent in weight one week after oviposition. After three weeks these eggs had increased 6 per cent in length, 34 per cent in width, and 62 per cent in weight. The increase in length is not statistically significant, but the increases in width and weight are significant at the one-tenth per cent level (*t* values are 1.4, 9.8, and 8.1, for length, width, and weight respectively). Munro (1949b:134) reported smaller increases (2 per cent in length, 22 per cent in width and 50 per cent in weight) for eleven eggs after 45 days of incubation.

The rate of increase in width and weight is related to the rate of embryonic development. From a clutch of seven eggs, four eggs were placed in a basement at 74°F, and three eggs were placed in a laboratory at a mean daily temperature of 80°F. The eggs in both lots were partially buried in moist sand. Seventeen days after oviposition, the eggs incubated in the basement had increased an average of three per cent in width and four per cent in weight, while those incubated at higher temperatures had increased 16 per cent in width and 23 per cent in weight. The increases in width and weight for those eggs incubated in the basement are not significant (t is 0.4 and 0.3). Because of the smallness of the sample, the eggs incubated at higher temperatures had increases that are only on the borderline of significance at the five per cent level (t values are 2.6 and 2.8 respectively).

Of 38 eggs from Harvey County from seven clutches that were laid in captivity, nine eggs (24 per cent) appeared abnormal at the time of oviposition. Of 28 eggs from six clutches that were incubated in captivity, only 17 (61 per cent) hatched (Table 24). However, some of these eggs were affected

TABLE 24. Abnormal Eggs and Hatching Success in Seven Clutches of Eggs Laid in Captivity by Western Hognose Snakes From Harvey County, Kansas.

Number of clutch	Number of eggs in clutch	Per cent abnormal at oviposition	Number of eggs incubated	Per cent hatched	Days in captivity before oviposition
1.....	4	0	4	50	3-4
2.....	7	0	7	100	3-6
3.....	7	14	6	33	8
4.....	5	0	5	100	25
5.....	5	60	1	100	31
6.....	5	100	5	0	36
7.....	5	0	0		5
Total....	38	24	28	61	

adversely by the conditions of captivity. Some of the eggs in the third clutch developed small ruptures when they were handled, and they later spoiled. Clutches nos. 5 and 6 were laid by snakes that had been in captivity for one month or more. This period of captivity may have caused abnormalities. The eggs were thin and weighed less than usual when they were laid. Four of the eggs in clutch no. 5 were opened, and only one had embryonic development. In clutches nos. 1, 2, and 4, 88 per cent of the eggs hatched. Other reports of hatching success include: 11 of 11 (Munro, 1949b); 12 of 12 (Mr. I. L. Traill, *in litt.*); one of five (Sabath, *loc. cit.*); and none of seven (partially desiccated before incubated; Werler, 1951:41). Under optimum conditions most of the eggs in clutches of the western hognose snake hatch, although adverse conditions may cause a whole clutch to be abnormal or to die.

Heterodon platyrhinos. Incubation periods and hatching dates of eggs of the eastern hognose that were incubated in captivity are listed in Table 25.

TABLE 25. Hatching Dates and Incubation Periods of Clutches of Eggs Laid by Eastern Hognose Snakes and Incubated in Captivity.

Hatching date	Incubation period	Locality of origin of snake	Authority
July 7.....	31 days	Carbondale, Illinois	Cagle, 1942:186
July 24.....	58 days	Harris Co., Texas	Kennedy, 1961:418
July 30.....	65 days	Harris Co., Texas	<i>Ibid.</i>
July 30.....	65 days	Harris Co., Texas	<i>Ibid.</i>
July 31.....	61 days	Harris Co., Texas	<i>Ibid.</i>
July 29-31.....	46-48 days	Dallas Co., Texas	Raun, 1962:3
Aug. 5.....	?	?	Brimley, 1903:262
Aug. 8.....	?	Indiana	Minton, 1944:456
Aug. 14.....	?	?	Brimley, <i>loc. cit.</i>
Aug. 14.....	50 days	Carbondale, Illinois	Cagle, 1942:187
Aug. 11-17.....	52-58 days	Illinois	Smith, 1961:190
Aug. 16-17.....	51-52 days	Harvey Co., Kansas	Platt
Aug. 19-22.....	52-54 days	Elgin Co., Ontario, Canada	Mr. H. T. Hiemstra, <i>in litt.</i>
Aug. 23-24.....	59-60 days	Miami Co., Kansas	Gloyd, 1932:403
Aug. 25.....	58 days	Woods Co., Oklahoma	Platt
Sept. 19.....	?	Indiana	Minton, <i>loc. cit.</i>
Sept. 26.....	75 days	Nashville, Indiana	Meyer, 1958:128
Oct. 16.....	88 days	Maryland	McCauley, 1945:66
?	approx. 8 weeks	Florida	Telford, 1952:179

Although in most cases the conditions of incubation were not reported, the majority of the incubation periods were between 50 and 65 days, similar to the incubation period of the eggs of the western species in the laboratory at normal variable summer temperatures.

In the years 1959, 1960, 1961, and 1962, the first hatchlings were caught on the study areas in Harvey County on August 20, August 27, August 26, and August 23. These snakes had already made significant growth and were

probably two to three weeks old (Table 28). The natural incubation period in this locality is approximately 60 days, with most hatching occurring from early August to early September.

Dates of hatching for eggs in natural nests or collected from natural nests shortly before hatching are listed in Table 26. Abbott (1885:289) reported

TABLE 26. Dates of Hatching of Eggs of the Eastern Hognose Snake Incubated in Natural Nests (Some Removed From Natural Nests Shortly Before Hatching).

Hatching date	Locality	Authority
July 4 to 12.....	Louisiana	Clark, 1949:248
Aug. 23 to 27.....	Nelson Co., Virginia	Dunn, 1915:37
Aug. 24.....	Crow Wing Co., Minnesota	Breckenridge, 1944:109
Sept. 6 to 8.....	Maryland	Hay, 1892a:116
Sept. 14.....	Long Island, New York	Cragin, 1879:710
Sept. 11 to 17.....	Ontario, Canada	Milnes, <i>in litt.</i>
Late Sept.....	Southern Illinois	Cagle, <i>loc. cit.</i>

that he found hatchlings in New Jersey in early July; Engelhardt, *et al.* (1915:3) stated that large numbers of young eastern hognose snakes were found on Rockaway Beach on Long Island, New York, in July and August; and Cagle (1942:187) reported that three newly hatched snakes were collected in Carbondale, Illinois, on September 10. All of these records indicate that the hatching period is prolonged, probably due, in large measure, to variability in temperatures during the incubation period. The records are insufficient to detect any geographical variation in hatching dates.

Edgren (1955:107) weighed three eggs seven days after oviposition, and the weights had increased four per cent. Kennedy (1961:420) reported that 23 eggs had increased 7 per cent in length, 19 per cent in width, and 47 per cent in weight after 24 days of incubation, but the shells of the eggs had become so thin that no further measurements were made.

Clutches of 32, 12, and 14 eggs were laid by the captive eastern hognose snakes kept by the writer. Of these three clutches the last two included only normal eggs, but the first clutch included 15 hard, yellow, abnormal eggs. Fourteen eggs from the first clutch were incubated, but only one of them hatched. A number of eggs were ruptured when they were measured. The 12 eggs in the second clutch hatched, and the third clutch was not incubated.

In 30 clutches of 583 eggs reported by other investigators, there are few reports of abnormal eggs. Of 120 eggs in five clutches laid by eastern hognose snakes from Harris County, Texas, there were four abnormal eggs (Kennedy, 1961:419-420, 1964:212). Of ten eggs in a clutch laid by a snake from Miami County, Kansas, there were two abnormal eggs (Gloyd, 1932:402).

The results of the incubation of 313 eggs from 16 clutches of the eastern hognose snake are available. Only 119 eggs (38 per cent) hatched. This low hatching success was probably due to the effects of captivity upon the female snake and the conditions of incubation in captivity, as a number of entire clutches failed to hatch. Reports of hatching success include: 0 of 31 (Milnes, 1946:2); 0 of 23 (Strecker, 1926b:6); 0 of 17 (Smith, 1961:190); 0 of 7 (Guidry, 1953:51); 1 of 14 (McCauley, 1945:66); 1 of 26 (Brimley, 1903:262); 37 of 99 ("too much water" added; Kennedy, 1961:421); 18 of 20 (Milnes, *in litt.*); 15 of 15 (Smith, *loc. cit.*); 8 of 8 (Gloyd, 1932:403); and 26 of 26 (Hay, 1892a:116).

Hatching and Hatchlings

Heterodon platyrhinus. The process of hatching in a clutch of 12 eggs required 55.5 hours from the time the first slit was noticed in an egg to the time that the last snake emerged from its shell. The first evidence of hatching was a slit in the shell made by the egg tooth that projects ventrally from the anterior end of the upper jaw of the snake. A number of slits were usually made, but most of them were cut lengthwise along the egg. In the 12 eggs, 28 longitudinal cuts and 8 transverse cuts were made. In each egg there was at least one longitudinal cut that extended more than one-half the length of the egg, and in two eggs only this one slit was made. Others had multiple cuts; one had five longitudinal slits and two transverse slits.

Soon after the slits were made, fluid began to leak out of the egg, and the opening appeared wet and sometimes frothy until after the snake emerged. A few hours after the slits were made, the snake extended its head through the opening. Periodically it withdrew and extended its head but never exposed its body until just before it was ready to leave the egg. The head was sometimes extended upside down. When the lid of the can was opened, those snakes whose heads were exposed immediately flicked their tongues. These snakes already seemed to have a diurnal rhythm, although the only light that could enter the can came through nail holes in the lid; few heads protruded from the eggs at night.

The mean time between the appearance of the first slit in an egg and the snake leaving the egg was 27.5 (15 to 44.5) hours. Although snakes emerged from eggs over a period of 36 hours, no snakes hatched during the middle of the night. Of eight snakes that hatched in a period of 24 hours, six emerged between 6:00 a. m. and 6:00 p. m.

The egg tooth was still present when the snake left the egg, but had dropped off of one hatchling within four hours. Another hatchling had not lost the egg tooth when it was 35 hours old.

When it hatched, the snake was wet but soon dried. The skin was loose but did not appear cloudy until the snake was a few hours old. The skin broke on the head, and the first moult began within 24 hours after hatching, but the moult was not completed until the snake was a few days old.

Brief descriptions of the hatching process by Hay (1892a:116-117), McCauley (1945:66), Kennedy (1961:421), and Raun (1962:4) agree in most details with my observations. However Kennedy reported that some snakes remained in the eggs for as long as three days after making the first slit, whereas Raun stated that the "longest that any snake remained within the opened shell was slightly over one hour." Hay reported that the young

snakes moulted shortly after hatching, and one had completed its moult by the time it was 2½ hours old. Kennedy stated that most of the hatchlings "shed their skin while crawling out of the shell."

Thirteen snakes that hatched in captivity in my study had a mean snout-vent length of 194 (176 to 210) mm. and a mean total length of 234 (218 to 250) mm. at the time of hatching. Other studies report shorter lengths. Ninety-eight hatchlings from other parts of the range of the eastern hognose snake had a mean total length of 192.4 mm. (data from Brimley, 1903:262; Gloyd, 1932:403; Cagle, 1942:187; Meyer, 1958:128; Kennedy, *loc. cit.*; Raun, 1962:3-4; Milnes, *in litt.*). Variability in length is evident. A group of 58 hatchlings from Texas averaged 199.3 mm. (Kennedy, *loc. cit.*; Raun, *loc. cit.*), whereas 18 hatchlings from Canada averaged 165 mm. (Milnes, *in litt.*). Some of this variability may have been caused by differences in measuring technique.

Variability in weight is even more extensive. Eleven snakes that hatched in captivity in my study had a mean weight of 7.9 (6.0 to 9.4) grams. Thirty-seven hatchlings weighed by Kennedy (*loc. cit.*) had a mean weight of 6.7 (3.7 to 10.0) grams, and 21 hatchlings weighed by Raun (*loc. cit.*) had a mean weight of 8.6 (6.9 to 10.8) grams. Mr. H. T. Hiemstra (*in litt.*) reported that some hatchlings from Canada weighed 5.0 to 5.5 grams.

The available evidence does not indicate any significant deviation from a one-to-one sex ratio at hatching. Of 13 eastern hognose snakes hatched in captivity in my study, six were males and seven were females. Sex ratios of two other litters have been reported: three males to five females (Gloyd, *loc. cit.*) and five males to nine females (Edgren, 1955:108). The 35 snakes from the above clutches included 14 males and 21 females. All litters had a preponderance of females, but the deviation from a balanced sex ratio is not statistically significant (chi-square is 1.0). In a sample of 137 young eastern hognose snakes in museum collections, 73 were males and 64 were females (Edgren, 1958:3).

Heterodon nasicus. Hatching in the western hognose is similar to that in the eastern species. In my study moulting occurred from 24 to 72 hours after hatching. Those snakes hatching at lower temperatures (72°F) required 24 to 48 hours to leave the egg, while those hatching at higher temperatures (mean of 80°F) were usually out in less than 24 hours.

Munro (1949c:134-135) described the hatching of a clutch of eleven eggs. Most of the snakes required 40 to 60 hours to leave the egg after making the first slit, the shortest time being 30 hours. Cool weather may have slowed emergence. Most hatching occurred in midafternoon, although three snakes left their eggs either late at night or in early morning. Most of the hatchlings had partially moulted in the egg, and three hatchlings completed the moult an hour after hatching.

Hatchling western hognose snakes are smaller than those of the eastern species in Harvey County. Twenty western hognose snakes hatched in my study from six clutches of eggs had a mean snout-vent length of 153 (128 to 167) mm., a mean total length of 177 (139 to 197) mm., and a mean weight of 3.8 (2.7 to 4.8) grams. Munro (1949c:136) stated that eleven hatchling western hognose snakes that he measured were approximately seven inches (178 mm.) in length and had a mean weight of 6.1 grams. Two of the twenty hatchlings in my study had open umbilical slits after hatching. In one

TABLE 27. Characteristics of the Reproduction of the Eastern and Western Hognose Snakes.

	Western Hognose Snake		Eastern Hognose Snake	
	Harvey County	Other parts of range	Harvey County	Other parts of range
Sexual maturity of males.....	12-24 months	12 months
Sexual maturity of females.....	20-34 months	20-22 months
Ovulation.....	Biennial	Annual (?)
Spring mating.....	May 13-29	Late April-May (?)	March 28-May
Oviposition.....	July 2-23	June 3-Aug. 4	June 18-early July	May 27-July
Size of clutch.....	7.5 eggs	10.8 eggs	13.0(?) eggs	22.7 eggs
Weight ratio of eggs to female.....	.66	1.14
Hatching.....	Aug.-Sept. (?)	Aug.-Sept.	early Aug.-early Sept.	July-Sept.
Hatchlings				
Total length.....	177 mm.	178 mm.	234 mm.	192.4 mm.
Weight.....	3.8 gms.	6.1 gms.	7.9 gms.	7.4 gms.
Primary sex ratio.....	1:1	1:1	1:1	1:1

the opening was approximately 10 mm. long and persisted during the one-month period that the snake survived. The sex ratio of the western hognose at hatching is probably one-to-one. Of the twenty hatchlings observed in my study, 11 were males and 9 were females.

Comparisons of reproductive patterns of eastern and western hognose snakes are summarized in Table 27.

GROWTH AND ECDYSIS

Growth

Growth was analyzed in my study as change in snout-vent length. Growth is expressed as a percentage of the initial length per month of activity and in mm. per month of activity (listed as mm. per month in the following discussion). A month of activity is defined as 30 days within the period from the average date of trapping the first snake in the spring to the average date of trapping the last snake in the autumn. Growth is much faster in the first part of the season of activity, but with the data available only average growth rates for the entire season could be computed in most instances.

Heterodon platyrhinos. Nine male and three female eastern hognose snakes were recaptured after periods of more than one month. Two males less than 450 mm. in snout-vent length had a mean growth rate of 16.5 mm. per month. Seven males more than 450 mm. in snout-vent length had a mean growth rate of 10.8 mm. per month. Three females with snout-vent lengths more than 500 mm. had a mean growth rate of 9.9 mm. per month.

Fitch (1949b:523, 531-532) demonstrated that capturing and handling rattlesnakes in California had a retarding effect on growth. Retardation of growth due to decreased nutrition would be accompanied by a proportionally greater decrease in weight relative to length. The records of nine male eastern hognose snakes were analyzed to detect such an effect. The total lengths and weights of these snakes when first captured and when last captured were compared to the theoretical regression of weight on length (Fig. 3). These nine snakes had a mean deviation from normal weight of +6.8 grams when first captured and of +0.6 grams when last captured. This difference is not statistically significant (t is 0.6 with eight degrees of freedom). Although it is probable that the snakes lost some weight after being handled, the sample is too small and the variability is too great to demonstrate it statistically. The effect of handling was small and probably lasted only a short time.

Hatchlings were captured on the study areas from August to October. Table 28 summarizes their growth during this period. They had already made substantial growth at the end of August when they were first captured. At hatching females were slightly larger than males and they made gains equivalent to half their initial lengths in the first two months, while the males increased from one-third to one-half in length. Yolk material in the abdomen may support growth during the first month, but hatchlings that were kept in the laboratory and not fed grew more slowly than those in the field during the first three weeks (Table 29).

Some of the hatchling males that were caught in October were retarded in growth because they had been unable to obtain sufficient food. Retarded snakes

TABLE 28. Growth of Hatchling Eastern Hognose Snakes in Harvey County, Kansas, as Determined From a Sample of 45 Snakes Measured in the Period From August to October.

	Number in sample	Mean snout- vent length in mm.	Growth rate in mm. per month	Percentage increase in length per month
MALES				
Hatching (in lab.).....	6	188(176-199)		
August (late).....	4	223(209-247)	31.0	14
September.....	8	254(233-329)		
October.....	13	260(224-318)	9.0	4
Mean growth rate (August to October)....			22.2	10
Mean growth rate (Hatching to October)...			33.9	18
Maximum growth rate ^a (Hatching to October)...			55.8	28
FEMALES				
Hatching (in lab.).....	7	199(186-211)		
August (late).....	3	239(218-256)	37.9	16
September.....	2	263(241-284)		
October.....	4	313(289-354)	50.0	19
Mean growth rate (August to October)....			45.3	19
Mean growth rate (Hatching to October)...			51.2	26
Maximum growth rate ^a (Hatching to October)...			65.0	31

a. Growth rate from maximum size recorded at hatching to maximum size recorded in October.

were probably more subject to capture because they were more actively searching for food. Many of these stunted snakes did not survive hibernation. Therefore, the mean snout-vent length of hatchlings that survived until the next spring was probably higher than the mean of this sample.

The growth rate is rapid but variable in first-year snakes and in young adults. Some fast-growing snakes may be longer than retarded individuals of an older age-class. Nevertheless, it is possible to separate the sample of younger male snakes caught in a particular month into probable age groups on the basis of their lengths (Fig. 21; Table 30). Growth records from recaptured

TABLE 29. Growth of Four Male and Seven Female Hatchling Eastern Hognose Snakes in the Laboratory Without Food (Water Was Supplied).

	Mean weight in grams	Mean snout-vent length in mm.	Growth rate in mm. per month
MALES			
Hatching, Aug. 19.	7.1(6.0-8.0)	192(184-199)	28.6
September 8.	7.4(6.3-8.5)	212(200-216)	
FEMALES			
Hatching, Aug. 19.	8.2(8.0-8.6)	199(186-211)	28.6
September 8.	8.2(7.4-8.7)	219(204-227)	

TABLE 30. Growth of First-year Eastern Hognose Snakes in Harvey County, Kansas, as Determined From a Sample of Snakes Measured in the Years 1959 to 1963.

	Number in sample	Mean snout-vent length in mm.	Growth rate in mm. per month	Percentage increase in length per month
MALES				
April-May.	14	309(269-383)	74.4	23
June.	12	376(314-448)		
July.	8	429(404-450)	49.8	13
October.	4	484(432-521)	17.4	4
FEMALES				
April-May.	6	321(240-385)	60.0	19
June.	3	373(349-383)		
July.	6	508(441-546)	109.5	29
Sept.-October.	2	536(525-546)	11.4	2

snakes help to identify certain size groupings as belonging to successive age groups. In the spring, growth of first-year males averaged more than two mm. per day. This was the period of most rapid growth in the life of the snake. Growth rate decreased to slightly more than one-half mm. per day in summer and autumn.

Fewer first-year females were available (Fig. 22; Table 30). The growth

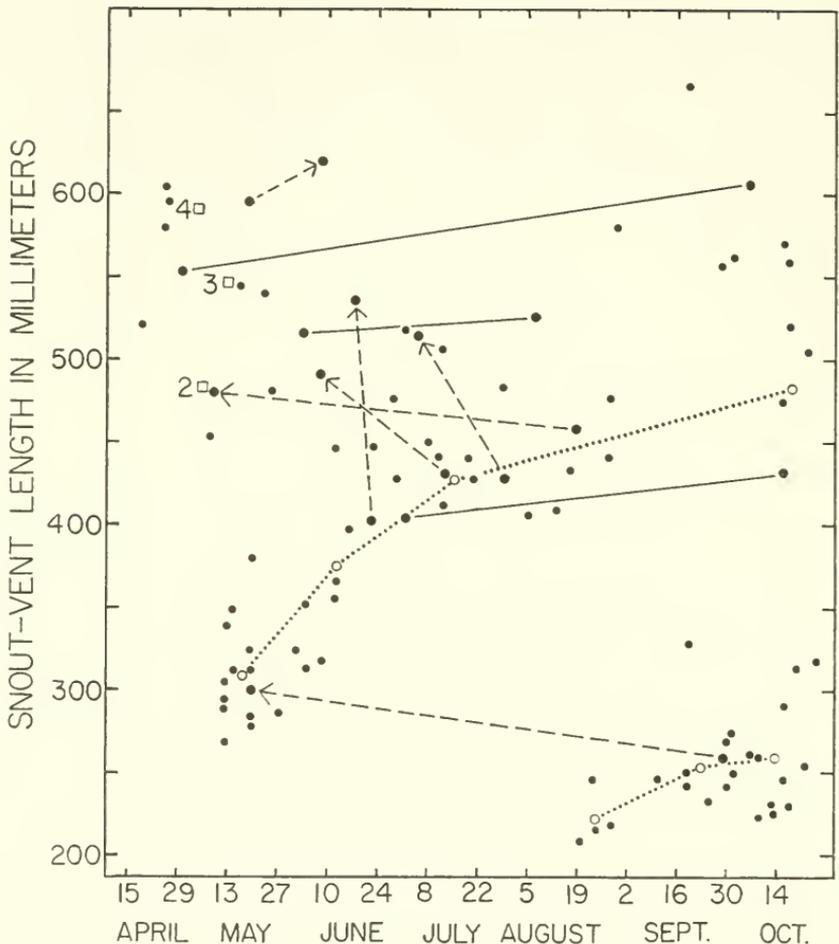


FIG. 21. Sizes of male eastern hognose snakes caught on different dates in the years 1959 through 1963 in Harvey County, Kansas. Records of size for an individual caught in two successive years are connected by a dashed arrow. Records of size for an individual caught more than once in a single season of activity are connected by a solid line. Circles represent the mean snout-vent lengths of snakes in succeeding periods through their first full year, and dotted lines indicate the growth curve. Numbered squares represent the mean snout-vent lengths of snakes in their second, third, and fourth springs.

rate of females for the entire season was larger than that of males. The most rapid growth of females occurred in late June and July, later than that of males.

Growth records from recaptured snakes and the length distribution of the sample of snakes captured in April and May were utilized to define probable age groups in terms of snout-vent length to the age of 45 months for male snakes and less certainly for female snakes (Figs. 21 and 22; Table 31). Female snakes are larger than males at all ages. At 21 months, when most snakes first breed, females were, on the average, more than 70 mm. longer than males. Probable growth rates at various ages for males and females can be estimated from the mean snout-vent lengths of the probable age groups (Table 31). The growth rates decrease with age, the most significant decrease occurring as

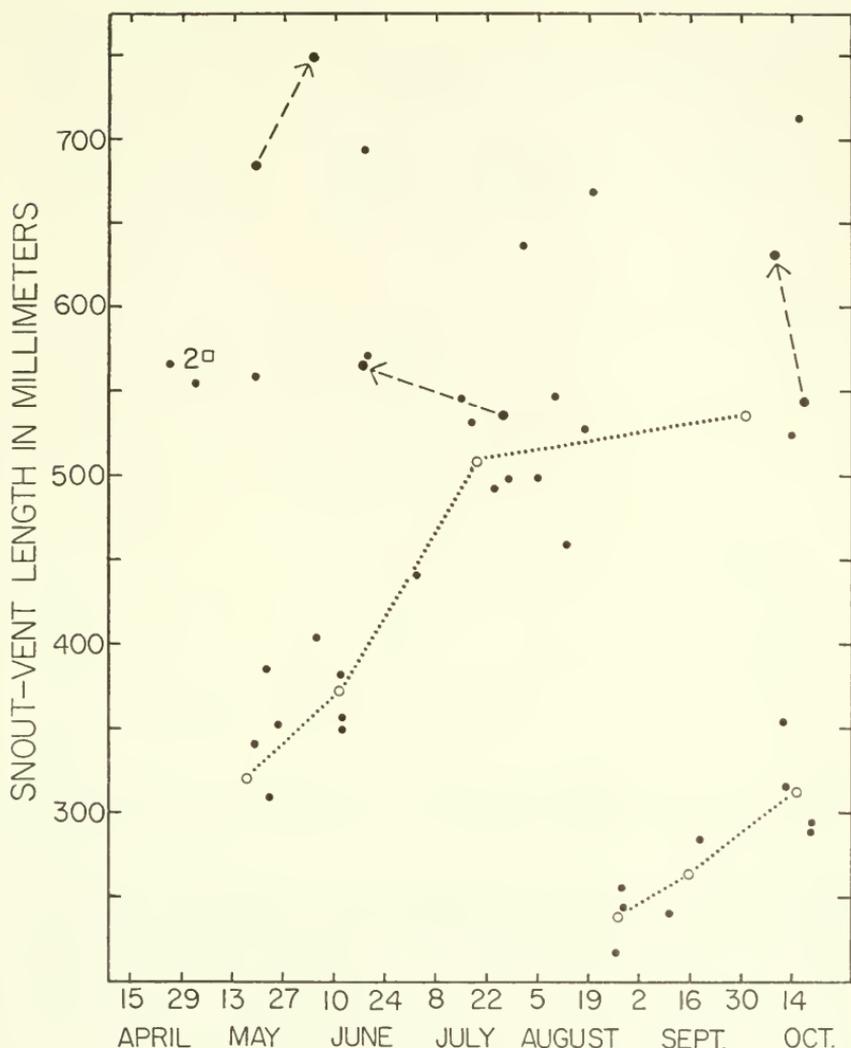


FIG. 22. Sizes of female eastern hognose snakes caught on different dates in the years 1959 through 1963 in Harvey County, Kansas. Records of size for an individual caught in two successive years are connected by a dashed arrow. Circles represent the mean snout-vent lengths of snakes in succeeding periods through their first full year, and the dotted lines indicate the growth curve. The numbered square represents the mean snout-vent length of snakes in their second spring.

sexual maturity is attained at an age of 21 months. Female snakes grow faster at all ages, but the greatest differential growth occurs between 9 and 21 months.

Although growth continues to decrease with age, the largest snakes that were recaptured made significant growth in the intervals between captures. A male that was captured on May 19, 1962, at a length of 597 mm. (probably 45 months old) was recaptured on June 8, 1963, when it was 621 mm. in length. Assuming a similar growth rate (3.9 mm. per month) for other large male snakes, the largest male snake that was captured during my study (653 mm. in snout-vent length) was probably more than five years old. However,

TABLE 31. Mean Snout-vent Lengths and Probable Growth Rates of Eastern Hognose Snakes of Various Probable Ages in a Sample of Snakes Captured in April and May in Harvey County, Kansas.

Probable age	Number in sample	Mean snout-vent length in mm.	Growth rate in mm. per month	Percentage increase in length per month
MALES				
Hatching (in lab.).....	6	188(176-199)	42.6	23
9 months.....	14	309(269-383)		
21 months.....	6	488(454-521)	11.1	2
33 months.....	3	546(540-553)	8.1	2
45 months.....	4	592(580-597)		
FEMALES				
Hatching (in lab.).....	7	199(186-211)	43.2	22
9 months.....	6	321(240-385)		
21 months.....	3	560(555-567)	45.0	14
33 months.....	0	630 ^a	12.3	2
45 months.....	1	685	9.6	2

a. Estimated from the growth record of a recaptured snake and the length of snakes in preceding age group.

this large snake may have grown somewhat more rapidly than average. Pope (1944:166) reported that an eastern hognose snake lived six years in captivity.

A female eastern hognose snake that was 685 mm. snout-vent length on May 19, 1962, was 748 mm. in length on June 4, 1963, a growth rate of 10.2 mm. per month. This was the largest female found in Harvey County during my study, and it was probably almost five years old when last captured.

Stallcup (1959:80-81) kept a large eastern hognose snake in captivity for 13 months and fed it two toads per week. It grew from 25 inches (635 mm.) to 30 inches (762 mm.), a rate of 9.8 mm. per month.

Heterodon nasicus. Capture and handling of western hognose snakes probably caused, at most, a slight decrease in the rate of growth. The total lengths and weights of 21 males at the time of their first capture and at their last capture were compared to the theoretical regression of weight on length for males of this species (Fig. 4). These snakes had a mean deviation from normal weight of +1.92 grams at the first capture and of -2.13 grams at the last capture. This difference is not statistically significant (t is 0.8 with 20 degrees of freedom).

Table 32 lists the mean growth rates for 33 western hognose snakes of different lengths that were recaptured after more than 30 days. The size

TABLE 32. Growth Rates of Western Hognose Snakes of Various Sizes From Harvey County, Kansas, as Determined From Records of Growth of Recaptured Snakes.

Snout-vent length in mm.	Number of snakes	Mean number ^a of days between captures	Growth rate in mm. per month
MALES			
Less than 351.....	7	185	6.8±3.1
351 to 400.....	7	189	5.7±0.7
401 to 450.....	3	115	5.3±2.4
More than 450.....	1	394	0.9
FEMALES			
Less than 351.....	1	83	41.7
351 to 400.....	4	117	13.9±3.4
401 to 450.....	4	144	7.7±2.5
More than 450.....	6	163	5.6±1.6

a. Includes only days within the season of activity.

groups are based on the median snout-vent length between the first and last capture of the snake. Although no growth records were available for hatchlings, the data indicate a decrease in growth rate with increase in length. However, the largest uninjured female snakes that were recaptured were still growing slowly. Only one male snake above 450 mm. snout-vent length was recaptured, and its change in length was within the margin of error. Females grew faster at all sizes than males. Rates of growth were variable, as indicated by the large standard errors.

Nine hatchling males from eggs incubated in the laboratory had a mean snout-vent length of 151 mm. No hatchling males were captured on the study areas in autumn. First-year males were first captured in June, at which time nine had a mean snout-vent length of 210 mm. In September and October three first-year snakes averaged 288 mm. in snout-vent length. This is a growth rate of 20.7 mm. per month during the first season of activity. A few western hognose snakes captured on the study areas and neighboring areas had snout-vent lengths of only 200 to 210 mm. in July or later. These snakes were retarded in growth, probably because of disease, injury, or insufficient nutrition. Moore (1953:173) collected a western hognose snake in Alberta, Canada, on July 13 that was only 7 $\frac{1}{2}$ inches (187 mm.) in total length and had made little growth during its first year. Most such retarded juveniles probably do not survive to maturity.

Sexual maturity usually occurs in male western hognose snakes at a snout-vent length of approximately 300 mm. In the size range from 282 to 326 mm. in May and June, six of seven males that were tested for spermatozoa had

completed their first spermatogenesis. These snakes must have been 21 months old. Some males in this size range were not sexually mature. Of those male snakes whose testes were studied histologically, three that were 296 to 302 mm. in snout-vent length when they were captured in July were in their initial spermatogenesis. A few snakes of this size may have been hatched the previous autumn and made exceptionally fast growth, but most were older individuals that were slow to mature sexually. A male that was 328 mm. in snout-vent length when it was captured on May 27, 1961, was not yet sexually mature. It had been captured previously on June 28, 1960, when it was already 326 mm. in snout-vent length.

In the sample of males captured in May and June, there was a continuous distribution within the range of 270 to 460 mm. in snout-vent lengths (Fig. 23).

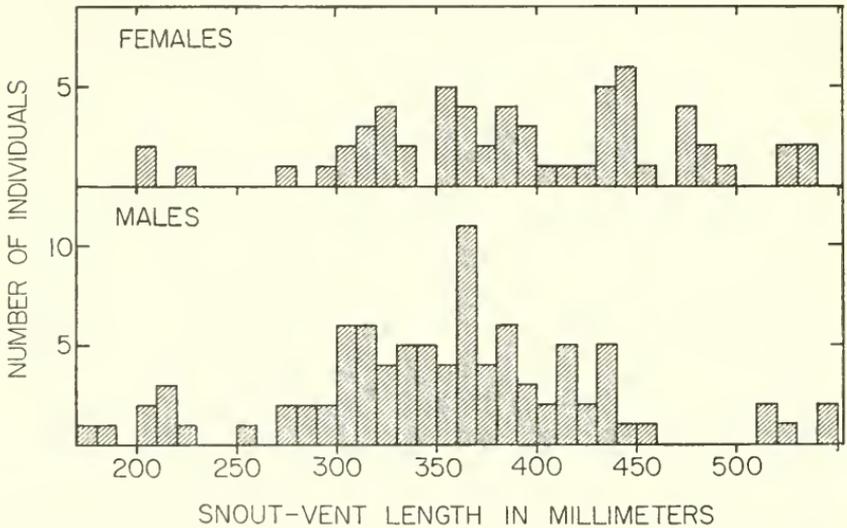


FIG. 23. Size distribution at intervals of ten millimeters of male and female western hognose snakes caught in May and June in the years 1959 through 1963. Three female snakes that had snout-vent lengths greater than 550 millimeters are omitted.

Due to the variability in growth rate, the overlap in size of snakes of various ages was great. However, on the basis of the peaks in this May and June series, the size-distribution in other months, and the growth records from recaptured snakes (Figs. 23 and 24), the sample of males captured in May and June can be divided into probable age groups for the first four years. Table 33 lists the snout-vent lengths of male western hognose snakes at probable ages. Probable growth rates computed from this distribution are also listed. These growth rates are comparable to those computed from recapture records alone (Table 32). The theoretical growth curve constructed from these data is compared to records of growth of recaptured snakes in Figure 24.

Two males (snout-vent lengths of 209 and 310 mm. and weights of 8.5 and 28 grams) in captivity were given small toads and lizards as often as they would eat them. The smaller snake grew at a rate of 24.9 mm. per month for 24 days but then moulted and refused food during the next three weeks. For

TABLE 33. Mean Snout-vent Lengths and Probable Growth Rates of Western Hognose Snakes of Various Probable Ages in a Sample of Snakes Captured in May and June in Harvey County, Kansas.

Probable age	Number in sample	Mean snout-vent length in mm.	Growth rate in mm. per month	Percentage increase in length per month
MALES				
Hatching (in lab.).....	9	151(143-161)	20.7	14
9 months.....	9	210(179-255)		
21 months.....	18	309(282-326)	18.6	9
33 months.....	15	342(330-356)	6.3	2
45 months.....	16	367(360-377)	4.8	1
FEMALES				
Hatching (in lab.).....	6	153(128-167)	29.3	19
9 months.....	5	242(206-296)		
21 months.....	25	354(312-398)	22.9	9
33 months.....	14	439(418-451)	16.6	5
45 months.....	7	481(471-490)	7.7	2

the entire 45 days its growth rate was 13.2 mm. per month. The larger snake grew at a rate of 3.9 mm. per month for a period of 39 days. Circumstances prevented the continuance of these tests for a sufficient time to measure maximum growth rates, but the rates recorded were slower than those determined for snakes of comparable size in the field.

The summary of growth of male western hognose snakes in Table 33 is valid only as an average. A fast-growing first-year snake may be larger than a slow-growing snake that is a number of years older. Table 34 lists records of exceptionally fast growth and slow growth by recaptured snakes. Two of the male snakes listed in this table, with rapid rates of growth, were captured at other times after having grown more slowly.

A few males grew to exceptionally large size (Fig. 23). The largest captured in my study, 546 mm. in snout-vent length, would have been at least 12 years old if it had grown at the average rates listed in Table 33 and if growth continued to decrease slowly as the snake aged. However, Klauber (1937:31-33) pointed out that, because of the variability of growth rates, the age of individual large snakes cannot be determined accurately from their lengths. The largest snakes probably had exceptionally fast growth rates. Most males captured in my study had snout-vent lengths of 270 to 460 mm. A male snake that grew at average rates to a snout-vent length of 460 mm. would be eight years old,

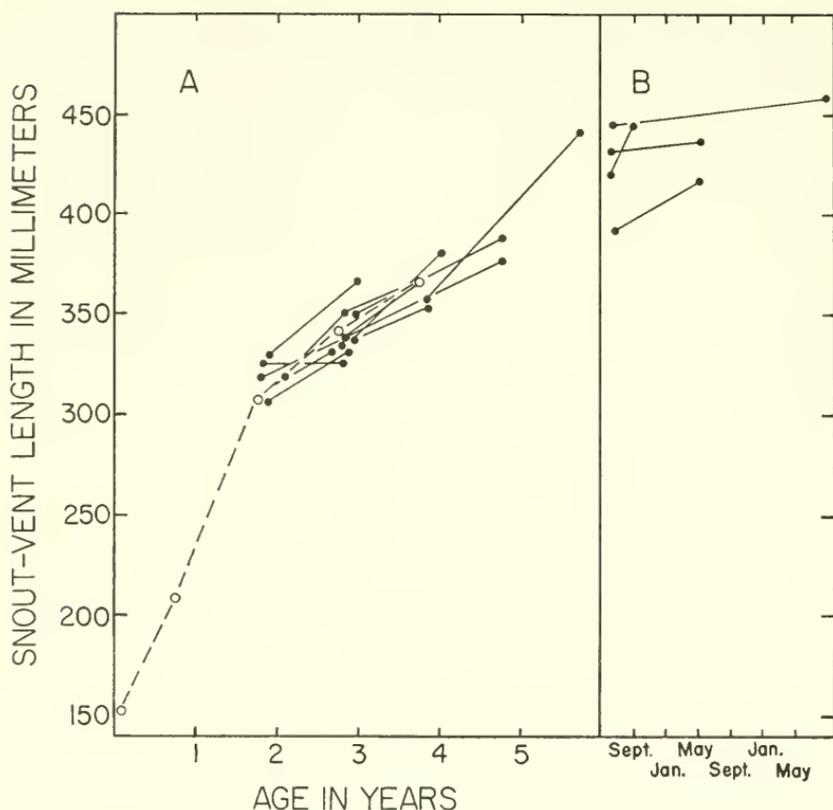


FIG. 24. Growth of male western hognose snakes. Circles represent the mean snout-vent lengths of snakes in successive probable age groups in the spring, and the dashed line indicates the growth curve. Solid lines indicate growth records of recaptured individuals. A. Growth records of snakes to which probable ages could be assigned at the time of their first capture. B. Growth records of larger snakes for which ages could not be reliably determined.

and this may be the maximum age for western hognose snakes in natural populations in Harvey County.

The growth rates and probable age-size relationships of females can be determined with less certainty from the data that are available. Six hatchling females from eggs incubated in the laboratory were approximately the same size as hatchling males (Table 33). Only four hatchling females were captured in the autumn. They had snout-vent lengths of 158 and 173 mm. on September 3 and 7 respectively, and of 201 and 206 mm. on October 17. These few records indicate a growth rate of 27.0 mm. per month. Few first-year snakes were captured.

Females captured in May and June fell into fairly distinct size groupings, some of which corresponded to the modal lengths of age classes (Fig. 23). There were two peaks of frequency between snout-vent lengths of 300 and 400 mm. However, most of the snakes in this size range were 21 months old. The lower peak was probably composed principally of slow-growing snakes.

TABLE 34. Records of Growth of Recaptured Western Hognose Snakes in Harvey County, Kansas, That Grew at Exceptionally Rapid Rates or That Grew Slowly or Not at All.

Sex	Days ^a between captures	Median snout- vent length in mm.	Growth rate in mm. per month
RECORDS OF RAPID GROWTH			
Male.....	38	335	25.2
Male.....	33	369	13.5
Male.....	118	357	11.1
Female.....	83	285	41.7
Female.....	182	366	23.1
Female.....	106	400	14.4
Female.....	48	455	13.2
Female.....	128	409	12.0
RECORDS OF SLOW GROWTH			
Male.....	146	433	0.9
Male.....	394	452	0.9
Male.....	139	327	0.3
Female ^b	218	471	2.7
Female ^b	100	651	0
Female.....	105	398	0

a. Includes days within season of activity only.

b. Injured between first and last capture.

There was evidence that at least two of the five snakes between 300 and 320 mm. in length were more than one year old. A few of these snakes may have been fast-growing individuals that were nine months old.

The mean snout-vent lengths of females of five age groups captured in May and June and their calculated growth rates are listed in Table 33. The theoretical growth curve is compared to recapture records in Figure 25. Most growth took place in the early part of the season of activity. Records of growth from recaptures within a single season of activity deviate widely from the theoretical growth curve.

The mean length computed for females 21 months old seems low, and the group may have had an unusually high proportion of slow-growing stunted snakes. Alternatively, several fast-growing nine-month-old snakes may have been included in this group. Many of the slow-growing snakes probably do not survive until the next growing season, and they have less effect on the

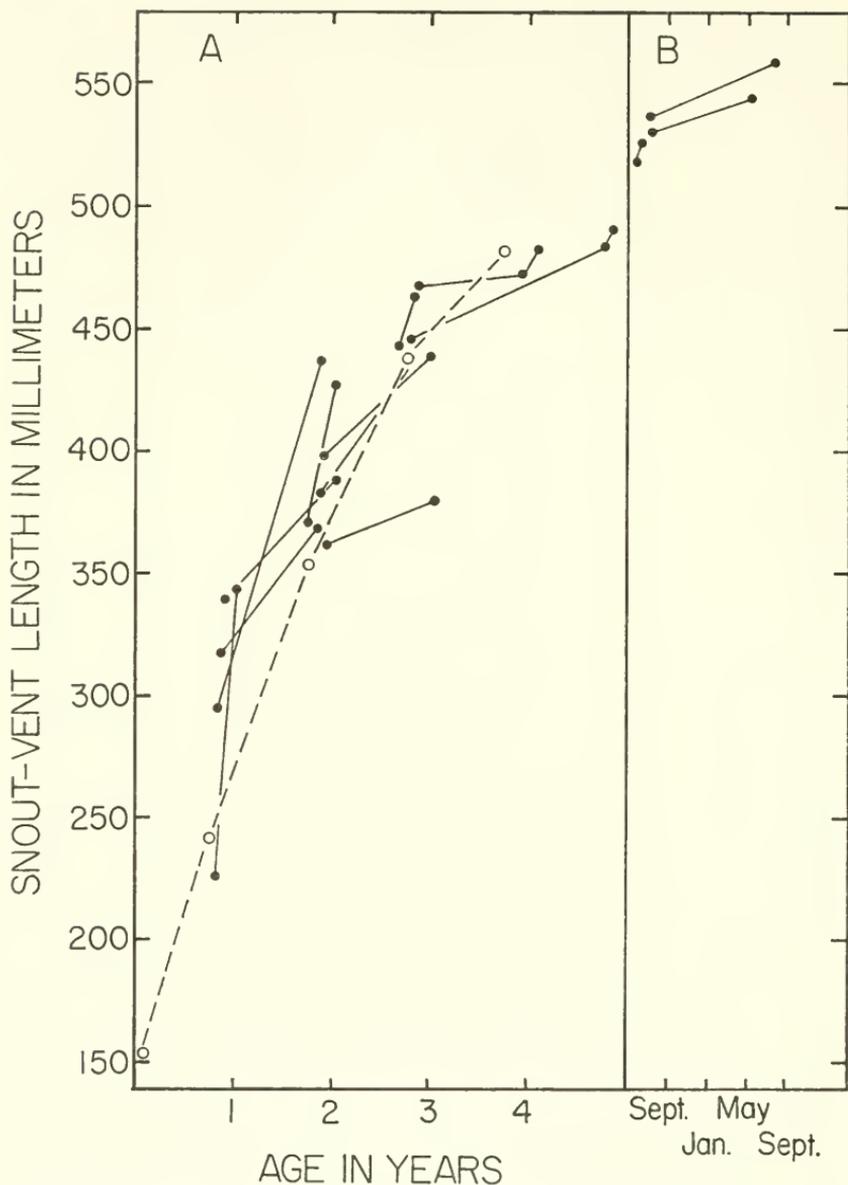


FIG. 25. Growth of female western hognose snakes. Circles represent the mean snout-vent lengths of snakes in successive probable age groups in the spring, and the dashed line indicates the growth curve. Solid lines indicate growth records of recaptured snakes. Growth was usually faster early in the season, and recaptures within one season diverge widely from the growth curve. A. Growth records of snakes to which probable ages could be assigned at the time of their first capture. B. Growth records of larger snakes for which ages could not be reliably determined.

average for the next year. Consequently, the growth rate calculated between 9 months and 21 months, as listed in Table 33, is probably too low, and the growth rate listed for snakes from 21 months to 33 months is probably high. The growth rates listed in Table 33 are comparable to those computed from recapture records (Table 32). Female snakes grow faster at all ages than males, particularly after 21 months.

Two small females (snout-vent lengths of 254 and 217 mm. and weights of 12.6 and 7.3 grams) were put in a cage and supplied with excess food from July 20 to September 3. In the first 24 days they each grew at a rate of 11.4 mm. per month. During the second three-week period, when both snakes moulted, one refused food, lost weight, and remained approximately the same length, while the other ate 3.1 grams of food, gained nine mm., and lost .5 grams in weight. Growth rates for the entire period of 45 days were 6.0 and 12.0 mm. per month for the two snakes. These growth rates are lower than those of snakes of comparable size in the field.

Variable growth rates seem to be more characteristic of females than of males; records of both rapid and slow growth in females are listed in Table 34. A snake that was 296 mm. in June and 436 mm. 13 months later (Fig. 25) seems to be an accelerated individual that was above normal length at an age of nine months and had grown to the size typical of 33-month-old individuals when it was 21 months old. Its weight was almost twice normal for its length when it was recaptured.

The largest female (707 mm. in snout-vent length) that was captured in my study would have been fourteen years old if it had grown at an average rate, but probably it had grown more rapidly since it was much larger than most large snakes. Length distribution of females is almost continuous up to 572 mm. and a female of this size would be seven or eight years old if it had grown at an average rate.

Female hognose snakes in Harvey County grow faster at all ages than males, and in both species the rate of growth decreases greatly when the snakes become sexually mature. Eastern hognose snakes are 25 to 30 per cent longer at hatching and grow much faster. The absolute growth rates of male eastern hognose snakes are almost twice as large as those of males of the western species at comparable ages. The absolute growth rates of female eastern hognose snakes in their first two years are from 50 to 100 per cent greater than those of females of the western species, but older females of both species grow at comparable rates. The differences in percentage increases are not as great (Tables 31 and 33).

Ecdysis

Heterodon nasicus. Munro (1952:37) reported that five western hognose snakes in captivity moulted soon after hatching, once in their first year, and twice or three times in their second year. He suggested that hognose snakes moult infrequently because they are short and stout and gain slowly in length. The data collected in my study indicate that young western hognose snakes moult more frequently than reported by Munro. However, only limited evidence is available concerning the periodicity of moulting in the field, because snakes preparing to moult are usually sluggish or inactive and hence not often trapped.

Moulting occurs within three days after hatching. Whether hatchling snakes moult again in the autumn is not known. Three first-year snakes in captivity moulted once on July 20, 24, and 25, and again on August 31 and September 1 and 9. If this period of approximately 42 days between moults is characteristic of first-year snakes in the field, they probably moult three or four times.

Adults moult at least twice during a season of activity. The first ecdysis of males is usually in May. In April and May, 1963, five of the nine sexually mature male snakes captured were in the initial stages of moult. Females moult in late June or early July before laying eggs. Three females kept in the laboratory for a few weeks before they laid eggs, moulted between June 23 and July 8, an average of 13 (12-14 days) before they laid eggs. Five females in captivity, that did not lay eggs, moulted between July 1 and July 29. One female snake captured in the field on June 19 had clouded ventrals preparatory to moult.

Most adults probably moult again during a period of inactivity in August or early September. Three snakes captured on August 1 and 9 were preparing to moult, and one captured on August 28 had recently moulted. Most snakes in captivity, both in cages and in an outdoor pen, moulted in August or September. There is no evidence of more than two moults per season by adult western hognose snakes living under natural conditions, although snakes in captivity occasionally moulted at short intervals.

Clouding of the ventral scales occurs 7 to 12 days before the moult in captivity. The eyes become clouded at the same time or a few days later. During this period prior to moult, western hognose snakes are sluggish, and some remain in a burrow. Female snakes moulting in June or July almost always spend this period in a burrow. Usually food is refused during the pre-moult period, especially that of the moult in August. Some snakes eat during the pre-moult period at other seasons. One or two days prior to the moult, the eyes become clear. The skin first splits on the head and is usually shed in one piece. Captive snakes may leave the skin on the surface or in a burrow.

Heterodon platyrhinos. Bogert (1955:207-209) and Schmidt and Inger (1957:213) published photographs of an eastern hognose snake shedding its skin, but Bogert (page 208) reported that the periodicity of ecdysis for this species was not known. Stallcup (1959:81) kept a large eastern hognose snake in captivity for 13 months, and in that time it moulted twice.

The periodicity of moulting is probably similar to that of the western species, although my data are scanty. There is a moult within a few days after hatching. A hatchling male, 209 mm. in snout-vent length when caught on August 20, had shed its skin in the trap. Two first-year males that were preparing to moult were captured on May 15 and May 19. A large female with clouded eyes was captured on August 18.

A large female kept in captivity from June to September moulted on July 20 and September 12. Three males that were in captivity from early July to September moulted once on August 20, August 31, and September 20.

FOOD HABITS

Feeding Behavior

Hognose snakes are slow in movements and reflexes, and in an outdoor pen are rarely able to pursue and catch frogs and toads. In small cages they can catch lizards and amphibians. A hungry snake becomes aware of the presence of potential prey through olfactory stimuli detected by Jacobson's organ. While the snake is searching for the prey, sight of movement stimulates the snake to attempt to grab any moving object. The snake does not strike but crawls quickly toward moving prey, attempting to seize the animal with wide open mouth and often attempting to hold the animal down with a coil of its body.

The eastern hognose sometimes preys on active amphibians in nature, as indicated by an observation recorded in my field notes:

"In the middle of the road was an eastern hognose snake attempting to swallow a large great plains toad (*Bufo cognatus*). Its body was partially wrapped around the toad. Only the toad's head was in the snake's mouth. Tracks showed that the snake had been crawling east along the middle of the road and turned out of its way to catch the toad. There was a sign of struggle only at the place where the snake turned out of its path."

Burt and Hoyle (1934:205) observed an eastern hognose snake "stalking a prairie swift (*Sceloporus undulatus consobrinus*)." Hognose snakes can probably capture active amphibians and reptiles in nature only by ambush or surprise encounter.

Many authors have stated that hognose snakes dig resting toads and lizards from their burrows in sand or soft soil (Curran and Kauffeld, 1937:126; Pope, 1944:167; Edgren, 1955:110; and others). However, there have been few reported observations of this behavior. Weaver (1965:296) observed eastern hognose snakes dig out southern toads (*Bufo terrestris*). Smith (1961:187) stated, "at intervals small craters are found where the [western hognose] snake has dug up resting toads." Mr. Ward M. Sharp (*in litt.* to Chief, Bureau of Biological Survey, August 13, 1938) reported: "Another case we have wherein the [western] hognose snake burrowed two-thirds the length of its body into a pocket in which Tiger Salamanders were laying up. The reptile was pulled out by its tail. It had a Salamander about $\frac{3}{4}$ swallowed." In the present study I observed no instances of predation by burrowing in the field. However, the large amount of sand found in digestive tracts and scats of hognose snakes indicates that capture and ingestion of prey may have taken place underground.

Captive hognose snakes respond to the scent of toads or lizards by burrowing. Some dry sand from a sack that had held toads for 24 hours was placed in a depression in moist sand in a cage with a female western hognose. The following description of the snake's response is taken from my notes:

"Immediately when I began to drop the sand into the cage, her tongue began to flick faster and she crawled over to the scented sand. She then began to crawl toward her water dish and then turned back, all the time flicking her tongue fast. She started to crawl toward the right of the scented sand and then turned back. When she got to the dry scented sand she

began to burrow in the edge of it and into the wet sand around it and then came out. She went over to a nearby burrow and flicked it with her tongue but turned back. She then began to burrow in the side of the dry sand again but came out. She began to burrow in the middle of the dry sand."

Similar behavior was observed when sand from a bag in which six-lined racerunners (*Cnemidophorus sexlineatus*) had been kept overnight was placed in the cage with another western hognose snake. Hognose snakes probably obtain most of their food in following by olfaction the tracks of toads, frogs, or lizards to the burrows in which they have sought shelter.

The following quotation from my notes describes the behavior of a small captive western hognose snake, typical of the sequence in ingestion of active prey:

"I placed a racerunner in the cage with a small western hognose snake. The snake raised its head and flicked its tongue twice. Both lizard and snake remained motionless for approximately one minute. The lizard then turned its head, and the snake jerked toward the lizard and grabbed the lizard's head. The lizard immediately began kicking, and the lizard and the snake kept twirling round and round. The snake did not try to coil around the lizard but allowed it to continue kicking. After approximately 1½ minutes the lizard quieted. For five minutes the snake attempted to swallow the lizard for only brief intervals. At this time the lizard still responded by moving its feet to touches by a probe. Then the snake began to swallow it in earnest, using each side of the jaw alternately. It paused for 20 to 40 seconds after three-fourths to one minute of working. When it came to the forelegs, one side of the upper jaw was used alone for awhile, followed by the other. At the end of 13 minutes there was no more response from the lizard. It took approximately one hour for the snake to swallow the lizard."

In this instance swallowing took an unusually long time because the lizard was large. Swallowing a moderate-sized lizard requires approximately 20 minutes, and a medium-sized frog or toad can be swallowed in five minutes or less. Often when the snake first grabs a lizard or amphibian, it throws a coil of its body over the prey to hold it down. Amphibians and lizards are usually seized by the head and swallowed head first.

Stallcup (1959:80) reported that a captive eastern hognose swallowed a large toad in 15 minutes. "The snake would push the toads against a coil of the body or against the side of the cage to help force the toad down the throat." Diener (1957:122) reported that one hour was required for an adult western hognose to swallow an adult collared lizard (*Crotaphytus collaris*).

Toads swell by inflating the lungs so that they are difficult for snakes to swallow. Van Duyn (1937:216) described the swelling of a toad on the approach of a southern hognose snake. Many authors have stated that the enlarged posterior teeth of hognose snakes function in puncturing and deflating toads (Pope, *loc. cit.*; Morris, 1944:83; Smith and White, 1955:138). However, if a hognose snake can seize a toad, the jaws are able to exert great pressure that could probably force deflation in most toads even if the toad was not punctured. Stallcup (*loc. cit.*) described an instance of a toad swallowed sideways in which the pressure on the body of the toad was great enough to force one of its lungs out through its mouth.

Minton (1944:455-456) suggested that the enlarged posterior teeth are useful in holding struggling prey. These teeth are also useful in manipulating an animal during swallowing. Because of its stout body and large head, a hognose snake is able to swallow relatively large animals. An eastern hognose having a weight of eight grams was observed to capture and swallow a frog that weighed 4.9 grams. The backward-pointing lance-like teeth on the posterior end of the maxillary maintain a tight hold on large prey while the animal struggles, often dragging the snake. If it is held by the body, a lizard usually bites the head and neck of a snake, but the snake maintains its grip. The snake may move its jaw back and forth so that the teeth pierce the body of the prey at a number of points, but it does not attempt to manipulate its prey until the tiring animal's struggles become less violent. This may require 10 to 15 minutes. The enlarged teeth may puncture vital organs or produce wounds that bleed freely and thus hasten the weakening of the prey. Also, salivary secretions that enter these wounds may have a mild toxicity for the prey or may hasten later digestion of a large food object.

Kapus (1964:138) and Weaver (1965:296-297) reported that the parotid element of the superior labial gland is well-differentiated and enlarged in western and southern hognose snakes but not in the eastern species. The parotid gland is associated with the development of more toxic constituents in the salivary secretions of some snakes. Evidence for the toxicity of the salivary secretions of hognose snakes on prey animals is meager. McAlister (1963) injected macerations of the inferior labial and superior labial salivary glands of eastern hognose snakes into mice, spring peepers (*Hyla crucifer*), Fowler's toads (*Bufo woodhousei fowleri*), and western chorus frogs (*Pseudacris tri-seriata*); and compared the effect to that of injections of macerated Harderian glands. The injection of macerated salivary glands had no effects on mice, but 15 of the 17 frogs died in 24 hours with hemotoxic symptoms. McAlister (pp. 136-137) concluded that the enlargement of the posterior maxillary teeth in the eastern hognose is not primarily for introduction of salivary secretions into prey, since the toxic effects of the saliva are too slow to be effective in subduing prey.

Weaver (1965:297) stated that toxic secretions of the southern and the western hognose snakes are probably useful in subduing prey. He reported that a fence lizard (*Sceloporus undulatus*) was killed by the bite of a southern hognose snake. In my study the skin of two six-lined racerunners were cut by the rear teeth of a moderate-sized western hognose. Another racerunner was seized by a western hognose and held struggling for more than a minute. It had a number of lacerations on its back when it was rescued. These lizards were still alive and active 24 hours after the injuries. Two other racerunners were rescued from western hognose snakes, one after it had been three-fourths swallowed and the other after it had been struggling with the snake for more than five minutes. Both lizards were active at the time they were released but died within 24 and 1½ hours, respectively. Death may have been due to injuries inflicted during the struggle, although the symptoms were similar to the symptoms of poisoning reported by McAlister (1963:134). The snakes had not fed for at least one month before these experiments. Although the evidence does not indicate a lethal effect of the salivary secretions that would be effective in killing prey, it does indicate a mild toxicity that might slow down the struggles of active prey.

The amount of food eaten by snakes varies according to availability. In captivity snakes may eat large amounts of food and grow rapidly, or if food is unavailable, they may survive for long periods without feeding at all. Huheey (1958:68) reported that a captive hatchling eastern hognose ate 34 cricket or chorus frogs, 5.3 grams of meat, and one dead salamander between September 13, 1956, and July 4, 1957, or an average of almost one item per week. Stallcup (1959:80) fed two toads per snake per week to captive eastern hognose snakes, but one snake went for six to eight weeks during the winter without food. A captive eastern hognose two feet long ate seven medium-sized toads in succession (Anderson, 1965:185). Between June 6 and July 24 three toads, an English sparrow, a fledgling robin, and a short-tailed shrew were fed by Munro (1949a:133) to a western hognose, 23 inches long.

Three small western hognose snakes (snout-vent lengths from 218 to 255 mm. and weights from 7.7 to 10.7 grams) were fed as many toads, frogs, and lizards as they would eat for a period of 59 days. The mean weight of food eaten per snake was 18.6 (17.3 to 20.4) grams. They ate at intervals of approximately one week during July and early August but refused food during the latter part of August and early September when they moulted. They had also moulted in the latter part of July, but without interruption in feeding. A larger western hognose (snout-vent length of 310 mm. and weight of 28 grams) ate seven six-lined racerunners, estimated to weigh a total of 40 grams, in 24 days.

A western hognose placed in a refrigerator at 7°C and given no food lost only 0.2 gram weight (from 40.7 to 40.5 grams) from July 13 to September 5. Hognose snakes often fasted for more than a month while they were active, and a few did not take food for more than four months. Three hatchling western hognose snakes and one hatchling eastern hognose were active for three months without having eaten. Then they were placed in a refrigerator on December 1, and all except one western hognose were still alive on March 8. They were dead in early April.

Digestion

The rate of digestion in a snake depends upon its physiological state and the size of the food items. Stallcup (1959:80-81) reported that a "lump" was evident in the body of an eastern hognose for as long as 72 hours after ingestion, and defecation of the residues of food eaten prior to the last meal occurred within 48 hours after ingestion. Three western hognose snakes from Harvey County were fed lizards, and the scats were collected after each of seven feedings. In all cases a scat defecated less than 45 hours after a lizard was eaten contained scales of that lizard. The last scat was collected five or six days after the feeding. In four instances this last scat still contained lizard scales, whereas in one instance it contained only insect fragments. In two instances a partially digested lizard (primarily skin and skeleton) was regurgitated five and eight days after feeding. In both instances the snake moulted a few days after regurgitation of the food item. Physiological changes may accompany moulting that sometimes slow digestion.

Composition of the Diet

Heterodon platyrhinos. Most of the published statements concerning the food habits of the eastern hognose indicate a decided preference for toads as the main food (Conant, 1951:44; Guidry, 1953:51; Oliver, 1955:205; Smith, 1956:227; Smith, 1961:190; Anderson, 1965:185; and others). Statements that mammals are an important food (Fowler, 1907:187; Guthrie, 1926:173; Haltom, 1931:24) were probably based on only a few observations or else pertained to an unusual local situation.

Some published and unpublished records of food eaten by eastern hognose snakes in nature in many parts of the species range are summarized in Table 35 (Surface, 1906:184-185; Wright and Bishop, 1915:157; Allen, 1932:13;

TABLE 35. Food Eaten by Eastern Hognose Snakes From Various Parts of the Species Range.

Food item	Percentage frequency (110 snakes)	Per cent of items (56 items eaten by 50 snakes)
Arthropods ^a (mainly insects) . . .	35.5	0
Earthworm ^a	0.9	0
Snails (<i>Triodopsis</i>) ^a	4.5	0
Amphibians	58.2	94.6
Toads	43.6	69.6
Frogs (<i>Rana</i> sp.)	7.3	14.3
Gray treefrogs (<i>Hyla versicolor</i>)	1.8	3.6
Eastern spadefoot (<i>Scaphiopus holbrooki</i>)	0.9	
Tadpole	0.9	
Salamanders	5.5	7.1
Reptiles	4.5	0
Lizards	2.7	
Eggs of lizard	0.9	
Turtle	0.9	
Birds	1.8	0
Mammals	2.7	5.4
Undetermined animal	1.8	0

a. Includes only those invertebrates reported to be primary prey.

Boyer and Heinze, 1934:194; Uhler, Cottam, and Clarke, 1939:619; Carr, 1940:79; Breckenridge, 1944:109; McCauley, 1945:65; Webb, 1952:157; Fouquette and Lindsay, 1955:411; Hamilton and Pollack, 1956:521-522; U. S. Fish and Wildlife Service files). Sixty-four of 110 snakes had eaten amphibians, and 53 of 56 items eaten by 50 snakes were amphibians, of which almost three-fourths were toads. In addition, Clark (1949:248) examined 86 eastern hognose snakes from Louisiana and found toads in all of those that contained food. Toads have been reported as an item of the diet in almost all localities where observations have been made. The following species of amphibians have been eaten in nature: *Bufo americanus*, *B. cognatus*, *B. terrestris*, *B. woodhousei*, *Rana pipiens*, *R. clamitans*, *Hyla versicolor*, *Scaphiopus holbrookii*, *Eurycea bislineata*, *Diemictylus v. viridescens*, *Plethodon* sp., and *Ambystoma opacum*. Hay (1892b:104) reported that eastern hognose snakes had eaten cricket frogs. Although salamanders were eaten in overall low frequency, four of 18 snakes (22 per cent) from Virginia and Maryland had eaten salamanders (U. S. Fish and Wildlife Service files; Uhler, *et al.*, *loc. cit.*).

Arthropods, especially insects, were the second most frequent class of items reported and were found in 35.5 per cent of the stomachs (including only those arthropods reported to be primary prey). Abbott (1885:289) stated that the eastern hognose burrows in search of earthworms and insect larvae, and Taylor (1892:349) reported that the principal foods are insects, insect larvae, and worms. However, many investigators have interpreted all insect fragments in the stomachs of hognose snakes as secondary items. Ruthven, *et al.* (1912:89) stated, "Insects are often found in the stomach, but there is no reason to believe that these are taken in any other way than in the stomachs of the toads they have swallowed." Uhler, *et al.* (*loc. cit.*) omitted from an analysis of stomachs with recognizable food items five stomachs that contained only insect fragments (U. S. Fish and Wildlife Service files).

Surface (*loc. cit.*), Wright and Bishop (*loc. cit.*), and Hamilton and Pollack (*loc. cit.*) recorded insect fragments as primary prey items. Hamilton and Pollack (1956:520) stated, "Since most of the vertebrates eaten were little digested and their viscera unexposed, we may discount the presence of secondary food organisms in virtually all of the snakes examined." Neill and Allen (1956:172-173) pointed out that hard parts of secondarily-ingested insects may remain in the stomach of a snake long after the primary prey has been digested. The presence of insect fragments in the stomach without partially digested vertebrate remains does not necessarily mean that they are primary items in the diet. Possibly a large proportion of the insects listed as primary food in the studies summarized in Table 35 were actually secondarily-ingested. Surface (1906:183-185, pl. 35) may have included a copperhead (*Agkistrodon contortrix*) in his sample of eastern hognose snakes, as he published a photograph of embryos taken from a female "hognose snake" (although the species is oviparous) and listed one stomach that was filled with cicadas (known to be favorite food of the copperhead).

All other prey listed in Table 35 were eaten with overall low frequency, although in local studies some amounted to substantial proportions of the diet. Reptiles (including *Cnemidophorus*, *Lygosoma*, and *Kinosternon subrubrum*) and eggs of lizards were eaten by five of 33 snakes (15 per cent) from Georgia (Hamilton and Pollack, 1956:521). Birds (including a nestling sparrow) were reported only from Ohio and Pennsylvania (Conant, *loc. cit.* and Surface,

1906:185). Mammals (including *Blarina brevicauda*, *Tamias striatus* and a microtine) were found in three of 18 snakes (17 per cent) from Virginia and Maryland (U. S. Fish and Wildlife Service files; Uhler, *et al.*, *loc. cit.*). Lockwood (1875:10) stated that eastern hognose snakes ate "the heads of the common eel, left on the shore by fishermen."

Foods eaten by snakes in captivity are only an indication of foods that may be eaten in nature. Foods may be eaten by some individuals in captivity that are not available or are not eaten in appreciable quantities in nature, and foods may be refused in captivity that are normally eaten in nature. Most reports state that eastern hognose snakes prefer to eat toads in captivity. Other items that have been recorded in the diet of captives are bullfrogs (*Rana catesbeiana*), southern cricket frogs (*Acris gryllus*), southern chorus frog (*Pseudacris nigrita*), dead red-backed salamander (*Plethodon cinereus*), fence lizard (*Sceloporus undulatus*), lined snakes (*Tropidoclonion lineatum*), ribbon snake (*Thamnophis sauritus*), small snakes, mice, grasshoppers, flies, and crickets (Howey, 1879:112; Gaines, 1894:959; Strecker, 1926b:6; Greenhall, 1936:171; Anderson, 1942:210; Conant, 1951:44; Huheey, 1958:68; Wegner, 1958:276). Foods refused in captivity include frogs, small birds, mice, and insects (Force, 1930:30; Gloyd, 1932:402; Clark, *loc. cit.*; Guidry, 1953:51; Stallcup, 1959:80). Wegner (*loc. cit.*) reported possible food imprinting in that a specimen from Avalon, Michigan, where toads were scarce, ate four frogs in captivity, although specimens from drier areas, where toads were common, refused frogs in captivity. In my study captives ate leopard frogs (*Rana pipiens*) and Rocky Mountain toads (*Bufo woodhousei*). Where choice was possible, they ate toads first. They refused prairie lizards (*Sceloporus undulatus*), six-lined racerunners, and mice (*Peromyscus* sp.), even on occasions when they did take amphibians.

The food habits of hognose snakes in Harvey County were studied by identification of regurgitated food items, analysis of stomach contents of preserved specimens, and analysis of scats. The analysis of scats is less definitive than the other two methods, because food items with little or no indigestible residue are poorly represented in scats. Also it is rarely possible to determine the number of items that the residue represents. However, since a larger number of scats can be collected, analysis of scats serves as a check on conclusions reached from analysis of stomach contents.

Of 154 eastern hognose snakes captured in Harvey County, 54.5 per cent had food in the stomach and/or provided scats. Only 13.6 per cent had food material that could be forced out of the stomach. Of 319 western hognose snakes examined for food, 48.6 per cent had food in their stomachs and/or provided scats, and 17.2 per cent provided records of stomach contents. Hamilton and Pollack (*loc. cit.*) reported that 33 of 42 eastern hognose snakes (78.6 per cent) had food in sufficient quantities to record. Uhler, *et al.* (1939:607) reported that only 10 of 27 (37 per cent) had usable stomach contents, but reference to the U. S. Fish and Wildlife Service files indicates that five records of stomachs containing only insect fragments were not tabulated. These studies were based on stomach contents removed from dead snakes. The lower percentage of snakes from Harvey County providing food records may have been due to my inability to detect all food residues in the digestive tracts of live snakes, to the possibility that snakes caught in traps were likely to have empty stomachs and to be searching for food, and/or to

the fact that snakes caught in traps often remained there for a few days before they were examined, and in the interval some food items were digested. I am inclined to believe that the first and last reasons were more important, since hognose snakes are also more subject to capture by hand-collecting when they are searching for food.

In the samples of food records there was no evidence of bias caused by snakes eating large numbers of animals that were in the traps. Many snakes with empty stomachs were found in the same traps with live frogs, lizards, or toads. Confinement in the trap was so disturbing to many snakes that they did not eat, even though potential prey was present. Many snakes refused to eat when they were first in captivity.

Thirteen eastern and 16 western hognose snakes were caught by hand in Harvey County and examined for food. The percentages of these snakes providing food records were higher than for those snakes caught in traps (61.5 per cent for eastern and 62.5 per cent for western hognose snakes), but they contained the same types of food as were recorded in the total samples.

Table 36 summarizes the food habits of eastern hognose snakes in Harvey County. The analysis of 21 stomach contents indicates that leopard frogs were the principal food, comprising almost two-thirds of the total. Leopard frogs were one of the most available foods, since they were abundant and, during part of the year, were commonly seen in the uplands as well as at the

TABLE 36. Records of Food Eaten by Eastern Hognose Snakes in Harvey County, Kansas.

A. REGURGITATED ITEMS OR STOMACH CONTENTS FROM 21 SNAKE.		
Food item	Percentage frequency	Per cent of items (32)
Leopard frogs (<i>Rana pipiens</i>)	61.9	65.6
Toads	42.9	28.2
Tiger salamander (<i>Ambystoma tigrinum</i>)	4.8	3.1
Caterpillar ^a	4.8	3.1

B. SCATS FROM 69 SNAKES	
Food item	Percentage frequency
Only insect fragments	52.2
Amphibians	17.4
Mouse (<i>Peromyscus</i> sp.)	1.4
Only unidentifiable material	29.0

a. This may be a secondary food item. It was regurgitated along with a small toad.

ponds. They were sometimes found in shallow burrows. When frogs were common in uplands, more than 500 were caught in traps within a three-day period. There were also large populations of bullfrogs on the study areas, but none were identified in the stomach contents of eastern hognose snakes. Bullfrogs were sometimes caught in traps, but they did not go far from ponds and probably did not burrow. Therefore, they were less available to the snakes.

Great plains toads and Rocky Mountain toads were second in importance of the food items recorded for the eastern hognose, whereas in most other studies toads have been reported to be the most important food. In the wet sand prairies of western Harvey County, the relative abundance of leopard frogs was a determining factor in the diet. The relatively high frequency of occurrence of toads in stomach contents is an indication of the snake's preference, since the toad population was much smaller than the population of leopard frogs. Seldom were as many as ten toads caught during a trapping period. However, a large percentage of the population of toads probably burrowed in the sand each day where they were subject to predation by hognose snakes.

The scats consisted primarily of insect fragments (Table 36), most of which were the residue of stomach contents of amphibians eaten by the snakes. They were primarily fragments of small insects, such as ants and small beetles. Hognose snakes that ate frogs in captivity produced scats with similar insect fragments. On only one occasion was a whole insect (caterpillar) forced up from the stomach of a hognose snake, while regurgitated material from blue racers (*Coluber constrictor*), that eat insects, often consisted of whole grasshoppers. Teeth of snakes were often found among the insect fragments in scats from hognose snakes. Normally a snake would not lose teeth in swallowing insects, but a tooth might remain imbedded in the skin of a large vertebrate that was swallowed. Those scats listed as containing amphibians had the same kinds of insect fragments, but they also contained amphibian remains, such as leg bones, a jaw, or a piece of skin from a toad. Usually the whole amphibian is digested, leaving no recognizable residues in fecal deposits.

Young eastern hognose snakes have been observed to eat crickets in captivity (Conant, 1951:44; and *in litt.*); and Pope (1944:167) and Conant (1958:138) have suggested that young snakes may feed on insects to a greater extent than do older individuals. There was no evidence in my study that insects were important items of food for young snakes. Those scats that contained fragments of grasshoppers, large beetles, or crickets, that might be primary prey, were from snakes that averaged 467 mm. in snout-vent length, whereas those that had only fragments of small insects were from snakes that averaged 418 mm. in length. This reflected a difference in the size of amphibians eaten rather than a diet of insects by young snakes. Hognose snakes of all sizes refused to eat crickets in captivity in my study, but young snakes did eat small amphibians. Three hatchlings that were two months old and weighed approximately eight grams ate leopard frogs weighing 4.8 and 4.9 grams for their first meal. A hatchling that was trapped on the study area and weighed only 12 grams had a Rocky Mountain toad in its stomach. Huheey (*loc. cit.*) reported that a hatchling in captivity ate small frogs and Raun (1962:5) reported that hatchlings ate small toads.

Tiger salamanders (*Ambystoma tigrinum*) and mice (*Peromyscus* sp.) were recorded as rare but acceptable items of food. Both were moderately common on the study areas.

Most feeding by eastern hognose snakes occurred in the middle of the summer. Of 73 snakes examined in June, July, and August, 72.6 per cent provided food records, whereas in April and May only 45.9 per cent of 37 snakes and in September and October only 31.8 per cent of 44 snakes provided food records.

Heterodon nasicus. The food habits of the western hognose are less well-known than those of the eastern species. Statements in the literature indicate a more varied diet that includes many reptiles (Stebbins, 1954:366; Wright and Wright, 1957:300; Smith, 1961:187). There are few records of the foods eaten by the western hognose in nature. Fourteen records from various parts of the species range are summarized in Table 37 (Branson, 1904:377; Ruthven,

TABLE 37. Food Eaten by 14 Western Hognose Snakes From Various Parts of the Species Range.

Food item	Percentage frequency	Per cent of items (24)
Amphibians.....	57.1	41.7
Toads (<i>B. cognatus</i> and <i>B. punctatus</i>).....	35.7	25.0
Western spadefoot toads (<i>Scaphiopus hammondi</i>)...	14.3	8.3
Leopard frogs (<i>Rana pipiens</i>)..	7.1	8.3
Reptiles.....	35.7	45.8
Lizards (<i>Eumeces septentrionalis</i> and <i>Uta stansburiana</i>)..	14.3	8.3
Eggs of lizards.....	14.3	37.5
Eggs of turtles.....	7.1
Birds (meadowlark and grasshopper sparrow).....	14.3	8.3
Mammals (<i>Peromyscus</i> sp.).....	7.1	4.2

1910:207; Little and Keller, 1937:220; Stanley, 1941:267; Breckenridge, 1944:113; Marr, 1944:484; Woodin, 1953:288; Gehlbach, 1956:369; Gehlbach and Collette, 1959:143; Dr. Henry S. Fitch, unpublished notes; Dr. Claude W. Hibbard, *in litt.*; Mr. W. Charles Kerfoot, *in litt.*; U. S. Fish and Wildlife Service files). An unpublished study of the food habits of the western hognose snake in two localities in western Nebraska is summarized in Table 38. Although toads were often recorded in these studies, other amphibians, lizards, eggs of reptiles, birds, and mammals were also reported in substantial numbers.

Brons (1882:566-567) reported that a western hognose snake had grasped and macerated the hind leg of an ornate box turtle (*Terrapene ornata*) and was sucking blood from it, and he suggested that this was a common occurrence. Ruthven (1910:208) suggested that the snake had probably seized the turtle's leg in order to swallow it, and being unable to do this, was also

TABLE 38. Previously Unpublished Records of Stomach Contents of 18 Western Hognose Snakes From Crescent Lake Refuge, Garden County, and Valentine Lakes Refuge, Cherry County, Nebraska (From Files of the United States Fish and Wildlife Service).

Food item	Percentage frequency	Per cent of items (47)	Percentage volume
Amphibians.....	44.4	25.6	42.3
Rocky Mountain toads (<i>Bufo woodhousei</i>).....	22.2	14.9	21.0
Leopard frogs (<i>Rana pipiens</i>)...	5.6	4.3	5.6
Tiger salamanders (<i>Ambystoma tigrinum</i>).....	16.7	6.4	15.7
Reptiles.....	38.9	59.5	26.6
Lesser earless lizards (<i>Holbrookia maculata</i>).....	11.1	4.3	1.5
Six-lined racerunner (<i>Cnemidophorus sexlineatus</i>)...	5.6	2.1	5.6
Prairie lizard (<i>Sceloporus undulatus</i>).....	5.6	2.1	5.6
Blue racer (<i>Coluber constrictor</i>)...	5.6	2.1	2.2
Yellow mud turtles—young (<i>Kinosternon flavescens</i>).....	5.6	4.3	0.6
Eggs of turtles (<i>Emydoidea blandingi</i> and <i>Terrapene ornata</i>)	11.1	44.6	11.1
Mammals.....	33.3	14.9	31.1
Voles (<i>Microtus</i> sp.).....	16.7	8.5	16.7
Deer mice (<i>Peromyscus</i> sp.).....	11.1	4.3	11.1
Pocket mouse (<i>Perognathus</i> sp.)..	5.6	2.1	3.3

unable to release its hold. Ornate box turtles were abundant on the study areas in Harvey County, but hognose snakes were never seen to attack them. Brons' statements are certainly exaggerated.

Food items that have been eaten in captivity include leopard frogs, bullfrogs, wood frogs (*Rana sylvatica*), spring peepers (*Hyla crucifer*), western chorus frogs, northern cricket frogs (*Acris crepitans*), Rocky Mountain toads, marbled salamanders (*Ambytoma opacum*), prairie lizards, collared lizards, "rainbow lizard," garter snakes, dead English sparrow, dead fledgling robin, live baby mice, dead adult mice, dead young rat, dead short-tailed shrew (Ruthven, 1910:207; Burt and Burt, 1929b:456; Force, 1930:30; Munro, 1949a:133; Swenson, 1950:74; Edgren, 1955:110; Fouquette and Lindsay,

TABLE 39. Records of Food Eaten by 54 Western Hognose Snakes in Harvey County, Kansas, as Determined by Identification of Regurgitated Items or Stomach Contents.

Food item	Percentage frequency	Per cent of items (92)	Percentage of food by weight		
			16 small snakes	30 medium snakes	8 large snakes
Amphibians.....	52.0	35.8
Leopard frogs (<i>Rana pipiens</i>).....	38.9	28.2	35.0	45.2	28.4
Bullfrog—tadpole (<i>Rana catesbeiana</i>)..	1.9	1.1	0.4
Toads.....	9.3	5.4	11.5	5.3	9.5
Tiger salamander (<i>Ambystoma tigrinum</i>).....	1.9	1.1	5.8
Reptiles.....	48.1	59.8
Six-lined racerunners (<i>Chemidophorus sexlineatus</i>).....	22.2	17.4	14.6	17.4	4.2
Prairie lizards (<i>Sceloporus undulatus</i>)..	5.6	3.3	7.9	1.1
Eggs of lizards.....	13.0	23.9	15.5	1.3
Plains garter snakes (<i>Thamnophis radix</i>).....	3.7	2.2	47.4
Eggs of snakes.....	3.7	6.5	8.0
Eggs of turtles.....	3.7	6.5	13.3
Birds.....	1.9	1.1	10.5
Mammals (<i>Peromyscus leucopus</i> and unidentified mice).....	5.6	3.3	9.7	8.0

TABLE 40. Records of Food Eaten by 132 Western Hognose Snakes in Harvey County, Kansas, as Determined by Analysis of Scats.

Food item	Percentage frequency
Only insect fragments.....	30.3
Amphibians.....	12.9
Reptiles	
Six-lined racerunners (<i>Cnemidophorus sexlineatus</i>) . . .	17.4
Prairie lizards (<i>Sceloporus undulatus</i>).....	2.2
Eggs of lizards.....	8.3
Eggs of turtles.....	0.8
Bird.....	0.8
Mammals	
Mice (<i>Peromyscus</i> sp.).....	5.3
Harvest mouse (<i>Reithrodontomys</i> sp.).....	0.8
Only unidentifiable material.....	24.2

1955:411; Diener, 1957:122; Mr. I. L. Traill, *in litt.*). Foods refused in captivity include leopard frogs and earthworms (Munro, *loc. cit.*; Swenson, *loc. cit.*; Edgren, *loc. cit.*). In my study captives ate leopard frogs, northern cricket frogs, Rocky Mountain toads, plains spadefoot toads (*Scaphiopus bombifrons*), six-lined racerunners, lesser earless lizards (*Holbrookii maculata*), and prairie lizards. When both lizards and frogs were offered, the snakes usually showed a preference for lizards.

The foods habits of western hognose snakes in Harvey County are summarized in Tables 39 and 40. Since the food items taken were of different sizes, total weight of live prey animals of each kind was calculated by multiplying numbers of individuals in records of stomach contents by an estimated average individual weight for each prey species. A percentage for each species was then calculated from this estimated total weight. This percentage by weight was calculated separately for small, medium, and large snakes, that had snout-vent lengths less than 350 mm., 351 to 500 mm., and more than 500 mm., respectively.

Amphibians were important in the diet of western hognose snakes in Harvey County. The predominance of leopard frogs in the diet as compared to the study in western Nebraska (Table 38) was due to the abundance of frogs on the study areas in Harvey County, Kansas. Records of feeding on leopard frogs were obtained in all months from May to October, except September. The largest number of records was from July. Great plains toads and Rocky Mountain toads were recorded only in May, June, and July; they were eaten in smaller numbers by western hognose snakes than by the eastern species.

Reptiles were the second most important food. Lizards were common foods of small and medium-sized snakes, whereas plains garter snakes (*Thamnophis radix*) were only eaten by large snakes. Six-lined racerunners were probably more available to hognose snakes than prairie lizards, because the population was larger and racerunners spend much time in burrows. Prairie lizards were more often above the ground on the trunks of willow trees or on logs. The absence of the lesser earless lizard among the food records from Harvey County is difficult to explain because this lizard was eaten in captivity, lives in burrows, and was common on the study areas in Harvey County. The species was eaten more commonly than other lizards in western Nebraska (Table 38). The six-lined racerunner was more important in the diet of small and medium-sized snakes; the prairie lizard was eaten primarily by small snakes. The racerunner was recorded as being eaten in May, June, July, August, and October, with the largest number of records in May and June. Records of the prairie lizard were from May, June, July, and October, with the largest number of records from June.

At least two different kinds of lizard eggs were eaten. The eggshells might have come from female lizards eaten when they were almost ready to lay. However, in only one instance was the eggshell accompanied by scales of a lizard. Eggs of lizards were eaten mostly by small snakes and only during June and July. Eggs of snakes, probably those of blue racers and eggs of turtles, probably those of ornate box turtles, were eaten in June and July by medium-sized snakes. Eggs of lizards, snakes, and turtles were dug out of nests soon after they had been laid, while the scent of the female still indicated the position of the nest. Mr. Ward M. Sharp (*in litt.* to Chief, Bureau of Biological Survey, August 13, 1938) observed a western hognose burrowing into the nest of a Blanding's turtle (*Emydoidea blandingi*) near Valentine, Nebraska. Stanley (*loc cit.*) reported an observation of a western hognose extracting the eggs of a turtle from a nest in Morgan County, Illinois.

Bird remains were recorded from two large snakes in Harvey County, but were not recorded in the study in western Nebraska. Mr. Marvin Plenert reported to me that he saw a large western hognose carrying a bird in Kearny County, Kansas.

Mice formed approximately nine per cent of the food of small and medium-sized snakes and were recorded from all months when snakes were active except July and October. Only *Peromyscus* and *Reithrodontomys* were identified in food remains from western hognose snakes in Harvey County. *Microtus* and *Perognathus* were both present on the study areas in Harvey County and were reported as food of the western hognose in western Nebraska, where rodents were recorded from one-third of the stomachs.

In scats containing only insect fragments, that residue probably came from the stomachs of amphibians and lizards eaten by the snakes. No evidence was obtained that small snakes feed on insects. Only nine scats contained remains of large insects such as grasshoppers and large beetles, and these were primarily from medium-sized and large snakes (mean snout-vent length of 403 mm. as compared to a mean of 375 mm. for snakes yielding scats with remains of small insects). Scats from three hatchling and first-year snakes, with snout-vent lengths of 201, 204, and 207 mm., contained scales of six-lined racerunners. A hatchling in captivity ate northern cricket frogs.

In Harvey County small western hognose snakes feed primarily upon leopard frogs, toads, six-lined racerunners, mice, and eggs of lizards. Medium-sized snakes eat leopard frogs, six-lined racerunners, eggs of snakes and turtles, and mice. The few records from large snakes indicate that they eat leopard frogs, racerunners, plains garter snakes, birds, and toads, but the proportions indicated by the small sample are probably unreliable. Most feeding occurs in June, July, and August. Of 239 snakes examined in those three months, 54.8 per cent provided food records, whereas in April and May only 35.2 per cent of 54 snakes and in September and October only 23.1 per cent of 26 snakes provided food records. Seasonal differences in the utilization of prey parallel the degree of activity of prey animals on the uplands. Lizards are eaten in greatest numbers in May and June, while frogs are eaten in greatest numbers in July (Fig. 19). In June and July eggs of reptiles are an important food. The western hognose snake has a much more varied diet in Harvey County than the eastern species.

Adaptations for Bufophagy

Smith and White (1955:138) listed a number of adaptations of hognose snakes for feeding on toads, including highly mobile maxillae, enlarged rear maxillary teeth, a broad head, an expansive gape, a thick body, and physiological resistance to the poisons produced by the skin glands of toads. The parotid secretions of toads include cholesterol, a bufotenine that stimulates secretion of epinephrine by the adrenal medulla, a bufagin (digitaloid), a bufotoxin (digitaloid) and epinephrine. The adrenal glands of hognose snakes are exceptionally enlarged (Smith and White, 1955:137-138). This enlargement may be necessary to produce sufficient epinephrine for normal functioning, since the tissues of hognose snakes seemingly are less sensitive to epinephrine (Edgren and Edgren, 1955:3). Secretions of the interrenal tissues may also play a role in resistance to the digitaloid poisons (Smith and White, 1955:141).

A histological study of the adrenal gland of the eastern hognose indicated normal proportions of interrenal and medullary cells, the enlargement of the gland involving both types of tissue. However, there is no certain correlation between volume of tissue and amount of secretion, and further studies are necessary to determine the significance of adrenal enlargement.

Huheey (1958:68) reported that a captive juvenal eastern hognose snake, that had probably never eaten toads, seized and held onto large toads with no ill effects. The resistance to toad poisons is inherent and not an individual adjustment to diet.

DISEASE AND MORTALITY

Parasites

Hognose snakes, particularly those of the eastern species, have many parasites. Wright and Bishop (1915:157) reported that 14 of 21 adult eastern hognose snakes from Georgia had parasites in the alimentary tract. The significance of parasitic infestations in causing debilitation or disease in hognose snakes is not known. However, individuals that appear healthy may have heavy infestations of flukes or other parasites (Goodman, 1951:65).

Corrington (1929:70) reported that captive hognose snakes often developed a skin infection characterized "by an ever increasing number of large oedemas just beneath the skin accompanied by sluggishness, loss of appetite, difficulty in or cessation of shedding, and a general wasting away culminating in death." I have also observed this condition in captive snakes and once in a wild snake.

Heterodon platyrhinus. Bacteria: *Leptospira ballum*, a bacterium causing leptospirosis in man and domestic mammals, was isolated from an eastern hognose in Illinois. The snake appeared healthy (Ferris, *et al.*, 1961: 408, 410).

Protozoa: The blood parasite, *Hepatozoon serpentium*, was found in three of five specimens of the eastern hognose from Texas (Hilman and Strandtmann, 1960:227). *Hypotrichomonas acosta* has been reported from this snake (Lee, 1960:397), and *Tritrichomonas batrachorum* has been cultured from the liver and kidney of a specimen captured in southern Illinois (Anderson and Levine, 1961:877).

Platyhelminthes: Eastern hognose snakes are commonly parasitized by lung flukes. The following species have been found: *Neoreniifer aniarum*, *N. elongatus*, *N. heterodontis*, *N. serpentis*, *N. validus*, *N. zschlockei*, *Renifer texanus* and *R. ellipticus* (Nicoll, 1911:677; Harwood, 1932:19-20, 22; Byrd and Denton, 1938:393-394; Hughes, Higginbotham, and Clary, 1941:38; Parker, 1941:31, 33; Ferris, *et al.*, 1961:408).

Nematoda: Morgan (1943:180) found the nematode *Physaloptera obtusissima* in one of nine specimens collected in Wisconsin. McCauley (1945: 65) reported that *Ophidascaris* sp. had been found in the stomach of a specimen from Maryland, and Ash and Beaver (1963:767-768) found *O. labiata-papillosa* in the stomach wall of five specimens collected on Avery Island, Louisiana. Harwood (1932:43, 51, 53-54, 63) examined four specimens from near Houston, Texas, and found the nematodes *Kalicephalus agkistrodontis* in the stomach of two, *Cosmocercoides dukae* in the rectum of two, *Rhabdias vellardi* in the lungs of one, and *Capillaria heterodontis* in the rectum of one.

Acarina: Edgren (1955:114) reported that mites had been seen on eastern hognose snakes, but they were not identified.

In my study snakes were examined for trematodes, nematodes, and external parasites. The "renifer" flukes that parasitize the respiratory and upper digestive tract are probably acquired by the snake when it eats an amphibian that is host to the metacercariae. These flukes parasitize the lungs, but they ascend the respiratory tract to the mouth and esophagus to lay eggs. The fluke, *Neoreniifer validus*, was found in the mouths of 15 of 137 individuals that were trapped in Harvey County. The number of flukes in the mouth varied from one to fourteen. All records of flukes were in the period from April 17 to July 5, with most records in May and June. This is undoubtedly the egg-laying period for the flukes.

The incidence of infection with *N. validus* was high in adult eastern hognose snakes. Of 17 large snakes (more than 500 mm. in snout-vent length) captured in May and June, 10 had flukes present in the mouth. However, of 34 snakes with snout-vent lengths less than 500 mm. captured in May and June, only three had flukes present in the mouth. Three preserved specimens that were more than 500 mm. in snout-vent length had large numbers of the fluke *N. validus* in the lungs and/or esophagus. Five preserved specimens of less than 500 mm. in snout-vent length had no flukes parasitizing the lungs.

Two of three large preserved specimens of the eastern hognose snake had

nematodes, *Physaloptera* sp., in the stomach. Five small specimens had no parasitic worms in the digestive tract. Only one mite was found on one juvenile in Harvey County, and this parasite was not identified.

Heterodon nasicus. There are no published records of parasites in the western hognose, primarily because this species has been little studied. The western species has a lower incidence of parasitic trematodes than the eastern species, because its diet does not consist so predominantly of amphibians. Of 25 preserved specimens from Harvey County, only one had flukes parasitizing the lungs or upper digestive tract. This specimen had two species of flukes, *Neoreniker validus* and *Reniker kansensis*. Of 288 live snakes that were examined, only four had flukes present in the mouth. These records were all in the period from May 9 to June 12. Only one or two flukes were present in each mouth.

Four of 25 preserved specimens had nematodes, *Physaloptera* sp., in the stomach. Mites were found on three snakes but were not identified.

Predation

Although a number of predators have been reported to eat them in captivity or in nature, hognose snakes are not common prey for any predator. Mr. William H. Stickel, who furnished records of predation on hognose snakes from the files of U. S. Fish and Wildlife Service, commented (*in litt.*), "In view of the many thousands of hawks, owls, crows, coyotes, foxes, and other animals whose stomach contents have been recorded and indexed in our files, it seems to me that the representation of *Heterodon* remains is quite low. These snakes are not rare, but I do consider them uncommonly secretive and I suspect that this protects them from a great deal of predation."

No instances of predation on hognose snakes were observed in my study. A few scats and pellets of opossums, striped skunks, red-tailed hawks, Mississippi kites, and screech owls were collected from the study areas or their immediate vicinity, but no remains of hognose snakes were found. The importance of predation as a mortality factor in hognose snake populations is not known.

Heterodon platyrhinos. The most commonly reported predators on the eastern hognose snake are other species of snakes. The kingsnake (*Lampropeltis getulus*) has been observed to eat them in captivity and in nature (Wright and Bishop, 1915:169-170; Wilson and Friddle, 1946:47-48; U. S. Fish and Wildlife Service files—one record). The kingsnake is rare on the study areas in Harvey County, but the related prairie kingsnake (*L. calligaster*) is moderately common. The prairie kingsnake eats few snakes, and no evidence of predation on hognose snakes has been collected.

The racer (*Coluber constrictor*) has been reported to eat the eastern hognose in captivity (Whitaker, 1931:84) and in nature (Hamilton and Pollack, 1956:523, recorded it from one of 57 stomachs; Klimstra, 1959:212, recorded one immature eastern hognose among 213 vertebrate prey items in 137 stomachs). The racer is common on the study areas in Harvey County, and it probably preys on hognose snakes occasionally, although examination of 55 stomach contents and 113 scats of the racer from western Harvey County revealed no remains of hognose snakes (Fitch, 1963:403).

Hamilton and Pollack (1956:523; 1955:3) found an eastern hognose in one of 45 stomachs of the eastern coachwhip (*Masticophis flagellum*) and in one of nine stomachs of the eastern cottonmouth (*Agkistrodon piscivorus*). A hatch-

ling black rat snake (*Elaphe obsoleta*) constricted and swallowed a hatchling eastern hognose in captivity (Hudson, 1947:178). The latter three species of snakes are not found on the study areas in Harvey County.

Over (1923:28) stated that red-tailed hawks feed their young on eastern hognose snakes, and there are records of predation by three hawks on four snakes in the files of the U. S. Fish and Wildlife Service. Red-tailed hawks are present on the study areas. There is one record of predation by the barred owl (*Strix varia*) on the eastern hognose (U. S. Fish and Wildlife Service files), but this owl is not present on the study areas.

There are no records of mammalian predators feeding on eastern hognose snakes. Raccoons, striped skunks, opossums, badgers, eastern moles, short-tailed shrews and coyotes are all moderately common on the study areas, all have been known to eat snakes, and doubtless they eat hognose snakes occasionally. However, snakes are not the principal prey of any of these predators, and the defensive behavior of hognose snakes may discourage predation by some of them (see p. 383).

Ornate box turtles (*Terrapene ornata*) and bullfrogs (*Rana catesbeiana*) are abundant on the study areas and may occasionally eat hatchling hognose snakes. The eastern box turtle (*Terrapene carolina*) and the bullfrog have been reported to eat snakes occasionally (Hensley, 1962:141; Hutchison and Vinegar, 1963:284; Korschgen and Basket, 1963:91, 96). Owens (1949:148) reported that a tarantula (*Eurypelma californica*) killed and fed on a newly hatched eastern hognose in captivity.

Heterodon nasicus. The only records of predation on the western hognose snake are those in the files of the U. S. Fish and Wildlife Service, that include the following predators: Swainson's hawks (two records), an unidentified *Buteo* hawk, a crow, and a coyote. These predators are found on the study areas in Harvey County. In addition, many of the predators listed for the eastern hognose may occasionally prey on the western species.

Other Causes of Mortality

Starvation is probably an important cause of death for hatchling hognose snakes. Some hatchlings that are unable to capture their first meal within an appropriate interval gradually become weak and emaciated so that their chances of finding and overpowering prey are reduced and survival becomes unlikely (see p. 353). A few mature snakes were captured in an emaciated condition resulting either from disease or starvation.

Both wild and domestic ungulates, such as deer, cattle, sheep, and horses kill snakes (Brons, 1882:565; Klauber, 1956:1033-1038). Mr. George Hawks, the caretaker at Harvey County Park, reported to me that he saw a sheep kill a snake. Such mortality may be important in heavily grazed pastures.

In many areas hognose snakes are killed by most human residents whenever they are seen (Conant and Bridges, 1939:40). Man may cause substantial mortality in Harvey County Park. Because they move slowly, hognose snakes are often killed by cars. In my study few DOR snakes were found on the unimproved roads near the study areas, but I found one DOR eastern and four DOR western hognose snakes in three years. Campbell (1956:124-125), who traveled extensively in New Mexico from 1951 to 1954, reported that the western hognose was the fourth most common snake found DOR. Bugbee (1945:373) found one DOR western hognose among 57 DOR

snakes found on a trip of 260 miles through western Kansas. Allin (1940:112) reported that many eastern hognose snakes were found DOR in the fall of 1933 in Ontario, Canada. Grant (1937:370) reported that the eastern hognose was "frequently seen dead on the roads of Sedgwick County," Kansas.

Injury

Hognose snakes, particularly those of the western species, can survive extensive injury. Eight of 124 eastern hognose snakes (6.5 per cent) that were captured alive were or had been injured. These injuries included: cuts or scars on the body (2), broken rostral region (2), tail badly cut (2), damage to skin below chin and on anterior ventrals (1), and damaged right eye (1). Eighteen of 241 snakes of the western species (7.5 per cent) had injuries that included: cuts or scars on body (7), scarred area on top of head, many scars on body, and damaged right eye (1), scarred area on body and missing ribs (1), scarred area on body, missing ribs, and appendage of skin healed but hanging loose (1), tail injured or end broken (5), right hemipenis everted and dried (1), broken and healed vertebral column (1) and three *Opuntia* thorns in head (1). One large western hognose was apparently dead when found at the side of a road. Its head had been run over by a car. When it was dissected four or five hours later, its heart was still beating strongly.

Some injuries, such as the broken rostral and puncture by thorns, were probably due to accidents. The more extensive injuries were probably the result of attempted predation or of the attempts of ungulates or man to kill the snake.

Defensive Behavior

Description. The stereotyped defensive behavior of hognose snakes, especially that of the eastern species, is well known. Descriptions of this behavior have been based on the snake's response to an encounter with man. Say (1819:261) wrote one of the earliest descriptions of the threatening components of this behavior but did not describe death-feigning. The total behavior pattern has been described by many authors, although many descriptions are incomplete and some statements are in error (for a list of references, see Wright and Wright, 1957:308).

The defensive behavior of hognose snakes in response to the presence of a person includes three phases. These phases in their usual sequence are:

1) Attempted escape or retreat phase—The snake may attempt to "freeze" upon the approach of a person. It is protectively colored and often overlooked (Taylor, 1892:347). As a person comes closer, the snake attempts to escape, often utilizing wide convulsive loops of the body. An attempt to escape may also follow the second phase of the behavior. If the snake's movement is obstructed, it suddenly and jerkily changes direction. If its movement is obstructed a number of times, the snake coils and the jerky movements become pseudo-strikes (see below).

2) Threatening phase—This phase includes some combination of the following behavior components: A. *Spreading-neck*—This is a threatening or bluffing posture consisting of broadening (laterally) and flattening (dorso-ventrally) the head and anterior one-third of the body. The neck may be stretched more than twice its normal width. This is accomplished by extending the well-developed ribs on the anterior body. As the skin between the scales is spread,

the color patterns on the anterior body of the snake appear brighter and more striking. The light-colored lips outline the sides of the head. While in this posture, the snake alternately swells and narrows the entire body by filling the lung and expelling air. Hissing usually accompanies this action and is especially loud during inspiration. Abbott's (1885:288) statement that the eastern hognose mimics the rattlesnake by vibrating its tail, sometimes rattling dead leaves, is in error (probably based on observations of the racer or other snakes), for the tail is held still and coiled. Often the head is raised above the spirally coiled posterior body. The mouth may be open or closed. This posture has been responsible for the hognose snake's fearful reputation. B. *Concealing-head*—The snake places its head under a part of its body or places its coiled tail over its head. Hissing may accompany this posture (Pl. 7, Fig. 1). C. *Pseudo-strikes*—Pseudo-strikes are oriented thrusts toward a person from the spreading-neck posture and with the mouth closed. The head of the snake may "bump" the person but usually does not. Sudden jerky movements may occur from any posture, such as a sudden switching of the head or tail by a snake concealing its head. These are analagous in adaptive function to pseudo-strikes.

3) *Death-feigning or letisimulation phase*—This phase of the behavior occurs as a response to a higher degree of stimulation and usually is initiated only after the snake has been mechanically stimulated. It is begun by vigorous writhing and convulsions, usually with the mouth wide open. Regurgitation and/or defecation, as well as secretion from the anal musk glands, often occur. The mucous membrane lining the mouth sometimes hemorrhages and the mouth becomes bloody. The body may become smeared with fecal matter or blood. After writhing, the snake lies still, completely limp, belly side up, often with the head partially covered by the body (Pl. 7, Fig. 2). If it is turned over onto its belly, the snake quickly turns back onto its dorsal side. If it is poked during this stage, it may respond with brief writhing. As the snake becomes active again, it first closes its mouth, then turns over its head, and begins to flick its tongue. It slowly rights the rest of its body and begins to move off. If it sees a person move at this time, the snake turns belly up and opens its mouth again. Letisimulation has given rise to the myth that after death the snake's "mate" will come and lick its wounds, and the dead snake will revive (Kilpatrick, 1893:208).

Physiological basis of the behavior. The stimulus that initiates defensive behavior in hognose snakes is the movement of a relatively large object (Raun, 1962:45). The escape and threatening phases of the defensive behavior of hognose snakes are obviously instinctive responses based primarily on central nervous reflexes. However, the letisimulation phase has been variously interpreted as fainting due to a nervous condition (Hulme, 1951:132), "tonic immobility" or paralysis due to the release of glandular secretions into the circulatory system when the snake is upside down (Beach, 1945:441; Bradt, 1949:417), shock (Mosimann and Rabb, 1952:25), or behavior controlled by central nervous reflex patterns (Edgren, 1955:114).

In order to test whether death-feigning might be caused by adrenal medullary action or by the paralyzing effects of neurohumors diffusing from nerve centers, Edgren and Edgren (1955) tested the effects on an eastern hognose of injections of epinephrine, nor-epinephrine, and acetylcholine chloride. Even large doses of these chemicals stimulated no death-feigning response. Death-

feigning is not a physiological response affecting the whole body. Heart rates of death-feigning hognose snakes may be as high as 104 or as low as 6 beats per minute; and there is no obvious change in heart rate when death-feigning is initiated.

The snake has not fainted or entered shock during letisimulation. Its senses are still alert, although many of its normal responses are inhibited. Sometimes responses are evident to strong mechanical or visual stimuli (Kilpatrick, 1893:209). The snake's response is rapid if it is placed on its belly.

The bulk of evidence suggests that death-feigning in hognose snakes is primarily a nervous response and is similar to the other components of defensive behavior. It is initiated by a period of convulsive muscular response. During death-feigning a particular posture is maintained, and many types of responses are inhibited (similar in many respects to "freezing" in young gallinaceous birds). The letisimulation phase is initiated by a higher level of fear or flight tendency than the other phases of defensive behavior.

Bartlett (1920:503) suggested that the variability in completeness of defensive behavior is due to conditions of the season, weather, and the development of the snake. I found no apparent relation between season or weather and behavior. Variability is probably due to inherent individual differences and changes in physiological state. Raun (1962:4) reported individual differences in the pattern of behavior in hatchlings in captivity.

After a period of repeated stimulation, as in captivity, many components of the defensive behavior of hognose snakes are extinguished. Death-feigning has the highest nervous threshold and is lost easily. Raun (1962:5) reported that death-feigning was lost by hatchling eastern hognose snakes after three or four days of handling and all defensive behavior was lost after ten days.

Although Munro (1949c:136) reported that young western hognose snakes did not show defensive behavior until they were at least one day old, it has been my experience and that of other investigators (Raun, 1962:4; Kennedy, 1961:421; Minton, 1944:455; Hay, 1892a:116-117) that many young eastern and western hognose snakes can perform the defensive behaviors as soon as they have hatched or even while they are still within the egg.

Adaptive value of defensive behavior. The defensive behavior of hognose snakes may have adaptive value in relation to predators, to domestic and wild ungulates that kill hognose snakes, and to man. There has been little observation of the response of predators to the defensive behavior of hognose snakes. Therefore, an interpretation of the adaptive value of this behavior in relation to predators must be speculative.

The response of a domestic cat to a western hognose is described in the following quotation from my notes. Of course, a well-fed domestic cat probably does not react in exactly the same manner that wild predators would react to the snake's behavior.

"The mother cat and one of her kittens became interested in the western hognose snake. It hissed and spread its neck to some degree but kept its head low—on the floor or just above it—with mouth closed. When the cat came close the snake made a jerky movement and hissed louder, and the cat jumped back. The mother cat soon became disinterested and left, but the young kitten continued teasing the snake. Sometimes it moved in on its coiled tail, and the snake made a pseudo-strike with its tail. The cat jumped

back. As the cat began to move in more often and touch it, the snake began to conceal its head. . . . The snake feigned death. The cat then grabbed the snake a few times and also licked it, particularly near the vent. Then it went off with the other cats."

If this defensive behavior allows only a few more snakes to survive, it will be adaptively maintained. This behavior can be assumed to have adaptive value if: 1) it postpones the killing of the snake by a predator, allowing time in which a distraction might permit the snake to escape; 2) it deters or discourages killing by less determined predators, such as those that are young, inexperienced, or relatively satiated; 3) it causes the predator to become less alert, allowing the snake sometimes to escape; 4) it discourages the killing of the snake by non-predatory animals, such as humans and ungulates.

The adaptive possibilities of escape or retreat are obvious. For a fast-moving snake, such as a racer, or for one living in dense vegetation, this is a successful response to a dangerous situation. However, hognose snakes are slow-moving and live in more open situations, so they cannot escape in this manner in many instances. Other types of defensive behavior have evolved (Sharp, 1893: 248; Morris, 1935:15).

The spreading-neck posture is a threatening behavior that makes the hognose snake appear to be larger and more aggressive. It evokes caution in another animal and may discourage attack. It may have adaptive values one, two, and four.

The behavior pattern of concealing the head makes less obvious the most vulnerable part of the snake. The head contains the venom apparatus of venomous snakes, so when the snake's head is concealed, the predator may become unsure of his position. By obviously displaying a coil of the tail, the snake encourages the predator to attack the least vital part of the body, thus postponing the kill. Also, since the snake appears less like an active, living animal, the predator or other animal may lose interest in the snake. This behavior pattern could have all four adaptive values.

Pseudo-strikes are the snake's response to close approach and probably cause the predator or other animal to move back, thereby discouraging and postponing the actual attack. Unoriented jerky movements accompanied by hissing would probably have the same effect.

The adaptive value of death-feigning is less obvious and, therefore, interpretation is more speculative. Some authors have suggested that it has no survival value (Hulme, *loc. cit.*; Mosimann and Rabb, 1952:25-26). However, it is difficult to explain the evolution of a complex behavior pattern in the absence of survival value. Raun (1962:6) suggested the possibility that death-feigning might eventually be lost through evolution because it was less effective than the other defensive behaviors. However, death-feigning is more uniformly developed in the three species of hognose snakes than the other phases of defensive behavior. Death-feigning has adaptive value four, since some animals are probably left for dead by grazing animals or man and afterwards escape. A number of hognose snakes have been observed that survived serious injury (see p. 379). Death-feigning may also in some cases postpone the actual killing of the snake by slowing down a predator's attack. Sometimes it might cause the predator to become less alert and allow the snake to escape. Some predators "lose interest" in prey that is not moving.

Many authors have commented on the almost invariable resumption of the belly-up position by death-feigning hognose snakes if they are placed belly-down. There have been few suggestions of adaptive value for this response. Some authors have suggested that this is a vital flaw in the behavior. Munyer (1967:669) suggested that this resumption of belly-up position may have been evolved for use in water where it would resemble the floating movements of a dead snake. However it is unlikely that this predominantly terrestrial snake is often preyed upon in the water and this would appear to be an insufficient argument. If letisimulation is to be most effective, a death-feigning animal must assume a posture that will be readily recognized as that of a dead animal. A snake lying belly-down is not obviously dead; it may be merely quiescent. The most obvious posture that no living snake would "normally" adopt is belly-up. If it is adaptive for a predator to assume that a hognose snake is dead, it would be adaptive for the snake to evolve behavior patterns insuring a close association between death-feigning and a posture that would make the above assumption more certain. Few predators, other than biologists, test a dead snake by deliberately placing it on its belly, so an appropriate response to this test has not been evolved.

Most of the known instances of predation on hognose snakes are by other snakes or by hawks. These predators would be least affected by the defensive behavior of hognose snakes. This behavior may lessen predation by mammalian predators and mortality by grazing animals. Although death-feigning probably reduces mortality by man (Breckenridge, 1944:109), some authors have suggested that the exaggerated threatening behavior causes the eastern hognose to be more greatly persecuted and killed by modern man (Morse, 1904:126; Bridges, 1939:124; Pope, 1944:168). The response of aboriginal populations to the defensive behavior of hognose snakes may also have been important in the reinforcement of this behavior.

Heterodon platyrhinus. The typical behavior of an eastern hognose when it first encounters a person is illustrated by the following two quotations from my field notes:

"As soon as I opened the trap, the eastern hognose snake spread its neck. As I picked it up by the tail, it spread its neck down to the second dorsal blotch, and hissed. When I put it down it reared its head, spread its neck, and hissed. It made a few pseudo-strikes; then it jerked its head backwards and began to writhe vigorously and feigned death. Within a minute it flicked its tongue, and then within two minutes it had turned its head over. It immediately turned ventral side up when I moved my hand near."

"The eastern hognose snake spread its neck as I approached the trap. When I touched the trap, it began to writhe, and then it turned over and feigned death. It regurgitated the legs of a leopard frog as it stopped writhing."

Conant (1951:43), McCauley (1945:65), and Myers and Arata (1961: 109-110) described instances in which an eastern hognose held its head and neck erect with its mouth wide open. Bogert (1954:1341) stated that, in the southern part of the United States, eastern hognose snakes imitate the cottonmouth (*Agkistrodon piscivorus*) by opening their mouths when threatening. However, this behavior is also sometimes seen in areas where cottonmouths are not found.

Heterodon nasicus. The following quotation from my field notes illustrates typical defensive behavior of the western hognose:

"When I picked up the western hognose snake, it began to hiss. I put it down and waved my hand at it. Each time my hand passed over it, it hissed and thrashed and coiled its body. It formed a round pancake coil with its head underneath and kept hissing. I kept touching it, and it writhed and kept hissing. Finally, after approximately three minutes, it turned belly up, opened its mouth, and quit hissing. It writhed for a few seconds. It then lay in a coil with its head on the inside, feigned death with its mouth partly open, and defecated."

Differences in behavior between Heterodon platyrhinos and H. nasicus. A number of authors have indicated that the western hognose has a defensive behavior pattern similar to that of the eastern species (Schmidt and Inger, 1957:213; Smith, 1961:187, 189-190; Anderson, 1965:187). However, Breckenridge (1944:112-113), Edgren (1955:113-114), and Bartlett (*loc. cit.*) have described differences in the behavior pattern of the western species. Hudson (1942:51) reported that western hognose snakes that he had observed did not "play possum."

Although there is much individual variation in the defensive behavior patterns of hognose snakes, I have found that certain sequences are typical of each species in Harvey County. Individuals of both species may attempt to escape when first confronted or after other phases of their defensive behavior. However, the western hognose continues the attempt longer and has a higher threshold for the other phases of defensive behavior. Taylor (1892:351) stated that the western hognose disappears quickly under loose sand or plowed ground. Breckenridge (1944:113) described a western hognose that attempted to escape and was surrounded by persons. Within a few minutes it burrowed under the sand. In another case he (Dr. W. J. Breckenridge, *in litt.*) observed one escape into an open hole in sandy ground. The eastern hognose may go directly into the threatening phase without attempting to escape.

In the threatening phase the eastern hognose typically spreads its neck, while the western species typically conceals its head. If the western hognose does attempt to spread its neck, this is never done to the degree that is characteristic of the eastern species and is often followed by the concealing-head posture. Bradt (1949:416) published photographs of a western hognose snake spreading its neck. Eighteen of 20 (90 per cent) eastern hognose snakes used the spreading-neck posture when they were first captured in traps or in the field, but only six of 29 (21 per cent) individuals of the western species spread their necks at the time of their first capture. Both species may engage in pseudo-strikes. Sometimes the western species feigns death immediately after attempting to escape, without any threatening phase except for sudden jerky movements of increasing frequency. Southern hognose snakes (*Heterodon simus*) may use either the spreading-neck or concealing-head posture (Myers and Arata, 1961:109).

The death-feigning phase is used by both species. Twenty-nine of 35 (83 per cent) eastern and 50 of 70 (71 per cent) western hognose snakes feigned death when first captured. However, in the defensive behavior of the eastern species, writhing is more energetic and lasts longer, regurgitation is more common, and death-feigning is more complete and usually lasts longer. During writhing, the eastern hognose may move five or six feet away, whereas a

western hognose does not move far. The inactive period of death-feigning for the eastern species after a single stimulation lasted from 30 seconds to 26 minutes in my study. However, with repeated stimulation they may remain inactive for an hour (McAtee, 1907:10). The period of reactivation after the snake has closed its mouth and righted its head until it moves away usually lasts a few minutes but lasted 20 minutes in one instance. The inactive period for western hognose snakes after a single stimulation usually lasts a few minutes (one to five minutes in my study). Sometimes after a period of writhing, a western hognose will attempt to escape rather than to feign death.

After a period in captivity, both species usually lose the exaggerated threatening behavior and death-feigning. However, these behaviors are lost sooner by western hognose snakes. Many hognose snakes were removed from the traps and taken to the laboratory for examination within 24 hours. Twenty-four of 41 (59 per cent) eastern hognose snakes that feigned death in the field also feigned death on examination in the laboratory, but only nine of 98 (nine per cent) individuals of the western species did so.

Significance of the difference in behavior. The differences in behavior between the eastern and western species are associated with differences in size, in susceptibility to predation, and possibly in habitat. In order for the spreading-neck posture to have sufficient intimidatory effect to make it of adaptive value, the hognose snake must be relatively large with respect to its common predators. Such behavior by an adult western hognose, 450 mm. long, probably would have little deterrent effect upon the large predators and ungulates encountered on the prairies. In fact, it might stimulate an ungulate to increase its attacks. It would also have little effect upon a *Buteo* hawk attacking suddenly from above, and those hawks are important predators of the prairies. Therefore this behavior is poorly developed. The spreading-neck posture of an adult eastern hognose, 850 mm. long, probably has deterrent effect even on some of the larger predators found in the deciduous forest.

The concealing-head behavior can be effective even when used by a relatively small snake, because it is not used to intimidate but to make the predator unsure of the danger of its position and to mislead its attack. It would also be less likely to excite an ungulate and would offer some protection against an ungulate's attack.

The large eastern hognose is more conspicuous. It is more susceptible to predation and has less chance of escaping and concealing itself. It depends upon intimidation or death-feigning for survival when it is discovered. The smaller western hognose can more easily escape into concealment. Therefore, its first reliance upon escape and its attempt to escape sooner after death-feigning are both probably adaptive.

POPULATION

Size of Population

Jolly (1965) presented a stochastic model for estimation of population parameters from capture-recapture data collected in a series of trapping periods. In each trapping period a sample, n , of a population is obtained, in which a certain number of individuals, m , have been previously marked. Also, a group of marked animals, s , is released. At trapping period i the size of the popula-

tion can be estimated if the proportion, a_1 , and the number, M_1 , of marked animals in the population can be estimated. The proportion of marked animals in the sample of animals trapped during trapping period i can be used as an estimate of a_1 , *i. e.*

$$\hat{a}_1 = \frac{m_1}{n_1}$$

Immediately after time i there are two groups of marked animals in the population: an unknown number, $M_1 - m_1$, that were marked before trapping period i but were not captured at time i ; and a known number of marked animals, s_1 , released at time i . Of the former, some individuals, Z_1 , are captured in subsequent trapping periods; and of the latter, R_1 are recaptured. Assuming that the probabilities of recapture of individuals in $M_1 - m_1$ and in s_1 are the same, the number of marked individuals in the population at time i can be estimated:

$$\hat{M}_1 = \frac{s_1 Z_1}{R_1} + m_1$$

The size of the population at time i can then be estimated:

$$\hat{N}_1 = \frac{\hat{M}_1}{\hat{a}_1}$$

Modification of the above method was necessary in order to estimate the size of populations of hognose snakes on my study areas, because the number of snakes obtained in any one trapping period was small. With small values of m_1 and R_1 , there will be an appreciable positive bias in the estimate of M_1 and the estimate of $1/a_1$. To eliminate this bias, and in particular, to get over the difficulty of R_1 or m_1 being zero, Mr. G. M. Jolly (*in litt.*) suggested the amalgamation of data from a number of consecutive trapping periods. In amalgamating the data from trapping periods i through k in estimating M_1 , R_1 is replaced by ρ_1 and s_1 is replaced by δ_1 . These new quantities may be defined: $\rho_1 = R_1 + R_{1+1} + \dots + R_k + 1$; $\delta_1 = s_1 + s_{1+1} + \dots + s_k + 1$. The formula for a_1 is modified by amalgamation of data from trapping periods prior to i :

$$\hat{a}'_1 = \frac{m_g + m_{g+1} + \dots + m_1 + 1}{n_g + n_{g+1} + \dots + n_1 + 1}$$

With small values for the various numbers involved, the standard errors of the estimates of population size calculated by using the equations given by Jolly (1965:237-238) with modifications due to the amalgamation of data are only approximations.

Estimates of the size of populations of hognose snakes on the study areas in Harvey County were made by amalgamating data for estimation of M_1 over periods of approximately one month. These estimates are made for the beginning date of each period and these dates are listed in the tables of population estimates (Tables 41 and 42). Estimates of the size of population of hognose snakes on the Graber Pasture study area are listed in Table 41. These estimates indicate the general magnitude of the size of the population, but

TABLE 41. Estimates of the Size of the Populations of Hognose Snakes on the Graber Pasture Study Area in Harvey County, Kansas.

Western Hognose		Eastern Hognose	
Date	Estimated population size	Date	Estimated population size
June 28, 1960.....	136 ± 128	September 22, 1961....	11 ± 12
August 2, 1960.....	181 ± 174	June 4, 1962.....	133 ± 125
June 14, 1961.....	43 ± 33	July 16, 1962.....	29 ± 22
August 15, 1961.....	206 ± 130	April 17, 1963.....	21 ± 17
April 26, 1962.....	133 ± 82	June 4, 1963.....	22 ± 18
June 4, 1962.....	199 ± 155	Mean Size.....	43
June 29, 1962.....	109 ± 73		
August 6, 1962.....	115 ± 83		
April 24, 1963.....	48 ± 37		
June 4, 1963.....	37 ± 36		
Mean Size.....	121		

their standard errors are so great as to yield incredible minimal values. The variability of the estimates is mainly due to the inadequacy of the data and probably has little biological significance. The mean estimate of 121 snakes for the population of western hognose snakes is the most reliable estimate. Amalgamating the data over slightly different time periods gave different individual estimates but a similar mean estimate. An estimate of the average population size in 1962 by Schnabel's (1938) method was 230 snakes, almost twice as high (calculated for me by Dr. Edward Batschelet). The variance of this estimate cannot be calculated, but this estimate lies within the 95 per cent confidence limits of all of the estimates for 1962 by Jolly's method. It is probable that the population was somewhat higher in 1962 than in the other years due to an influx of snakes to feed on the large numbers of frogs around the drying ponds.

The estimates of population size are only for the trappable portion of the population and do not include the hatchlings that were poorly represented in the samples of western hognose snakes. Also the probability of catching a snake in its first spring was lower than the probability for older snakes. After hatching in the autumn, the population on the Graber Pasture study area was probably at least 200 snakes, and in the spring the trappable population was approximately 120. The size of the Graber Pasture study area was approximately 50 acres. However the traps caught snakes from immediately adjacent

areas, so the mean trappable population density in the spring was approximately 1.5 snakes per acre. The actual population density was probably at least 2.5 snakes per acre at certain times.

The mean estimate of the size of the population of eastern hognose snakes on the Graber Pasture study area was 43, approximately one-third as large as the population of the western species (Table 41). Most of the estimates are for the spring and early summer months. Although hatchlings were caught in the autumn, the recaptures were inadequate for population estimates, so the degree of population increase at that time is not known.

Estimates of the size of populations of hognose snakes on the Harvey County Park study area (Table 42) are based on fewer records. Populations

TABLE 42. Estimates of the Size of the Populations of Hognose Snakes on the Harvey County Park Study Area in Kansas.

Western Hognose		Eastern Hognose	
Date	Estimated population size	Date	Estimated population size
July 2, 1960.....	50 \pm 51	September 19, 1959....	15 \pm 18
August 2, 1960.....	51 \pm 50	July 5, 1960.....	5 \pm 6
June 20, 1961.....	83 \pm 70	Mean Size.....	10
July 3, 1962.....	57 \pm 29		
August 28, 1962.....	42 \pm 30		
Mean Size.....	57		

of both species were smaller (mean estimate of 57 western and 10 eastern hognose snakes). The Harvey County Park study area of unpastured land contained approximately 50 acres, but since adjacent areas on three sides were pastured, the population density was not uniform over the area from which the traps sampled.

Sex Composition

Heterodon nasicus. The primary sex ratio of the western hognose is probably one male to one female (see p. 347). The populations on the study areas contained approximately equal numbers of males and females, and the two sexes were equally active. On the Graber Pasture study area, 77 males and 84 females were captured, and in Harvey County Park 46 males and 34 females were captured. The sex ratio in museum collections is similar (131 males and 115 females; Edgren, 1952a:64-65).

Female western hognose snakes may have been lost from the populations either by emigration or death at a slightly higher rate than males, but the differences are not significant. Of 75 male western hognose snakes marked from 1959 to 1961, 21 per cent were recaptured after a period of at least one month. Of 80 females marked in this same period, 14 per cent were re-

captured. A contingency test indicated that this difference is not significant (chi-square is 1.6). The mean periods between first and last captures for all recaptures were 272.7 days for males and 188.6 days for females. The difference is not statistically significant (t is 1.2).

Heterodon platyrhinos. The primary sex ratio of eastern hognose snakes is probably one-to-one, although the few litters studied had a slight preponderance of females (see p. 345). The sex ratio in the samples captured on the study areas in Harvey County was more than two males for every female (87 males and 38 females). This is significantly different from an equal sex ratio at the one per cent level (chi-square is 19.2). The sex ratio was even more unbalanced in the sample of hatchlings trapped on the study areas (24 males and 9 females). Samples in some museum collections do not have this unbalanced sex ratio (221 males and 220 females; 37 males and 52 females; Klau and David, 1952:364, 368). The unbalanced sex ratio in the sample from Harvey County was probably due, in large part, to greater activity by males than by females.

Percentages of recapture were similar for male and female eastern hognose snakes. Of 63 males (nine months or older) marked and released on the study areas, 13 per cent were recaptured after periods of more than one month. Of 29 females, 10 per cent were recaptured. If there were equal numbers of the two sexes, the probability of catching females was approximately one-half that of catching males and a lower percentage of recaptures of females would have been expected. Also if females were in smaller numbers due to lower survival rates as adults, a lower percentage of recaptures would have been expected. However, similar rates of recapture in the two sexes can be explained, without assuming an unbalanced sex ratio for juveniles, by assuming that migration of males from and to the study areas was greater or that males have larger home ranges. The first explanation is consistent with the difference in the mean period between first and last capture for recaptured male and female eastern hognose snakes (194.8 days for males and 261.3 days for females), although this difference is not statistically significant.

Age Composition and Population Dynamics

Table 43 lists the percentages of western hognose snakes of various probable ages in a sample from the population on the Graber Pasture study area. The age groups are based on size of the snake (Table 33). There were no hatchling snakes in this sample, and the number of first-year snakes was obviously low. Immature western hognose snakes have a lower probability of capture. The proportions in various age groups of mature snakes captured were probably similar to their proportions in the population. The older age class represents years five through eight.

Table 44A lists the percentages of western hognose snakes in the various age groups that were recaptured in the first, second, or third years after marking, or later. The percentage of recapture is affected both by mortality and emigration. Survival in the population was relatively low for immature snakes. Tables 43 and 44A both provide evidence of high survival rates for young mature snakes and survival of a relatively large proportion to old age. However, comparison of the two tables suggests that emigration and immigration may have had an important effect on percentages of recapture, especially for young mature snakes.

TABLE 43. Age Distribution in Samples of 133 Western Hognose Snakes and 53 Eastern Hognose Snakes Trapped in 1960, 1961, and 1963, on the Graber Pasture Study Area in Harvey County, Kansas.

Western Hognose Percentages			Eastern Hognose Percentages			
Age group	Total sample	Mature snakes (N=117)	Total sample	Mature snakes (N=16)	Autumn sample (N=23)	Spring sample (N=30)
Hatchlings.....	0	28	65
First-year.....	12	41	18	60
Second-year.....	30	33	19	63	4	30
Third-year.....	26	30	6	19	9	3
Fourth-year.....	12	14	2	6	4	0
Older.....	20	23	4	12	0	7

Table 45 lists the size distribution of female western hognose snakes in a sample trapped on the Graber Pasture study area in 1960, 1961, and 1963. Assuming an equal sex ratio and a total trappable population of 120 snakes on the study area in the spring, the female population was 60. Fecundity can be estimated from mean clutch size and per cent of females breeding at various sizes. Total production of 188 eggs is a minimum estimate, since it is based on biennial reproduction by mature females, and some females may have reproduced more often. There were an estimated 36 second-year snakes in the population in the spring (30 per cent of 120). The product of the percentage of eggs hatching and the percentage survival to 21 months would therefore be approximately 19 per cent.

The age distribution in a sample of eastern hognose snakes from the Graber Pasture study area is listed in Table 43. Sixty-nine per cent of the individuals in this sample were immature (hatchling and first-year snakes). This proportion varied from 60 per cent in the spring to 83 per cent in the autumn. Approximately 50 per cent of the first-year snakes survived to become mature. Most snakes died before they were two years old. Other studies have indicated high mortality of hatchlings (Klau and David, 1952:371).

Table 44B lists percentages of recaptures for eastern hognose snakes of different ages. No snakes in this sample were recaptured after the season following their initial capture. These data also indicate low survival of eastern hognose snakes.

An estimate of the fecundity of the eastern hognose population can only be approximate because of the small amount of data available. The estimate of fecundity in Table 45 is based on a population estimate of 40 snakes, an equal sex ratio, the proportion of females of different sizes in a sample from the Graber Pasture study area, an annual ovulatory cycle, and mean clutch sizes

TABLE 44. Recapture Percentages in Samples of Western and Eastern Hognose Snakes Marked and Released on the Graber Pasture Study Area in Harvey County, Kansas, in 1960 and 1961.

A. WESTERN HOGNOSE SNAKES				
Age group (year c)	Number marked (year c)	Percentage recaptured (year c+1 or after)	Percentage recaptured (year c+2 or after)	Percentage recaptured (year c+3 or after)
Hatchlings	7	0	0	0
First-year	14	7%	0	0
Second-year	31	19%	6%	3%
Third-year	25	20%	8%	0
Older	22	14%	5%	0

B. EASTERN HOGNOSE SNAKES			
Age group (year c)	Number marked (year c)	Percentage recaptured after more than one month	Percentage recaptured (year c+1)
Hatchlings	14	7%	7%
First-year	18	11%	6%
Second-year	4	0	0
Third-year	2	0	0
Fourth-year	0	0	0
Older	1	0	0

equal to those calculated from records from various parts of the species range. The first-year and second-year classes in the spring had an estimated 24 and 12 snakes respectively (60 per cent and 30 per cent of 40). The product of the percentage of hatching and the percentage of survival to nine months was approximately 15 per cent and the product of percentage of hatching and percentage of survival to 21 months was seven per cent.

Survivorship curves for the two species can be approximated by smoothing out the age distributions, utilizing evidence from recapture data (Fig. 26). There is little evidence on which to base an estimate of the survival of immature snakes. The survival rate of immature western hognose snakes is based on an estimated production of 188 eggs by a trappable population of 120 snakes and

TABLE 45. Size Distribution and Fecundity of Females in Populations of 120 Western Hognose Snakes and 40 Eastern Hognose Snakes on the Graber Pasture Study Area in Harvey County, Kansas.

Snout-vent length in mm.	Percentage of sample	Estimated numbers of females in population	Estimated numbers of females reproducing	Mean clutch size	Total eggs
WESTERN HOGNOSE SNAKES					
Less than 360..	21	13	0
360 to 399.....	19	11	3	5.1	15.3
400 to 439.....	13	8	4	5.1	20.4
440 to 489.....	26	15	8	6.8	54.4
490 or more....	21	13	7	14.0	98.0
Total.....	100	60	19	188.1
EASTERN HOGNOSE SNAKES					
Less than 560..	61	12	0
560 to 609.....	23	5	5	17.1	85.5
610 to 724.....	12	2	2	22.2	44.4
725 or more....	4	1	1	37.9	37.9
Total.....	100	20	8	167.8

40 per cent hatching success. The survivorship curve for hatchling eastern hognose snakes is based on an estimated production of 168 eggs, 40 per cent hatching success, and the assumption that the proportion of hatchlings caught in the autumn was similar to the proportion in the total population.

The estimates in this analysis of population size and dynamics in hognose snakes are only indicators of general magnitude because the standard errors are large and there are many unknown factors. However, differences in the population dynamics of eastern and western hognose snakes in Harvey County are obvious and consistent. Fecundity of individuals of the western species is relatively low, but survival after maturity is high. The rate of turnover of the breeding population is relatively low. Fecundity of individual eastern hognose snakes is higher, but survival after maturity is relatively low, and population turnover is more rapid. Because of the higher fecundity of individuals of the eastern species, estimates of the total production of eggs by the two species are nearly equal even though the population of the western species is three times as large and contains a larger percentage of mature snakes. Second-year snakes contribute most to the production of eggs by eastern hognose populations, whereas in the western species, older snakes are more important.

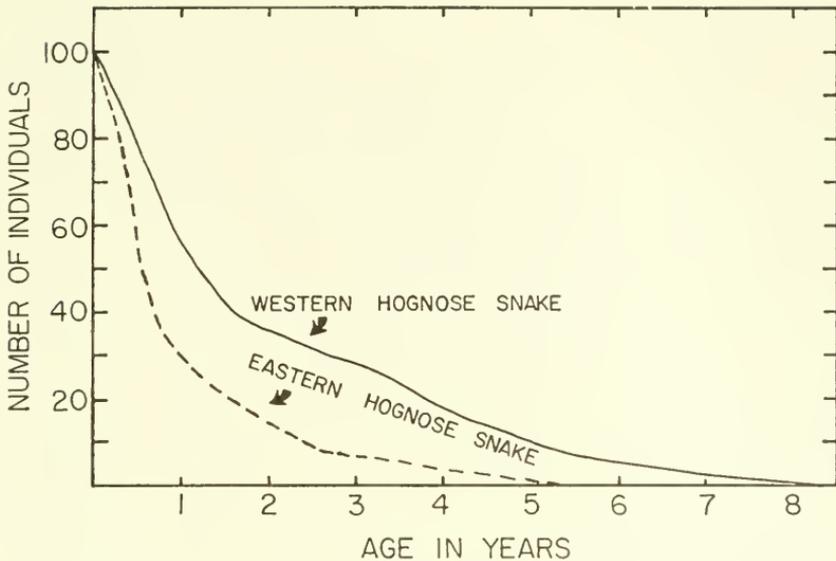


FIG. 26. Estimated numbers of individuals surviving at successive ages from a group of 100 hatchlings of eastern hognose snakes and a group of 100 hatchlings of western hognose snakes on the Graber Pasture study area in Harvey County, Kansas.

RELATION TO MAN

Some investigators, particularly in the southeastern United States, have reported that large populations of eastern hognose snakes survive in close association with man. Published statements include:

"found frequently in this area in gardens and cultivated fields" (Llewellyn, 1940:150, in West Virginia); "ruderal situations; frequently seen in green-houses and ferneries" (Carr, 1940:79, in Florida); found in "dry, sandy lots in Augusta," Georgia (Neill, 1950:116); "Outbuildings and fields seem to be favorite haunts of this species" (Allen, 1932:13, in Mississippi); "usually found in plowed fields" (Funkhouser, 1945:24, in Kentucky); "found in gardens, golf courses, or open meadows" (Force, 1925:27, in Oklahoma).

Elsewhere, especially in the North, the numbers of eastern hognose snakes have declined since 1900. Logier (1939:21) presented evidence of decrease in numbers in some parts of Ontario. Creaser (1944:239) reported that the eastern hognose was rare in the Douglas Lake region of northern Michigan, although it had been fairly common 15 years earlier. Hudson (1954:71) stated that this species was rare in Montgomery and Bucks counties, Pennsylvania, except in "inaccessible or protected areas." Conant (1966:54) cited evidence of a decline in numbers on Kelleys Island, Ohio, and other islands in Lake Erie. Some authors have suggested that reduction in numbers in certain localities has been caused by persecution by man (Schmidt and Necker, 1935:68; Conant and Bridges, 1939:40). This species seems to be more sensitive to human disturbance near the limits of its range.

There are no published reports on changes in populations of western hognose snakes after settlement by white men. It is possible that some local colonies in eastern Kansas have been exterminated by human disturbance (see p. 289).

Both species were more abundant on the highly-disturbed Graber Pasture study area than on the undisturbed Harvey County Park. Human disturbance that opens up dense vegetative cover may increase favorable habitat for hognose snakes in some regions, although intensive cultivation is detrimental.

Many authors have stated that, even though the eastern hognose is harmless, there is widespread popular belief in the poisonous nature of its bite or even its breath (Evermann and Clark, 1915:346; Logier, 1939:22; Conant, 1951:44; and others). This belief is still common today, although many persons that recognize hognose snakes know that they are harmless. Løennberg (1894:328) was told of "two or three cases in which spreading adders [eastern hognose snakes] are said to have bitten. . . . In one of these cases it was said that the hand of the bitten man swelled up considerably." Schneck (1878:585-587) pointed out the circumstantial nature of most reports of poisoning by this species and stated that its bite had no adverse effects on a cat, a chicken, and a man. Hay (1892b:104) stated, "A number of scientific men have reported that they have allowed themselves to be bitten by this snake and have received no harm." Blatchley (1891:33) stated of the eastern hognose, "by experience I know that its bite is no more painful than that of a mouse." Anderson (1965:181-182) caused an eastern hognose to bite his thumb while the snake was attempting to feed on a toad. He also rubbed saliva from the snake in an open wound on the dorsal surface of his hand. No toxic symptoms developed.

Bragg (1960:121-123) was bitten by a hungry western hognose that attempted to ingest his thumb after he had been handling frogs. The dorsal surface of his hand, wrist, and distal forearm swelled and was painful for several days, although the swelling did not involve the site of the wound. Western hognose snakes handled in my study never attempted to bite. However, I twice cut my finger on one of the enlarged posterior teeth sufficiently to cause bleeding, but no toxic symptoms developed.

Investigations have shown that a number of relatively harmless snakes, including hognose snakes, have mildly venomous toxins for small vertebrates (McAlister, 1963:132-133). There is no evidence that the saliva of the eastern hognose is toxic to man. Although the western hognose may be slightly venomous to man, the reaction reported by Bragg could have been an individual sensitivity to a component in the saliva. Neither snake is dangerous to man, since hognose snakes usually cannot be induced to bite unless the feeding reaction is stimulated by the odor of prey.

ECOLOGICAL COMPARISONS

Both eastern and western hognose snakes are slow-moving and diurnal and are found most commonly in relatively open disturbed habitats. They are specialized for burrowing and for eating relatively large prey. Although many aspects of their morphology and behavior are similar, there are important differences in the ecology of the two species.

The habitat requirements of the two species are similar in many respects; and in some areas they are sympatric and are found in identical habitats. However, optimum habitat for the eastern species is sandy, open woods or forest edge, and optimum habitat for the western species is sandy, short grassland. The eastern hognose prefers more moist sites in some parts of its range. The western species is a more specialized burrower in having relatively shorter

body, tail, and head; skull more modified for support of the rostral region; and more modified rostral projection. This species may be more dependent on burrowing for shelter and obtaining prey. The eastern hognose has a more specialized diet. Amphibians, primarily toads, comprise more than 90 per cent of its food in most localities. Although the diet of the western species includes large numbers of amphibians (35 to 50 per cent of the diet), it also includes appreciable quantities of reptiles, eggs of reptiles, and mammals.

There are important ecological differences between the two species in individual growth and population dynamics. These differences probably affect energy requirements and other aspects of the ecology of the two species. The eastern hognose is larger and has a more rapid rate of growth. In Harvey County individuals of the eastern species grow almost twice as fast as those of the western species in the first year.

The fecundity of female eastern hognose snakes is higher than that of females of the western species. Most individuals of both species first reproduce when they are 21 months old, but a larger percentage of female western hognose snakes may not mature until they are more than two years old. The larger size of clutches of eggs laid by the eastern species is related, in part, to the larger size of this species. However, a female of the eastern species lays a clutch of eggs that is heavier on the average than a clutch laid by a western hognose of similar size. In Harvey County a smaller percentage of mature females of the western species than of the eastern species breed each year.

In Harvey County mortality of eastern hognose snakes is greater than that of the western hognose at all ages. Mortality of adults may not be as great in some other parts of the range of the eastern species, for the largest snakes caught in Harvey County were only three-fourths of the maximum length attained elsewhere. The factors responsible for mortality in hognose snakes are inadequately known, but factors causing greater mortality of the eastern species probably include: 1) greater susceptibility to predation and greater likelihood of being killed by man or ungulates, because it is larger, more conspicuous, more active, and less secretive; and 2) greater sensitivity to food shortage because it has greater nutritional requirements, especially during the early periods of rapid growth. The more highly developed defensive behavior of eastern hognose snakes may be related to the first factor.

Individuals and populations of eastern hognose snakes probably have higher nutritional requirements than those of the western species, as indicated by their more rapid growth, larger size, greater activity, higher fecundity, and more rapid population turnover. Some of the differences in seasonal behavior and movements of the two species may be related to nutritional requirements. The eastern hognose has a longer season of activity, with definite peaks of activity in both spring and fall. The western hognose has a pronounced peak of activity in the spring, but after late summer is relatively inactive. The earlier oviposition of the eastern hognose allows a post-hatching period of growth before hibernation that is at least a week longer than that for hatchlings of the western species. The eastern hognose is apparently more sensitive to shortened summer seasons in the north. Records of movement of recaptured snakes indicate that eastern hognose snakes travel over larger areas in obtaining food and other necessities.

Large numbers of hatchling eastern hognose snakes, but few hatchlings of

the western species, were trapped in the autumn in Harvey County. The significance of this difference is not known. It may be related to lower fecundity of the western species or more probably to less activity, smaller size, or other differences in behavior of hatchlings of this species.

The fossil record indicates that the *pre-platyrrhinus* line and the *pre-nasicus* line have been separated as eastern and western forms at least since the Middle Pliocene and probably much earlier. In this long period of separate evolution, morphological modification has been minor and is related to more important ecological differences. The center of evolution of the western species was in the xeric grasslands that have periods of extended drought. Its adaptations reflect this adverse environment. Amphibians were probably an important food of ancestral hognose snakes. However, amphibians were not plentiful in the more xeric grasslands, and terrestrial amphibians had short periods of activity. Since there were other burrowing animals and their eggs that could be utilized as food, evolution of more generalized food habits by the western hognose was adaptive. The climatic pattern of late summer drought and high temperatures was probably important in the evolution of a relatively short season of activity. The *nasicus* line evolved the adaptive pattern of slower and more variable growth, more effective burrowing adaptations, lower fecundity, and greater survival. If biennial breeding is common in populations of the western species, this, together with a tendency toward later sexual maturity, may be the most important adaptation for lowered fecundity and lower nutritional requirements for reproduction. The smaller western hognose was less subject to predation than its larger ancestor. The defensive behavior of the ancestral hognose snake (probably similar to that of modern *H. platyrrhinus*) was less effective in its smaller descendant, *H. nasicus*, and became modified and somewhat degenerate.

The eastern hognose evolved in more mesic habitats in deciduous forest, and developed or retained a specialized preference for toads and frogs as food. Amphibians were relatively abundant for long seasons and fewer burrowing animals were available in the deciduous forest. Studies of the diet of the eastern species in certain localities show that it can utilize alternative food resources when necessary. The adaptive pattern of fast growth and large size with greater nutritional requirements was developed or retained, for there was abundant food in the form of large populations of amphibians in its optimum habitat. A large conspicuous slow-moving snake is subject to high mortality. Therefore, the highly specialized defensive behavior and high fecundity that also increased nutritional requirements were important adaptations.

The eastern hognose is not commonly found on the short grass steppe on fine-textured soils. Some of the reasons may be: 1) Greater mortality from predators and ungulates; 2) insufficient amphibians available to supply needs; 3) inability to burrow effectively in dry compact soils. In the grasslands eastern hognose snakes are common only in sandy situations where they can effectively burrow, or on more mesic sites where amphibians are abundant. Even in such areas, at least in Harvey County, mortality of large snakes is high.

The factors that prevent expansion of the range of the western species into the forest are not clearly evident, but may be associated with the denser vegetation of both the forest and tall grassland. Competition with the eastern species is probably not important. Both species are uncommon in the tall grasslands and are sympatric on suitable sites.

Sympatric populations of eastern and western hognose snakes are found on the southern and central grasslands, primarily on sandy soils and on the sites of relict colonies of western species. The *nasicus* line and *H. platyrhinos* have been sympatric in Kansas since the upper Pliocene. Studies of closely related sympatric species have been popular with ecologists in attempts to "prove" or "disprove" the Volterra-Gause or competitive exclusion principle. This principle that no two species that occupy similar ecological niches and effectively compete can coexist sympatrically has been the subject of much controversy (Hardin, 1960:1292-1297; Cole, 1960:348-349; Patten, 1961:1599-1601; and others). It has become obvious that, until more information is available on the dynamics of interaction of sympatric species, discussion concerning the importance of the competitive exclusion principle is futile.

Andrewartha (1961:174) defined competition as utilization of common resources that are in short supply. Two sympatric species that utilize a common resource will compete if the resource is in short supply relative to the needs of both species or if the population of either species can grow to utilize the entire resource, but they will not compete if other factors limit population growth so that each species only utilizes a fraction of the resource.

Overlap in some aspects of the ecological niche does not involve potential competition. For example, predation, although it may be related to a limited resource such as shelter, is not in itself a limited resource for the prey population. Two sympatric species that have common predators may interact in a variety of ways. The results of such interactions will depend on many factors, including the degree of specialization of the predators and the reproductive potential of the two prey species.

Sympatric populations of eastern and western hognose snakes in Harvey County have substantial overlap in ecological niches with respect to habitat, shelter, diet, diel rhythms, and seasonal activity. There is no evidence of character displacement caused by competitive interaction in the area of sympatry, with the possible exception of increased differences in the size of hatchlings (see p. 398). Habitat requirements of the two species in Harvey County are similar. In the western or eastern parts of the sympatric range, one species may be more restricted in habitat than the other, but this restriction is caused primarily by environmental adversity rather than biotic competition between the two species. Shelter requirements are also similar, but sites for burrowing are effectively unlimited, and both species can easily burrow in the sand of the study areas. In habitats where burrowing is more difficult and the snakes depend on holes and crevices already present, potential competition might exist.

The food habits of both species in Harvey County are similar to food habits in other parts of their ranges. Their diets are similar in the large component of amphibians, and in Harvey County both species eat more amphibians than in some other localities. This is due to the abundance of amphibians, especially leopard frogs, on the study areas. Both species seek food at the same time of day. Although their seasons of activity are not identical, both concentrate feeding activity in late spring and summer when frogs are most active. However, predation by hognose snakes did not materially affect the large populations of leopard frogs on the study areas during wet seasons. Competition for food probably does not occur, except possibly during drought.

Mortality of hatchlings is high, especially for the eastern hognose. Part of this mortality may be caused by lack of food, since hatchlings have narrower

food requirements especially with regard to size of prey, frogs and toads are less available in autumn, and hatchlings are less experienced in capturing prey. Potential competition between hatchlings of the two species is greater than between adults, because hatchlings are numerous, more similar in size, and appear in the population at approximately the same time. Vertebrates small enough to be utilized as food are limited in availability. Hatchling eastern hognose snakes are larger and more active than hatchlings of the western species. These and other differences may reduce competition, but more information is needed concerning the biology of hatchlings of the two species before a reliable evaluation can be made. The mean length of hatchling eastern hognose snakes in Harvey County was more than 20 per cent greater than the mean length of hatchlings reported from other localities. This difference may be the result of differences in the technique of measuring. If the difference in size is real, it may be an adaptive modification increasing differences in the size of hatchlings to reduce competition of the two species in the area of sympatry.

The importance of various factors causing mortality of adult hognose snakes is little known. However, the differences in population dynamics indicate that these factors are not equally effective for the two species. No predators specialize in preying on hognose snakes. Differences in ecological niche with respect to predation probably result from differences in body size. The differences in defensive behavior are also indicative of differences in some mortality factors.

Differences in ecology of the two species probably would be reflected in different degrees of adaptability to climatic cycles in Harvey County. The size of the population of eastern hognose snakes may be more variable. Because of its more specialized diet, higher nutritional needs, and more rapid turnover, the population of the eastern species would be affected more by drought, with its consequent decrease in numbers of frogs on areas lacking permanent water. When frogs again become abundant and widely distributed in a wet season, high reproductive potential would allow the population of eastern hognose snakes to grow more rapidly in response. Since there was no drought in the period of study, the above prediction could not be tested.

SUMMARY

Populations of eastern hognose snakes (*Heterodon platyrhinos*) and western hognose snakes (*H. nasicus*) on a heavily-grazed pasture and on an ungrazed wildlife refuge in sand prairie in western Harvey County, Kansas, were studied from 1959 to 1963. Snakes were caught in wire funnel traps and marked for individual recognition by clipping subcaudal scales. In the five seasons 241 western hognose snakes were captured 314 times, and 124 eastern hognose snakes were captured 144 times. Supplementary studies were made on 55 hognose snakes that were collected outside the study areas, killed, and preserved, and on snakes that were kept in cages and in an outdoor pen. The scattered literature and unpublished information concerning the ecology of the two species in other geographic areas were reviewed and, combined with my field data,

served for comparative accounts of the ecology and life history of both species.

The genus *Heterodon* with three existing species is a member of the family Colubridae, most closely related to the South American genera *Lystrophis* and *Xenodon*. Hognose snakes differ from most other colubrids in having a short broad head, a short stout body, a ridged projection on the rostral region of the head that involves modifications of the premaxillary bone and the rostral scale, azygous scales, a complete ring of ocular scales, diacranterian dentition on extremely loose and mobile maxillae, and enlarged adrenal glands. Most of these characteristics are adaptive for burrowing, for capturing and swallowing large prey, or for bufophagy. Hognose snakes have myological and osteological characteristics that are primitive for colubrid snakes and that suggest relationship to viperids.

Heterodon platyrhinos is a monotypic but variable species. Three subspecies of *H. nasicus* (*H. n. nasicus*, *H. n. kennerlyi*, and *H. n. gloydi*) are currently recognized, but the validity of *H. n. gloydi* is questionable. The population in Harvey County is intermediate between *nasicus* and *gloydi*.

Sexual dimorphism in hognose snakes is evident in bodily proportions that are associated with a more posterior placement of the vent and umbilicus in females—namely a larger number of ventrals, fewer subcaudals, more middorsal blotches on the body, and a shorter tail. Female eastern hognose snakes in Harvey County have more somites than males. Positive allometric growth of the tail is evident in young male hognose snakes, but in females the growth of the tail is proportional to that of the body. The mean total lengths of males in my samples from populations in Harvey County were approximately 90 percent of the mean lengths of females.

There are differences in coloration between the eastern and western hognose snakes, and also morphological differences as follows: (1) the eastern hognose is longer (maximum total length 1155 mm.) than the western species (maximum total length 895 mm.); (2) a western hognose is heavier than an eastern hognose of the same length; (3) the eastern species has more caudal somites and a longer tail; (4) the western species has a shorter head; (5) the western species has a rostral projection that is more concave dorsally and that has a thinner free edge; and (6) the western species has a shorter maxilla and fewer teeth. Most of these morphological differences indicate a greater degree of specialization for burrowing in the western hognose.

Both species burrow by thrusting movements of the head, causing the free edge of the rostral projection to loosen sand or soil. The western hognose prefers fine sand to loam or coarse sand as a substrate in which to burrow. Burrowing is used to obtain food and to excavate temporary shallow burrows for shelter, deeper shelter burrows, nests, and hibernacula. Hognose snakes burrow in response to the scent of prey and to cold temperatures.

Both species are diurnal or crepuscular. Cloacal temperatures of active hognose snakes are relatively high. The normal activity range for the western hognose in Harvey County was 21.4°C to 36.2°C (mode was 31°C to 33°C) and for the eastern species was 22°C to 34°C. The critical maximum temperature for the western hognose was above 40°C and the critical minimum temperature for both species was approximately 7°C.

The average dates of entering and leaving winter dormancy in Harvey County in the period of study were October 20 and May 2 for the eastern species and October 18 and May 9 for the western species. Soil temperature was an important factor affecting the length of the period of dormancy. The largest numbers of eastern hognose snakes were caught in mid-May and mid-October, and few were caught in early September. Seasonal differences in success of trapping were related primarily to marked seasonal changes in the size of the population of first-year snakes and hatchlings and to inherent seasonal rhythms in activity. The greatest activity of western hognose snakes occurred in the period from May to early August. Dormancy and moulting occurred in late August, and there was little resurgence of activity in autumn. Western hognose snakes were most active in sunny periods of rising temperatures. The differences in seasonal activity between the two species were related to differences in inherent rhythms and to the relatively few captures of hatchling and first-year western hognose snakes. Females of the eastern species were less active than males, but male and female western hognose snakes had equal total activity in a season. Males of both species were active earlier in the spring when they were searching for females during the breeding season. The mean distance of movement of recaptured western hognose snakes was less than one-half that of individuals of the eastern species. Both species made shorter movements on the pasture than on the ungrazed grassland.

Growth of western hognose snakes is slow and variable. Eastern hognose snakes grow more rapidly at all ages. In Harvey County hatchlings of the eastern species were larger (mean total length

234 mm.) than hatchlings of the western species (mean total length 177 mm.) and had a growth rate $1\frac{1}{2}$ to two times as rapid. At an age of 21 months males of both species were usually sexually mature, and male eastern hognose snakes had a mean snout-vent length of 488 mm., whereas males of the western species had a mean of 309 mm. Females of both species grow faster than males. Most females of the eastern species were sexually mature at an age of 21 months when they averaged 560 mm. in snout-vent length. Some female western hognose snakes that grew rapidly became sexually mature at 21 months and at a snout-vent length between 350 and 400 mm., but many did not mature until they were 33 months old.

Males of both species have a postnuptial spermatogenesis, and spermatozoa are stored in the ductus deferens during hibernation. The principal mating season was in April and May for the eastern hognose in Harvey County and May 13 to 29 for the western species. Some mating also occurred in autumn. The egg-laying season in Harvey County for the eastern species was in the last half of June and early July (egg-laying dates from May 27 to August in its total range), whereas oviposition by the western hognose occurred from July 2 to July 23 (June 3 to August in its total range). Fifty-nine clutches laid by eastern hognose snakes from various geographic areas had a mean size of 22.3 (4 to 61) eggs, and 31 clutches from the western species had a mean size of 9.4 (4 to 23) eggs. Averages for clutches from Harvey County were 13.0 and 7.5 eggs respectively. Larger snakes laid larger clutches of eggs. There was no evident geographic variation in the size of clutches. The eggs of the eastern hognose were larger and clutches of eggs laid by eastern hognose snakes weighed more relative to the weight of the female.

Eggs of both species are laid in nests a few inches below the surface of the ground. Although most female eastern hognose snakes probably lay a clutch of eggs each season, typical females of the western species ovulate every other year in Harvey County. The natural incubation period for both species is 50 to 60 days, and hatching of eastern hognose snakes occurred from early August to early September and of the western hognose in August and September in Harvey County. Primary and secondary sex ratios for populations of both species were not significantly different from one-to-one.

Amphibians, primarily toads, constitute more than 90 percent of the diet of the eastern species over its total range. Leopard frogs, because of their abundance, were the main food of the eastern hognose on the study areas in Harvey County. The diet of the

western hognose included large numbers of amphibians, but it also included appreciable numbers of reptiles, eggs of reptiles, and mammals. Small western hognose snakes ate larger percentages of prairie lizards and eggs of lizards than did the larger snakes. However, the smaller snakes did not eat birds or other snakes, both of which were among the items of food recorded for large snakes. The enlarged ungrooved posterior teeth of hognose snakes function primarily in the manipulation of large prey and the deflation of toads. Salivary secretions introduced into the wounds made by the teeth have a slight toxicity for certain prey but do not kill captured animals before they are swallowed.

The mean population density of the western hognose on the study area in the pasture was 1.5 snakes per acre, and at times the population probably increased to at least 2.5 snakes per acre. The population of the eastern species was approximately one-third as large and is probably more variable. On the ungrazed study area population densities of both species were less than half those on the pasture.

Studies of reproduction and age structure of the populations in Harvey County indicated that fecundity of western hognose snakes was relatively low, but survival of individuals after maturity was relatively high. In an estimated population of 120 on the pasture, the fecund females produce a minimum of 188 eggs in a season, and from these approximately 36 young snakes survive until their second spring. Fecundity of eastern hognose snakes was higher, but mortality was also greater at all ages. In an estimated population of 40 on the pasture, the mature females produced an estimated 168 eggs, and from these approximately 12 snakes survived until their second spring. The maximum age of snakes in natural populations in Harvey County was approximately five years for the eastern species and eight years for the western species.

Hognose snakes are slow-moving and occur in open habitats where they are relatively easily captured by predators and are subject to mortality from grazing animals and man. Starvation may eliminate some, especially hatchlings and juveniles. No predators specialize in feeding on hognose snakes. No records of predation were obtained on the study areas, but predators there that may feed on hognose snakes, at least occasionally, include blue racers, king snakes, red-tailed hawks, Swainson's hawks, crows, coyotes, raccoons, striped skunks, opossums, badgers, shrews, moles, ornate box turtles and bullfrogs. A large number of parasites, notably eight species of flukes of the genera *Renifer* and *Neorenifer* and

certain parasitic nematodes, have been reported parasitizing the eastern hognose. A large proportion of the adult snakes on the study areas were parasitized by *Neoreniker validus* and *Physaloptera* sp. Western hognose snakes were less commonly infected with *Neoreniker validus*, *Reniker kansensis*, and *Physaloptera* sp. There was no evidence that parasitic disease was an important cause of death for either species.

Complex but stereotyped responses occur in defense against predators and man. This behavior includes an attempted escape phase, a threatening phase, and a letisimulation phase. The threatening phase in the eastern species involves flattening and widening the neck and head, hissing, and making pseudo-strikes. The behavior is not so well-developed in the western species, which usually attempts to conceal its head rather than spread its neck. This stereotyped defensive behavior is probably adaptive in discouraging or postponing the actual killing of a snake by some predators or non-predatory animals. The differences in behavior between the two species are associated with differences in size, susceptibility to predation, and possibly habitat.

The eastern hognose is typical of open deciduous forest, pine forest, or forest edge, and is especially abundant in disturbed or sandy habitats near water, where amphibians are abundant. The eastern hognose has invaded the grasslands along river valleys and occurs in numbers in sandy or savanna habitats. The western hognose is typical of the short grass and mixed grass prairie, being particularly abundant in sandy or disturbed habitats. The continuous geographic range is limited on the east by the tall grass prairie and forest, although isolated colonies in Minnesota, Iowa, Illinois, and Missouri are relicts of a more eastern distribution during the Xerothermic period. The ranges of both species are probably limited on the north by requirements for high summer temperatures and for certain minimum lengths of the summer season. The western species extends into areas with colder temperatures and shorter summer seasons. The study areas in Harvey County were at the eastern edge of the continuous range of the western species and in a peripheral part of the range of the eastern species.

The fossil record indicates that the pre-*platyrhinos* line and the pre-*nasicus* line have been separately evolving at least since the Middle Pliocene. The western hognose evolved in xeric grasslands that have periods of extended summer drought. Adaptations oc-

curing in this evolutionary line included the evolution of more generalized food habits, more effective burrowing, a shorter season of activity, and lower nutritional requirements due to slower growth, lower fecundity, and slower population turnover. The defensive behavior of the relatively large ancestral hognose snake was less effective for its smaller descendant, *H. nasicus*, and became modified and somewhat degenerate.

The eastern hognose evolving in a more mesic habitat of the deciduous forest developed or retained a larger size and a more specialized diet with preference for toads and frogs. The longer season of activity, with greater nutritional requirements for more rapid growth and for high fecundity, is adaptive in utilizing the resources available in optimum habitat with large populations of amphibians. Such a large conspicuous slow-moving snake is subject to relatively high mortality, hence important compensatory adaptations of high fecundity and defensive behavior with an accentuated threatening phase have developed.

Sympatric populations of eastern and western hognose snakes in Harvey County have substantial overlap in ecological niches with respect to habitat, diel rhythm, shelter, seasonal activity, and diet. Differences in size, defensive behavior, population dynamics, and perhaps in behavior of hatchlings probably indicate important differences in the factors that limit the populations of the two species.

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PLATE 1



FIG. 1. The Tall Grassland community in the Harvey County Park study area, June, 1963. The large grove of trees in the distance is along the Little Arkansas River in the recreation area of the park.



FIG. 2. The Weedy Lovegrass community in the Harvey County Park study area, June, 1963. The grove of trees in the background is along the east boundary of the study area.

PLATE 2

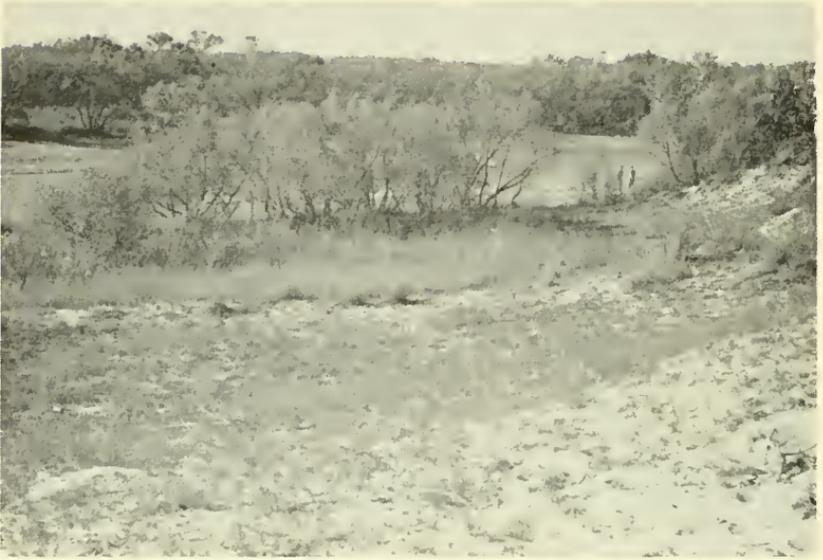


FIG. 1. Open sand and Weedy Upland Grass on the side of a ridge in the Graber Pasture study area. Lowland Grass, Willow Groves, and a small pond are in the distance. Photo was taken by Lloyd C. Hullbert.



FIG. 2. Lowland Grass community on the Graber Pasture study area, November, 1963.

PLATE 3

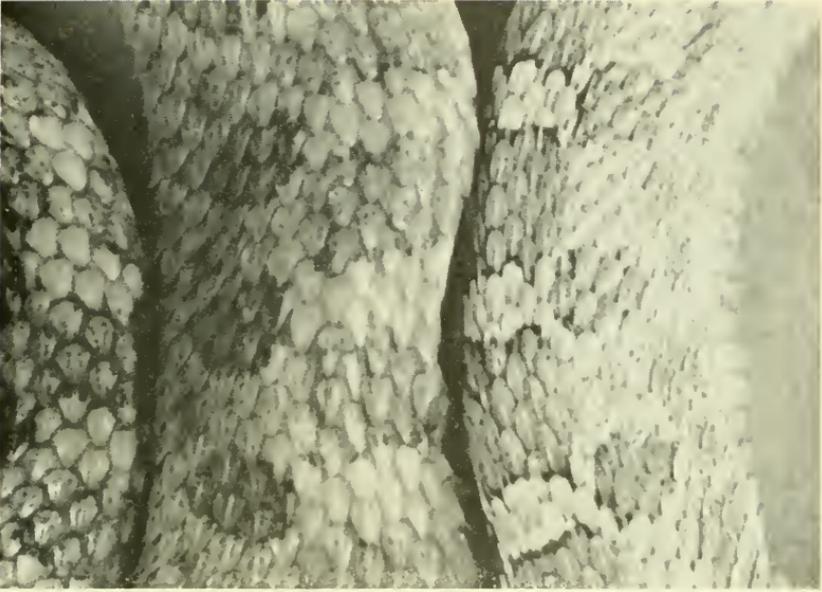
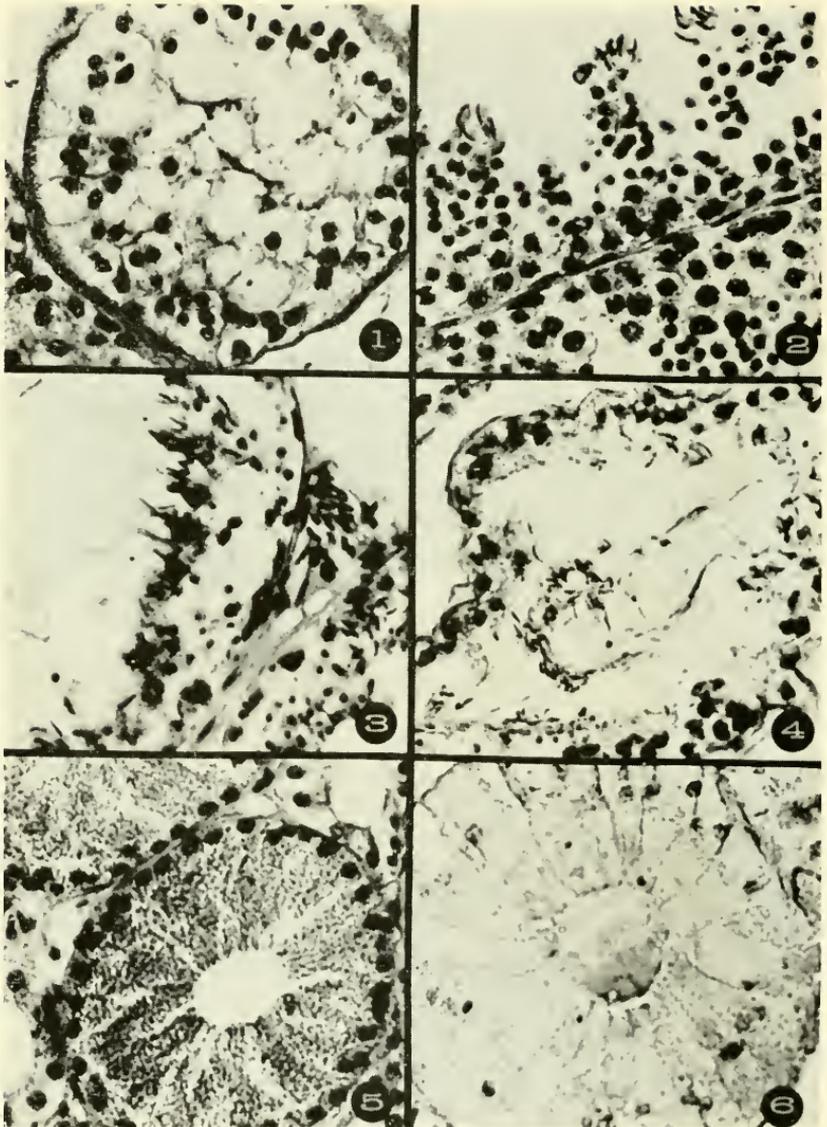


FIG. 1. Dorsal view of the bodies of two specimens of *Heterodon nasicus gloydi* from Texas (Texas Coop. Wildl. Mus. 335 on left and center from Colorado County and 3236 on right from Brazos County). The snake on the right has distinct dark borders on the dorsal blotches.



FIG. 2. A specimen of *Heterodon nasicus* from Harvey County, Kansas, on right (DRP 350) and a specimen of *H. n. gloydi* from Colorado County, Texas, on left (Texas Coop. Wildl. Mus. 184). There is an obvious difference in spacing of dorsal blotches but not in distinctness of blotches.

PLATE 4



Cross sections of the testes and kidneys of mature male western hognose snakes collected in Harvey County, Kansas. Figs. 1 to 4 are cross sections of seminiferous tubules of specimens killed on May 13, July 19, September 8, and October 20, respectively. Figs. 5 and 6 are cross sections of the pre-terminal or "sexual" segments of the renal tubules from specimens killed on May 13 and September 8, respectively. All figures are approximately $\times 375$.

PLATE 5



FIG. 1. Cage used to test the preference of hognose snakes for burrowing in different substrates, approximately $\times \frac{1}{4}$. Fine sand is on the right and coarse sand is on the left. The openings of two burrows can be seen.



FIG. 2. Track left by a small western hognose snake in loose sand at the edge of a road in western Harvey County, Kansas, on July 26, 1961, approximately $\times \frac{1}{3}$.

PLATE 6

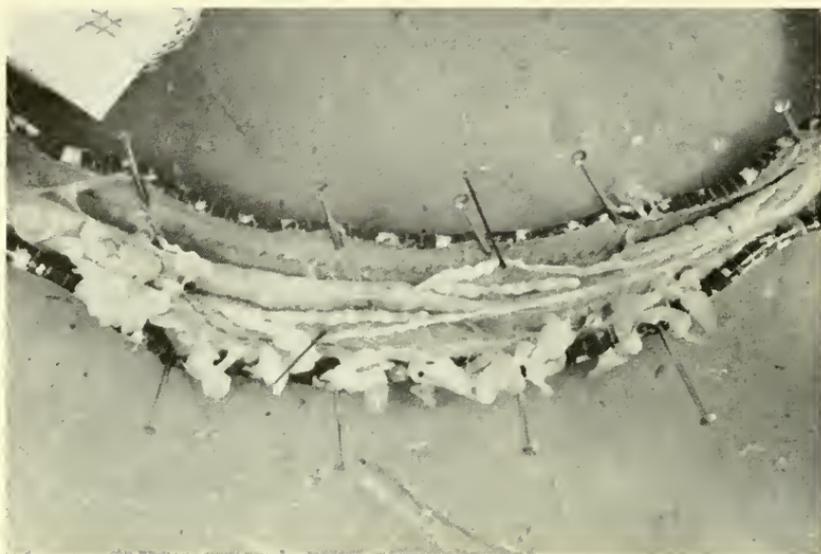


FIG. 1. Dissection of an immature female western hognose snake (DRP 350) from Harvey County, Kansas, approximately $\times \frac{1}{2}$. The oviducts (near black pins) are thin and relatively straight.



FIG. 2. Dissection of a mature parturient female western hognose snake (DRP 358) from Harvey County, Kansas, approximately $\times \frac{1}{2}$. The oviducts (indicated by arrows) are thick and convoluted.

PLATE 7



FIG. 1. The concealing-head posture of the threatening phase of the defensive behavior of the western hognose snake.

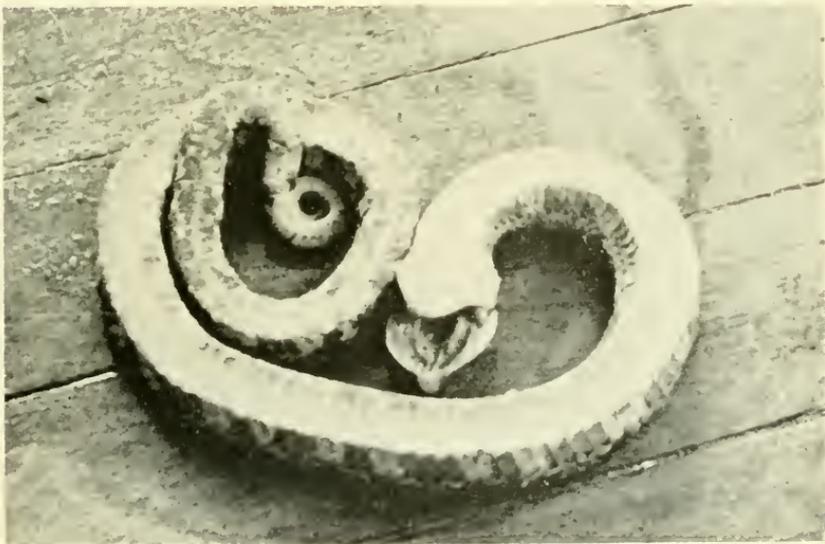


FIG. 2. Death-feigning by an eastern hognose snake.

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Comparative Ecology of Pinyon Mice
and Deer Mice in
Mesa Verde National Park, Colorado

BY

CHARLES L. DOUGLAS

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INTRODUCTION

Centuries ago in southwestern Colorado the prehistoric Pueblo inhabitants of the Mesa Verde region expressed their interest in mammals by painting silhouettes of them on pottery and on the walls of kivas. Pottery occasionally was made in the stylized form of animals such as the mountain sheep. The silhouettes of sheep and deer persist as pictographs or petroglyphs on walls of kivas and on rocks near prehistoric dwellings. Mammalian bones from archeological sites reveal that the fauna of Mesa Verde was much the same in A. D. 1200, when the Pueblo Indians were building their magnificent cliff dwellings, as it is today. One of the native mammals is the ubiquitous deer mouse, *Peromyscus maniculatus*. The geographic range of this species includes most of the United States, and large parts of Mexico and Canada.

Another species of the same genus, the pinyon mouse, *P. truei*, also lives on the Mesa Verde. The pinyon mouse lives mostly in southwestern North America, occurring from central Oregon and southern Wyoming to northern Oaxaca. This species generally is associated with pinyon pine trees, or with juniper trees, and where the pinyon-juniper woodland is associated with rocky ground (Hoffmeister, 1951:vii).

P. maniculatus rufinus of Mesa Verde was considered to be a mountain subspecies by Osgood (1909:73). The center of dispersion for *P. truei* was in the southwestern United States, and particularly in the Colorado Plateau area (Hoffmeister, 1951:vii). The subspecies *P. truei truei* occurs mainly in the Upper Sonoran life-zone, and according to Hoffmeister (1951:30) rarely enters the Lower Sonoran or Transition life-zones. *P. maniculatus* and *P. truei* are the most abundant of the small mammals in Mesa Verde National Park, which comprises about one-third of the Mesa Verde land mass.

Under the auspices of the Wetherill Mesa Archeological Project, the flora of the park recently was studied by Erdman (1962), and by Welsh and Erdman (1964). These studies have revealed stands of several distinct types of vegetation in the park and where each type occurs. This information greatly facilitated my study of the mammals inhabiting each type of association. The flora and fauna within the park are protected, in keeping with the policies of the National Park Service, and mammals, therefore, could be studied in a relatively undisturbed setting.

Thus, the abundance of these two species of *Peromyscus*, the botanical studies that preceded and accompanied my study, the relatively undisturbed nature of the park, and the availability of a large area in which extended studies could be carried on, all contributed to the desirability of Mesa Verde as a study area.

My primary purpose in undertaking a study of the two species of *Peromyscus* was to analyze a number of ecological factors influencing each species—their habitat preferences, how the mice lived within their habitats, what they ate, where they nested, what preyed on them, and how one species influenced the distribution of the other. In general, my interest was in how the lives of the two species impinge upon each other in Mesa Verde.

Physiography

The Mesa Verde consists of about 200 square miles of plateau country in southwestern Colorado, just northeast of Four Corners, where Colorado, New Mexico, Arizona and Utah meet. In 1906, more than 51,000 acres of the Mesa Verde were set aside, as Mesa Verde National Park, in order to protect the cliff dwellings for which the area is famous.

The Mesa Verde land mass is composed of cross-bedded sandstone strata laid down by Upper Cretaceous seas. These strata are known locally as the Mesaverde group, and are composed, from top to bottom, of Cliff House sandstone, the Menefee formation, the Point Lookout sandstone, the well known Mancos shale, and the Dakota sandstone, the lowest member of the Cretaceous strata. The Menefee formation is 340 to 800 feet thick, and contains carbonaceous shale and beds of coal.

There are surface deposits of Pleistocene and Recent age, with gravel and boulders of alluvial origin; colluvium composed of heterogenous rock detritus such as talus and landslide material; and alluvium composed of soil, sand, and gravel. A layer of loess overlays the bedrock of the flat mesa tops in the Four Corners area. The earliest preserved loess is probably pre-Wisconsin, possibly Sangamon in age (Arrhenius and Bonatti, 1965:99).

The North Rim of Mesa Verde rises majestically, 1,500 feet above the surrounding Montezuma Valley. Elevations in the park range from 8,500 feet at Park Point to about 6,500 feet at the southern ends of the mesas. The Mesa Verde land mass is the remnant of a plateau that erosion has dissected into a series of long, narrow mesas, joined at their northern ends, but otherwise separated by deep canyons. The bottoms of these canyons are from 600 to 900 feet below the tops of the mesas.

The entire Mesa Verde land mass tilts southward; Park Headquarters, in the middle of Chapin Mesa (Fig. 1), is at about the same elevation as is the entrance of the park, 20 miles by road to the north.

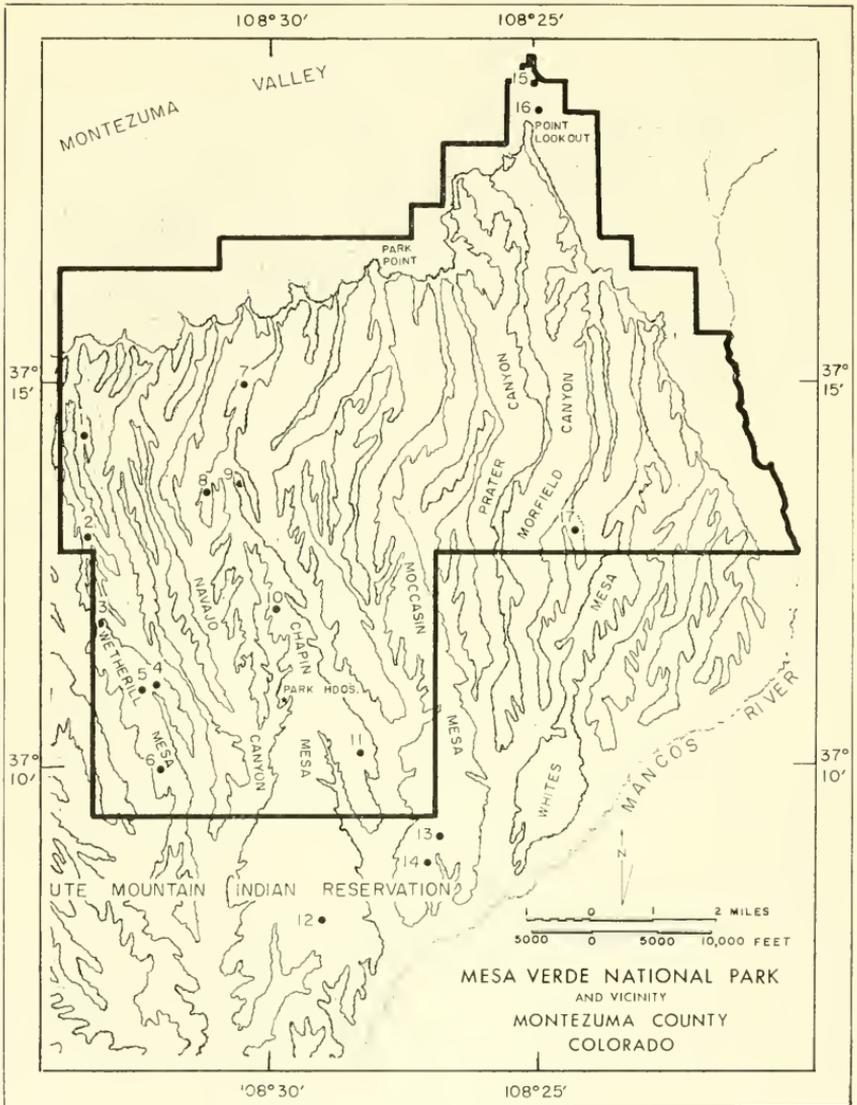


FIG. 1: Map of Mesa Verde National Park and vicinity, showing major trapping localities from 1961-1964. Trapping localities are designated in the text as follows: 1) North End Wetherill Mesa 2) Rock Springs 3) Mug House 4) Bobcat Canyon Drainage 5) North of Long House 6) Juniper-Pinyon-Bitterbrush Site 7) Navajo Hill 8) West of Far View Ruins 9) South of Far View Ruins, also general location of trapping grid 10) M-2 Weather Station 11) East Loop Road Site 12) Big Sagebrush Stand, Southern end Chapin Mesa 13) Grassy Meadow, Southern end Moccasin Mesa 14) Bed-rock Outcroppings, Southern end Moccasin Mesa 15) $\frac{1}{4}$ mi. SE Park Entrance 16) Meadow, 1 mi. SE Park Entrance 17) Morfield Ridge.

Vegetation and Climate

Mesa Verde is characterized by pinyon-juniper woodlands that extends throughout much of the West and Southwest. Although the pinyon-juniper woodland dominates the mesa tops, stands of Douglas fir occur in some sheltered canyons and on north-facing slopes. Thickets of Gambel oak and Utah serviceberry cover many hillsides and form a zone of brush at higher elevations in the park. Aspens grow in small groups at the base of the Point Lookout sandstone and at a few other sheltered places where the supply of moisture suffices. Individual ponderosa pine are scattered through the park, and stands of this species occur on some slopes and in the bottoms of some sheltered canyons.

Tall sagebrush grows in deep soils of canyon bottoms, and in some burned areas, and was found to be a good indicator of prehistoric occupation sites.

The climate of Mesa Verde is semi-arid, and most months are dry and pleasant. Annual precipitation has averaged about 18.5 inches for the last 40 years. July and August are the months having the most rainfall. Snow falls intermittently in winter, and may persist all winter on north-facing slopes and in valleys. In most years, snow is melting and the kinds of animals that hibernate are emerging by the first of April.

Because of the great differences in elevation between the northern and southern ends of the mesas, differences in climate are appreciable at these locations. Winter always is the more severe on the northern end of the park, owing to persistent winds, lower temperatures, and more snow. The northern end of the park is closer to the nearby La Platta Mountains where ephemeral storms of summer originate. They reach the higher elevations of the park first, but such storms dissipate rapidly and are highly localized. The northern end of the park therefore receives much more precipitation in summer and winter than does the southern end.

The difference in precipitation and the extremes in weather between the northern and southern ends of the mesas affect the distribution of plants and animals. Species of mammals, plants, and reptiles are most numerous on the middle parts of the mesas, as also are cliff-dwellings, surface sites, and farming terraces of the prehistoric Indians.

Anderson (1961) reported on the mammals of Mesa Verde National Park, and Douglas (1966) reported on the amphibians and reptiles. In each of these reports, earlier collections are listed and earlier reports are summarized.

I lived in Mesa Verde National Park for 28 months in the period July 1961 to September 1964, while working as Biologist for the Wetherill Mesa Archeological Project, and the study here reported on is one of the faunal studies that I undertook.

ACKNOWLEDGMENTS

This study could not have been completed without the assistance and encouragement of numerous persons. I am grateful to Dr. Olwen Williams, of the University of Colorado, for suggesting this study and helping me plan the early phases of it.

Mr. Chester A. Thomas, formerly Superintendent, and Mrs. Jean Pinkley, formerly Chief of Interpretation at Mesa Verde National Park, permitted me to use the park's facilities for research, issued collecting permits, and in 1965 appointed me as a research collaborator in order that I might complete my studies.

Dr. H. Douglas Osborne, California State College, Long Beach, formerly

Supervisory Archeologist of the Wetherill Mesa Project, took an active interest in my research and provided supplies, transportation and laboratory and field assistance under the auspices of the Wetherill Project. His assistance and encouragement are gratefully acknowledged.

Mrs. Marilyn A. Colyer of Mancos, Colorado, ably assisted in analyzing vegetation in the trapping grid; Mr. Robert R. Patterson, the University of Kansas, assisted me in the field in October of 1963 and in August of 1965. Mr. James A. Erdman, United States Geological Survey, Denver, formerly Botanist for the Wetherill Mesa Project, and Dr. Stanley L. Welsh, Brigham Young University, identified plants for me in the field, and checked my identifications of herbarium specimens. I owe my knowledge of the flora in the park to my association with these two capable botanists.

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Mr. Harold Shepherd of Mancos, Colorado, Senior Game Biologist, Colorado Department of Fish, Game and Parks, obtained permission for me to use the department's trapping grid near Far View Ruins, and provided me with preserved specimens of mice.

Mr. Fred E. Mang Jr., Photographer, National Park Service, processed large numbers of photomicrographs of plant epiderims. Dr. Kenneth B. Armitage, The University of Kansas, offered valuable suggestions for the study of water consumption in the two species of *Peromyscus*, and permitted me to use facilities of the Zoological Research Laboratories at The University of Kansas. Dr. Richard F. Johnston, The University of Kansas, permitted me to house mice in his controlled-temperature room at the Zoological Research Laboratories. I am grateful to all of the above mentioned persons for their aid.

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Travel funds provided by the Kansas Academy of Science permitted me to work in the park in August, 1965. The Wetherill Mesa Project was an interdisciplinary program of the National Park Service to which the National Geographic Society contributed generously. I am indebted to the Society for a major share of the support that resulted in this report. This is contribution No. 44 of the Wetherill Mesa Project.

DESCRIPTIONS OF MAJOR TRAPPING LOCALITIES

Trapping was begun in September of 1961 in order to analyze the composition of rodent populations within the park. I used the method of trapping employed by Calhoun (1948) in making the Census of North American Small Mammals (N. A. C. S. M.). It consisted of two lines of traps, each 1,000 feet long having 20 trapping stations that were 50 feet apart. The lines were either parallel at a distance of 400 feet from each other, or were joined to form a line 2,000 feet long. Three snap traps were placed within a five-foot radius of each station, and were set for three consecutive nights. More than a dozen areas were selected for extensive trapping (Fig. 1). Some of these were retrapped in consecutive years in order to measure changes in populations.

One circular trapline of 159.5 feet radius was established in November 1961, and was tended for 30 consecutive days to observe the effect of removing the more dominant species (Calhoun, 1959).

Other mouse traps and rat traps were set in suitable places on talus slopes, rocky cliffs, and in cliff dwellings. Most of these traps were operated for three consecutive nights.

In order to test hypotheses concerning habitat preferences of each of the species of *Peromyscus*, several previously untrapped areas that appeared to be ideal habitat for one species, but not for the other, were selected for sampling. In the summers of 1963 and 1964 snap traps were set along an arbitrary line through each of these areas. Traps were placed in pairs; each pair was 20 feet from the adjacent pairs.

A mixture of equal parts of peanut butter, bacon grease, raisins, roman meal and rolled oats was used as bait. Rolled oats or coarsely ground scratch feed was used in areas where insects removed the mixture from the traps.

Rodents trapped by me were variously prepared as study skins with skulls, as flat skins with skulls, as skeletons, as skulls only, or as alcoholics. Representative specimens were deposited in The University of Kansas Museum of Natural History. In the course of my study, traps were set in the following areas:

Morfield Ridge

In July 1959 a fire destroyed more than 2,000 acres of pinyon-juniper forest (*Pinus edulis* and *Juniperus osteosperma*) in the eastern part of the park. The burned area extends from Morfield Canyon to Waters Canyon, encompassing several canyons, Whites Mesa, and a ridge between Morfield Canyon and Waters Canyon that is known locally as Morfield Ridge (Fig. 1). Beginning on September 4, 1961, three pairs of traplines were run on this ridge at elevations of 7,300 to 7,600 feet.

Vegetation in the trapping area consisted of dense growths of grasses and herbaceous plants, which had covered the ground with seeds. In this and in the following accounts, the generic and specific names of plants are those used by Welsh and Erdman (1964). The following plants were identified from the trapping area on Morfield Ridge:

<i>Lithospermum ruderalis</i>	<i>Bromus inermis</i>
<i>Chenopodium pratericola</i>	<i>Bromus japonicus</i>
<i>Achillea millefolium</i>	<i>Oryzopsis hymenoides</i>
<i>Artemisia tridentata</i>	<i>Calochortus nuttallii</i>
<i>Aster bigelovii</i>	<i>Linum perenne</i>
<i>Chrysothamnus depressus</i>	<i>Sphaeralcea coccinea</i>
<i>Chrysothamnus nascosus</i>	<i>Polygonum sawatchense</i>
<i>Helianthus annuus</i>	<i>Solidago petradoria</i>
<i>Helianthella</i> sp.	<i>Wyethia arizonica</i>
<i>Lactuca</i> sp.	<i>Nicotiana attenuata</i>
<i>Lepidium montanum</i>	<i>Fendlera rupicola</i>
<i>Quercus gambelii</i>	<i>Penstemon linarioides</i>
<i>Agropyron smithii</i>	

Only *Peromyscus maniculatus*, *Perognathus apache* and *Reithrodontomys megalotis* were taken in this area (Table 1). Many birds inhabit this area, including hawks, ravens, towhees, jays, juncos, woodpeckers, doves, sparrows and titmice. Rabbits, badgers and mule deer also live in the area. Only two reptiles, a horned lizard and a collared lizard, were seen.

South of Far View Ruins

Two parallel trap lines were established on October 4, 1961, in the area immediately south of Far View Ruins (Fig. 1). In altitude, latitude and geographical configuration the area is similar to that trapped in the Morfield burn, but the Chapin Mesa site had not been burned.

Canopy vegetation is pinyon-juniper forest. A dense understory was made up of *Amelanchier utahensis* (serviceberry), *Cercocarpus montanus* (mountain

mahogany), *Purshia tridentata* (bitterbrush), and *Quercus gambelii* (Gambel oak). The ground cover consisted of small clumps of *Poa fendleriana* (mutton-grass), and *Koeleria cristata* (Junegrass), intermingled with growths of one or more of the following:

<i>Artemisia nova</i>	<i>Eriogonum racemosum</i>
<i>Solidago petradoria</i>	<i>Eriogonum umbellatum</i>
<i>Sitanion hystrix</i>	<i>Polygonum sawatchense</i>
<i>Astragalus scopulorum</i>	<i>Amelanchier utahensis</i>
<i>Lupinus caudatus</i>	<i>Purshia tridentata</i>
<i>Eriogonum alatum</i>	<i>Comandra umbellata</i>
<i>Penstemon linarioides</i>	

Seeds of *Cercocarpus montanus* covered the ground under the bushes in much of the trapping area, and large numbers of juniper berries were on the ground beneath the trees. Individuals of *P. truei* and *P. maniculatus* were caught in this area (Table 1).

Several deer, rabbits, one coyote, and numerous birds were seen in the area. No reptiles were noticed, but they were not searched for. A mountain lion was seen in this general area two weeks after trapping was completed.

West of Far View Ruins

Three pairs of traplines were run west of Far View Ruins in an area comparable in vegetation, altitude, general topography, and configuration to the area previously described. The elevations concerned are typical of the middle parts of mesas throughout the park. This area differs from the trapping area south of Far View Ruins and the one on Morfield Ridge in being wider and on the western side of the mesa.

The woody understory was sparse in most places, and where present was composed of *Cercocarpus montanus*, *Purshia tridentata*, *Fendlera rupicola* (fendlerbush), *Amelanchier utahensis*, *Quercus gambelii*, and *Artemisia tridentata* (sagebrush). The herbaceous ground cover was dominated by *Solidago petradoria* (rock goldenrod), and grasses—including *Poa fendleriana*, *Oryzopsis hymenoides*, and *Sitanion hystrix*. Other herbaceous species were as follows:

<i>Echinocereus coccineus</i>	<i>Yucca baccata</i>
<i>Achillea millefolium</i>	<i>Linum perenne</i>
<i>Aster bigelovii</i>	<i>Eriogonum racemosum</i>
<i>Wyethia arizonica</i>	<i>Eriogonum umbellatum</i>
<i>Lepidium montanum</i>	<i>Polygonum sawatchense</i>
<i>Lupinus caudatus</i>	<i>Delphinium nelsonii</i>
	<i>Penstemon linarioides</i>

Fresh diggings of pocket gophers were observed along the trap lines. Badger tunnels were noted in numerous surface mounds that are remnants of prehistoric Indian dwellings, but no badgers were seen. Numerous deer and several rabbits were present. Juncos, two species of jays, and woodpeckers were seen daily. No reptiles were observed.

Both *Peromyscus maniculatus* and *P. truei* were caught in this area (Table 1).

Big Sagebrush Stand, South Chapin Mesa

A circular trapline, 1,000 feet in circumference, was established on November 16, 1961, in a stand of big sagebrush, and was operated for 30 consecutive nights.

The vegetation of the trapping area was predominantly *Artemisia tridentata* (big sagebrush), interspersed with a few scattered seedlings of pinyon and juniper. This stand was burned in 1858 (tree-ring date by David Smith) and some charred juniper snags still stood. The deep sandy soil also supported a variety of grasses and a few other small plants. The following species were common in this area:

<i>Bromus inermis</i>	<i>Sitanion hystrix</i>
<i>Oryzopsis hymenoides</i>	<i>Solidago petradoria</i>
<i>Poa fendleriana</i>	<i>Orthocarpus purpureo-albus</i>

The 15 to 20 acres of sagebrush were surrounded by pinyon-juniper forest. The trapping station closest to the forest was approximately 100 feet from the edge of the woodland. More *P. truei* than *P. maniculatus* were caught here (Table 1).

East Loop Road, Chapin Mesa

The trapping area lies north of Cliff Palace, eastward of the loop road, at elevations of 6,875 to 6,925 feet. Two pairs of traplines were run from January 9, 1962, to January 12, 1962, and from February 13 to 15, 1962.

Vegetation was pinyon-juniper woodland with an understory of mixed shrubs. One to four inches of old snow covered the ground during most of the trapping period, but the ground beneath trees and shrubs was generally clear, providing suitable location for traps.

Numerous juncos and jays were seen in this area; deer and rabbits also were present.

Individuals of *P. truei* and of *P. maniculatus* were taken (Table 1).

Navajo Hill, Chapin Mesa

Navajo Hill is the highest point (8,140 feet) on Chapin Mesa. The top of the hill is rounded and the sides slope gently southward and westward until they level out into mesa-top terrain at elevations of 7,950 to 8,000 feet. The northern and eastern slopes of the hill drop abruptly into the respective canyon slopes of the East Fork of Navajo Canyon and the West Fork of Little Soda Canyon. The gradually tapering southwestern slope of the hill extends southward for one mile and is bisected by the main highway, which runs the length of the mesa top.

Heavy growths of grasses cover the ground; *Amelanchier utahensis*, *Cercocarpus montanus*, and *Fendlera rupicola* comprise the only tall vegetation. Trees are lacking on this part of the mesa, except on the canyon slopes, where *Quercus gambelii* forms an almost impenetrable barrier.

Four traplines were run from May 4-7, 1962, and from May 9-12, 1962. *P. maniculatus* was taken but *P. truei* was not present here in 1962, or in 1964 or 1965 when additional trapping was performed as a check on populations (Table 1).

Other species trapped include the montane vole, long-tailed vole, and Colorado chipmunk. Mule deer and coyotes were abundant in the area. Striped whipsnakes, rattlesnakes and gopher snakes are known to occur in this vicinity (Douglas, 1966).

North End Wetherill Mesa

In 1934 a widespread fire deforested large areas of pinyon-juniper woodland on the northern end of Wetherill Mesa. The current vegetation consists of shrubs with a dense ground cover of grasses. Many dead trees still remain on the ground, providing additional cover for wildlife.

The trapping area was a wide, grassy meadow, three and a half miles south of the northern end of the mesa. A pronounced drainage runs through this area and empties into Rock Canyon. Four traplines were run parallel to each other. The first lines were established on May 23, 1962, and the second pair on June 3, 1962.

Another pair of lines was run in a grassy area two miles south of the northern escarpment of Wetherill Mesa. This area was one and a half miles north of the above-mentioned area. These lines ran along the eastern side of a drainage leading into Long Canyon. The vegetation was essentially the same in both areas, and they will be considered together.

The vegetation was composed predominantly of grasses. *Quercus gambelii* and *Amelanchier utahensis* were the codominant shrubs. *Artemisia tridentata* and *Chrysothamnus depressus* (dwarf rabbitbrush), were common. Plants in the two areas included the following:

Juniperus scopulorum
Symphoricarpos oreophilus
Artemisia ludoviciana

Sitanion hystrix
Stipa comata
Astragalus scopulorum

Artemisia tridentata
Chrysothamnus depressus
Helianthus annuus
Tetradymia canescens
Quercus gambelii
Bromus tectorum
Poa fendleriana

Lupinus caudatus
Yucca baccata
Sphaeralcea coccinea
Eriogonum umbellatum
Amelanchier utahensis
Fendlera rupicola
Lomatium pinatasectum

Individuals of *P. maniculatus* and of *Reithrodontomys megalotis* were caught (Table 1).

TABLE 1.—Major Trapping Localities in Mesa Verde National Park, Colorado. Vegetational Key as Follows: 1) Pinyon-Juniper-Muttongrass 2) Pinyon-Juniper-Mixed Shrubs 3) Juniper-Pinyon-Bitterbrush 4) Juniper-Pinyon-Mountainmahogany 5) Grassland with Mixed Shrubs 6) Big Sagebrush 7) Pinyon-Juniper-Big Sagebrush 8) Grassland.

Locality	Date	No. trap nights	<i>P. truei</i>	<i>P. man.</i>	Type of vegetation
Morfield Ridge.....	Sept. 1961	1080	0	83	5
	Oct. 1963	360	0	13	5
S. of Far View.....	Oct. 1961	360	10	13	2
W. of Far View.....	Oct. 1961	1080	22	17	2
South Chapin Mesa.....	Nov.-Dec. 1961	3600	16	9	6
East Loop Road.....	Jan. 1962	720	6	2	2
Navajo Hill.....	May 1962	720	0	18	5
	Aug. 1964	20	0	2	5
	Aug. 1965	50	0	8	5
N. Wetherill Mesa.....	May-June 1962	1080	0	57	5
Bobcat Canyon Drainage	June 1962	360	0	0	6
N. of Long House.....	June 1962	1080	3	4	1
Mug House—Rock Springs.....	Aug. 1962	720	8	14	4
	Aug. 1963	720	9	7	4
S. Wetherill Mesa.....	Aug. 1962	720	0	5	3
1 mi. SE Park Entr.....	June 1963	50	0	16	7
¼ mi. SE Park Entr.....	July 1963	100	0	7	8
M-2 Weather Sta.....	May 1964	25	2	0	1
8 mi. S North Rim Moccasin Mesa.....	Aug. 1964	100	0	3	8
10 mi. S North Rim Moccasin Mesa.....	Aug. 1964	25	2	0	2

Bobcat Canyon Drainage

Bobcat Canyon, a large secondary canyon on the eastern side of Wetherill Mesa, is a major drainage for much of the mesa at its widest part. The mesa top drains southeast into a pour-off at the head of Bobcat Canyon. A stand of big sagebrush, *Artemisia tridentata*, grows in the sandy soil of the drainage, and extends northwest for several hundred yards from the pour-off. The sagebrush invades the pinyon-juniper forest at the periphery of the area.

Two traplines were set in the drainage, with trapping stations at intervals of 25 feet. The lines traversed elevations of 7,000 to 7,100 feet, and were run from June 26 to 29, 1962.

Grasses are the most abundant plants in the ground cover. *Artemisia dracunculus* is common in the drainage, and *A. nova* grows around the periphery of the drainage. Other species occurring in this stand include:

<i>Aster bigelovii</i>	<i>Calochortus gunnisonii</i>
<i>Tetradymia caesceus</i>	<i>Sphaeralcea coccinea</i>
<i>Tragopogon pratensis</i>	<i>Phlox hoodii</i>
<i>Bromus tectorum</i>	<i>Eriogonum umbellatum</i>
<i>Poa fendleriana</i>	<i>Peraphyllum ramosissimum</i>
<i>Sitanion hystrix</i>	<i>Purshia tridentata</i>
<i>Stipa comata</i>	<i>Penstemon linarioides</i>
<i>Lupinus argenteus</i>	

No mice were caught in three nights of trapping (360 trap nights), and only one mammal, a *Spermophilus variegatus*, was seen.

North of Long House, Wetherill Mesa

Pinyon-juniper forest with a dominant ground cover of *Poa fendleriana* was described by Erdman (1962) as one of the three distinct types of pinyon-juniper woodland on Wetherill Mesa. Such a woodland occurs adjacent to the Bobcat Canyon drainage, and is continuous across the Mesa from above Long House to the area near Step House. Plants in the ground cover include:

<i>Cryptantha bakeri</i>	<i>Phlox hoodii</i>
<i>Opuntia rhodantha</i>	<i>Eriogonum racemosum</i>
<i>Chrysothamnus depressus</i>	<i>Eriogonum umbellatum</i>
<i>Solidago petradoria</i>	<i>Cordylanthus wrightii</i>
<i>Koeleria cristata</i>	<i>Pedicularis centranthera</i>
<i>Lupinus argenteus</i>	<i>Penstemon linarioides</i>
<i>Yucca baccata</i>	<i>Penstemon strictus</i>

Two traplines were run from July 9 to 12, 1962, in the area south of the Bobcat Canyon drainage at an elevation of 7,100 feet. No mice were caught in three nights of trapping. Four additional lines were established on July 24, 1962, and were run for three nights, in the area north of the Bobcat Canyon drainage at elevations of 7,100 to 7,150 feet.

P. maniculatus and *P. truei* were caught here (Table 1). This vegetational association may have few rodents because there is a shortage of places where they can hide. Although *Poa fendleriana* is abundant, the lack of shrubs leaves little protective cover for mammals.

Mug House—Rock Springs

A juniper-pinyon-mountain mahogany association extends from the area of Mug House to Rock Springs, on Wetherill Mesa. On that part of the ridge just above Mug House, the understory is predominantly *Cercocarpus montanus* (mountain mahogany), but northward toward Rock Springs the understory changes to *Fendlera rupicola*, *Amelauchier utahensis*, *Cercocarpus*, and *Purshia tridentata*. The ground cover is essentially the same as that in the pinyon-juniper-muttongrass association described previously.

Four traplines were run from July 31 to August 2, 1962, and from August 13 to 15, 1963. These lines ran northwest-southeast, starting 1,000 feet south-

east of, and ending 3,000 feet northwest of, Mug House. The lines traversed elevations of 7,225 to 7,325 feet. Individuals of *P. maniculatus* and *P. truei* were caught here (Table 1).

Deer and rabbits inhabit the trapping area. Bobcats have been seen, by myself and by others, near Rock Springs. Lizards of the genera *Cnemidophorus* and *Sceloporus*, as well as gopher snakes were seen in this area.

Juniper—Pinyon—Bitterbrush

Three pairs of traplines were run from August 7-9, 1962, in a juniper-pinyon-bitterbrush stand on the southern end of Wetherill Mesa, starting 200 yards southwest of Double House (Fig. 1).

The forest on the southern end of the mesas consists of widely-spaced trees, which reflect the low amounts of precipitation at these lower elevations. Juniper trees are more numerous than pinyons, and both species are stunted in comparison to trees farther north on the mesa. *Purshia tridentata* (bitterbrush) is the understory codominant. *Artemisia nova* (black sagebrush) is present and grasses are the most abundant plants in the ground cover. Herbaceous species in the sparse ground cover include the following:

<i>Opuntia polyacantha</i>	<i>Lupinus caudatus</i>
<i>Solidago petradoria</i>	<i>Yucca baccata</i>
<i>Lathyrus pauciflorus</i>	<i>Phlox hoodii</i>
<i>Penstemon linarioides</i>	

Only *P. maniculatus* was caught in this stand; all mice were caught in the first night of trapping.

Five areas were selected for trapping in the summers of 1963 or 1964, in order to test hypotheses concerning habitat preferences of each of the species of *Peromyscus*. Four of these areas appeared to be ideal habitat for one species, but not for the other. The fifth area was expected to produce both species of *Peromyscus*. Each of these areas is discussed below.

One Mile Southeast of Park's Entrance

A small stand of *Artemisia tridentata*, occurring one mile southeast of the entrance to the park, is bordered to the north and northeast by a grassy meadow, discussed in the following account. Kangaroo rats have been reported in this general area, and I wanted to determine whether *P. maniculatus* and *Dipodomys* occurred together there. Fifty trap nights in this sagebrush, on June 20, 1963, yielded only *P. maniculatus* (Table 1).

Meadow, One-Quarter Mile Southeast of Park's Entrance

A grassy meadow lies just to the east of the highway into the park, one-quarter of a mile southeast of the park's entrance. On July 30, 1963, one hundred traps were placed in two lines through the meadow, and were run for one night. Only individuals of *P. maniculatus* were caught (Table 1).

M-2 Weather Station, Chapin Mesa

The M-2 weather station of the Wetherill Mesa Archeological Project was on the middle of Chapin Mesa at an elevation of 7,200 feet. This site was in an old C. C. C. area, about one mile north of the park's U. S. Weather Bureau station. The vegetation surrounding the M-2 site was a pinyon-juniper-muttongrass association. It was thought that both species of *Peromyscus* would occur in this habitat.

On May 10, 1964, 25 traps were placed in this area and were run for one night. Only individuals of *P. truei* were caught (Table 1).

Grassy Meadow, Southern End Moccasin Mesa

This large meadow is located eight miles south of the northern rim of Moccasin Mesa. The meadow lies in a broad, shallow depression that forms the head of a large drainage (Fig 1). To the south of the meadow the drainage deepens, then reaches bedrock as it approaches the pour-off.

On August 23, 1964, one hundred traps were set in pairs in a line through the middle of the meadow; adjacent pairs were 20 feet from each other. Only individuals of *P. maniculatus* were caught (Table 1).

Grasses are dominant in the ground cover, and *Sphaeralcea coccinea* (globe mallow) is codominant. The abundance of globe mallow is due to the present and past disturbance of this meadow by a colony of pocket gophers. Trees are absent in the meadow. Species of plants include the following:

<i>Opuntia polyacantha</i>	<i>Gutierrezia sarothrae</i>
<i>Chenopodium</i> sp.	<i>Tetradymia canescens</i>
<i>Artemisia ludoviciana</i>	<i>Tragopogon pratensis</i>
<i>Chrysothamnus nauscosus</i>	<i>Bromus tectorum</i>
<i>Koeleria cristata</i>	<i>Sphaeralcea coccinea</i>
<i>Poa pratensis</i>	<i>Eriogonum racemosum</i>
<i>Lupinus ammophilus</i>	<i>Polygonum sawatchense</i>
<i>Calochortus gunnisonii</i>	<i>Comandra umbellata</i>
<i>Erigeron speciosus</i>	<i>Penstemon strictus</i>

Bedrock Outcroppings, Southern End Moccasin Mesa

Two miles south of the preceding site, much of the mesa is a wide expanse of exposed bedrock, which extends approximately 100 feet inward from the edges of the mesa. Pinyon-juniper-mixed shrub woodland adjoins the bedrock.

On August 23, 1964, 25 traps were placed along the bedrock, near the edge of the forest. Only two mice, both *P. truei*, were caught. (Table 1).

HOME RANGE

In order to learn how extensively mice of different ages travel within their habitats, whether their home ranges overlap, and how many animals live within an area, it was necessary to determine home ranges for as many mice, of each species, as possible (Hayne, 1949; Mohr and Stumpf, 1966; Sanderson, 1966).

In 1961, the Colorado Department of Fish, Game and Parks established a permanent trapping grid in the area south of Far View Ruins (Fig 1). The grid was constructed and used by Mr. Harold R. Shepherd, Senior Game Biologist, and his assistant, in the summers of 1961 and 1962, in a study concerning the effect of rodents on browse plants used by deer. The Department of Fish, Game and Parks allowed me to use the grid during 1963 and 1964, and also permitted me to use its Sherman live traps.

The grid is divided into 16 units, each with 28 stations (Fig. 2). Traps at four stations (1a, 1b, 1c, 1d) are operated in each unit at the same time, with two traps being set at each station. The traps are moved each day in a counter-clockwise rotation to the next block of four stations (2a, 2b, 2c, 2d) within each unit. The stations are arranged so that on any given night, traps in adjacent units are separated by at least 200 feet. As a result, animals are less inclined to become addicted to traps, for even within one unit they must move at least 50 feet to be caught on consecutive nights.

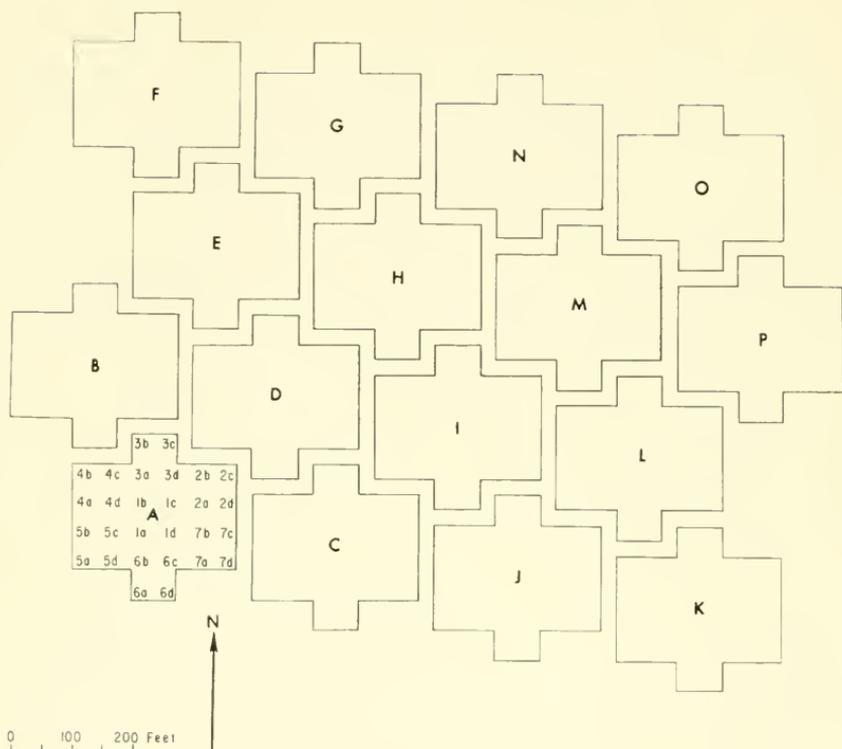


FIG. 2: Diagram of trapping grid for small mammals, showing units of subdivision. Trapping stations were numbered in each unit as shown in unit A.

Traps were carefully shaded and a ball of kapok was placed in each trap to provide protection against the killing temperatures that can develop inside. In spite of these precautions, mice occasionally succumbed from heat or cold. The traps were baited with coarsely-ground scratch feed.

Mammals trapped in the grid were inspected for molt, sexual maturity, larvae of botflies, anomalies, and other pertinent data. Each animal was marked by toe-and ear-clipping and then released. Four toes were used on each front foot, and all five toes were used on each hind foot; two toes were clipped on the right front foot to signify number nine. The tip of the left ear was clipped to signify number 100, and the tip of the right ear was clipped to signify 200. If 300 or more animals had been captured, the tip of the tail would have been clipped to represent number 300. A maximum of 799 animals could have been marked with this system, which was used by Shepherd. I continued with it, starting my listings with number one.

Only two mice were caught that had been marked in the previous season by Shepherd.

Live traps were operated in the trapping grid from July 9 through October 25, 1963, and from June 25 through August 21, 1964. Traps were rotated through all stations five different times (35 days) in 1963, and twice (14 days)

in 1964. Approximately three man hours were required each day to service and rotate the traps to the next group of stations. By the autumn of 1964, a total of 282 mice had been captured, marked and released; these were handled 817 times. In 1963, 235 mice were caught for an average of 20 captures per day; in 1964, 47 mice were caught for an average of 9 captures per day.

Calculations of Home Range

A diagrammatic map of the trapping grid was drawn to scale with one centimeter equal to 100 linear feet. Trapping stations were numbered on the diagram to correspond with stations in the field. An outline of this drawing also was prepared to the same scale, but station numbers were omitted. Mimeographed copies of such a form could be placed over the diagrammatic map and marks made at each station where an animal was caught. A separate form was kept for each animal that was caught four or more times.

In calculating home range, it was assumed that animals would venture half-way from the peripheral stations, at which they were caught, to the next station outside the range. A circle having a scaled radius of 25 feet (half the distance between stations) was inscribed around each station on the periphery of the home range by means of a drafting compass. The estimated range for each animal was then outlined on the form by connecting peripheries of the circles. Both the inclusive boundary-strip method and the exclusive boundary-strip method (Stickel, 1954:3) were used to estimate the ranges. The area encompassed within the home ranges was measured by planimetry of the outline of the drawing. At least two such readings were taken for each home range; then these planimeter values were converted into square feet.

The customary practice in delimiting home ranges on a scaled map of a grid is to inscribe squares around the peripheral stations at which the animal was trapped, and then to connect the exterior corners of these squares (Stickel, 1954:3). If the distance between stations was 50 feet, such squares would have sides 50 feet long. An easier method is to inscribe a circle having a scaled radius of 25 feet around the peripheral stations by means of a drafting compass. To my knowledge this method has not been used previously and consequently has not been tested by experiments with artificial populations.

To test the accuracy of this method, a "grid of traps" was constructed by using 8½ by 11 inch sheets of graph paper with heavy lines each centimeter. The intersects of the heavier lines were considered as trap stations. A "home range" of circular shape, 200 feet (4 cm.) in diameter, with an area of 31,146 square feet (0.71 acre), was cut from a sheet of transparent plastic. Another "home range" was made in an oblong shape with rounded ends. This range measured 2 by 65 centimeters (100 by 325 feet) and had an area of 32,102 square feet (0.74 acre). Each plastic range was tossed at random on sheets of graph paper for fifty trials each. The range was outlined on the graph paper, then circles having a scaled radius of 25 feet were inscribed around each "trap station" within the range. The peripheries of the inscribed circles were then connected and the estimated home range was delimited by the exclusive boundary-strip method. The estimated range was measured by planimetry, and the data were compared with the known home range (Table 2).

It was found that when calculated by the exclusive boundary-strip method, the circular home range was overestimated by 2.22 per cent. The oblong home range was overestimated by only 1.50 per cent. Stickel (1954:4) has shown that the exclusive boundary-strip method is the most accurate of several methods of estimating home ranges, and in her experiments this method gave an overestimate of two per cent of the known range. Thus, my method of encircling the peripheral stations yields results that are, on the average, as accurate as the more involved method of inscribing squares about the trap stations, and saves a great deal of time as well. My method probably yields better accuracy; a perfect circle is easily drawn by means of a compass, whereas a perfect square is more difficult to construct without a template.

It is generally understood that the estimated home range of an animal tends to increase in size with each additional capture; this increase is rapid at first, then slows. Theoretically, the more often an animal is captured, the more reliable is the estimate of its home range. Most animals, however, rarely are captured more than a few times. The investigator must decide how many captures are necessary before the data seem to be valid for estimating home ranges.

An animal must be trapped at a minimum of three stations before its home range can be estimated, and even then the area enclosed in the triangle will be much less than the actual home range. Some investigators have plotted home ranges from only three captures (Redman and Selander, 1958:391), whereas others consider that far more captures are needed to make a valid estimate of range (Stickel, 1954:5).

In my study, 161 individuals of *P. truci* were caught from one to 13 times each. The estimated home ranges of 10 individuals of *P. truci*, each caught

TABLE 2—Summary of Data from Experiments in Calculating Home Ranges for an Artificial Population.

Series	No. of trials	Trap spacing in ft.	Shape of range	Actual area of range in ft.	Calculated area of range by exclusive boundary-strip method	± S. D.
A	50	50	Circular	31,146	31,782	9,600
B	50	50	Oblong	32,102	32,583	9,466

from eight to 13 times, were plotted and measured after each capture from the fourth to the last. The percentage of the total estimated range represented by the fourth through tenth captures was, respectively, 52, 65, 73, 85, 88, 93, and 96 per cent.

Ninety-seven individuals of *P. maniculatus* were caught from one to 10 times each. For five individuals that were each caught from seven to 10 times, the percentage of total estimated range represented by the fourth through seventh captures was, respectively, 59, 69, 85, and 93 per cent.

The above percentages do not imply that the true home range of individuals of these species can be reliably estimated after seven or 10 captures; the average percentages do, however, indicate a fairly rapid increase in

known size of home ranges between the fourth and tenth captures. The estimated home ranges of *P. maniculatus* tended to reach maximum known size at about seven captures, whereas the estimated ranges of *P. truei* tended to attain maximum known size after nine or more captures. The controversy over the number of captures of an individual animal required for a reliable estimate of its home range was not settled by my data.

I initially decided to estimate home ranges for animals caught five or more times and at three or more stations. Of the 282 animals caught and marked, only 48 were caught five or more times. Because of the small numbers of *P. maniculatus* that were caught five or more times, I wanted to determine whether mice caught four times had an estimated range that was significantly smaller than that of mice caught five times. Eight individuals of *P. maniculatus* were caught four times each, and it seemed desirable to use the data from these mice if such use was justified. Data from the 48 mice caught five or more times were used for this testing.

By means of a T-test, I compared the estimated ranges of those 48 mice following their fourth capture with ranges estimated after the fifth capture. The results did not demonstrate significant differences between the two sets of estimates; therefore, I decided to use data resulting from four or more captures, and at three or more stations.

Table 3 shows estimations of the home ranges of males and females of each species of *Peromyscus*. When the inclusive boundary-strip method is used, the area encompassed by the range tends to be larger than the area of the same range when estimated by the exclusive boundary-strip method. Stickel (1954:4) has shown that the inclusive boundary-strip method overestimates the home range by about 17 percent.

Analysis of Home Range by Inclusive Boundary-Strip Method

When all age groups were considered, the ranges of 16 males of *P. truei* averaged 20,000 to 80,000 square feet (ave. 47,333; S. D. 19,286). The sizes of home ranges were not significantly different ($P > 0.05$) between adult and subadult (including juveniles and young) males.

All females of *P. truei* (22) had ranges encompassing 16,666 to 83,333 square feet (ave. 40,666; S. D. 17,566). Sizes of home ranges between adult and non-adult females did not differ significantly. The mean range of adult males of *P. truei* did not differ from that of adult females ($P > 0.05$).

Fifteen males of *P. maniculatus* had ranges of 16,666 to 66,666 square feet (ave. 34,222; S. D. 16,000); six adult males had ranges of 33,333 to 53,333 square feet (ave. 38,666). Sizes of home ranges of adult and non-adult males of this species did not differ significantly.

Five females of *P. maniculatus* had ranges of 33,333 to 76,666 square feet (ave. 51,333; S. D. 15,913); of these, four adults had ranges of 33,333 to 53,333 square feet (ave. 45,000). Sizes of home ranges of adult males of this species did not differ ($P > 0.05$) from those of adult females.

The ranges of adult males of *P. truei* were compared with ranges of adult male of *P. maniculatus*; likewise the ranges of adult females of each species were compared. In each case no difference was demonstrable in sizes of ranges between the species.

The largest home range of any *P. truei* was that of animal number 18, a young male with an estimated home range of 133,333 square feet. This animal

was caught only five times, and his home range appeared unusually large in relation to that of other young males of this species; hence some of the widely-spaced sites of capture probably represent excursions from the animal's center of activity, rather than the true periphery of his range. These data were, therefore, not used in further computations. Stickel (1954:13) pointed out the advisability of removing such records from data to be used in calculations of home range.

Number eight had the largest home range of any female of *P. truei*; she was captured ten times, and had a range of 83,333 square feet. The vegetation within her range was pinyon-juniper woodland with understories of *Amelanchier*, *Artemisia nova* and *Purshia*. Most of her home range was in the western half of unit II, but extended into parts of units D, I, G and N.

The largest home range for adult males of either species was number three of *P. truei*; he had a range of 80,000 square feet. The largest range for an adult of *P. maniculatus* was 66,666 square feet (Table 3).

Analysis of Home Range by Exclusive Boundary-Strip Method

Stickel (1954:4) has shown that under theoretical conditions the exclusive boundary-strip method is the most accurate of several methods of estimating home range. This method overestimates the known range by only two percent.

Table 3 shows a comparison of home range calculations obtained for each species, when calculated by inclusive and exclusive boundary-strip methods.

The data for males and for females of each species were compared in the same manner as in the inclusive boundary-strip method. The ranges of 16 male individuals of *P. truei* encompassed 14,000 to 56,666 square feet (ave. 34,333; S. D. 13,266); of these, the ranges of 10 adult males were from 23,333 to 53,333 square feet (ave. 39,733). Twenty-two females of this species had ranges of 13,333 to 50,000 square feet (ave. 27,199; S. D. 8,820). Eighteen adult females had the same extremes, but the average size of range, 28,000 square feet, was larger. Sizes of home ranges of males and females did not differ significantly.

The ranges of fifteen males of *P. maniculatus* encompassed 13,333 to 46,666 square feet (ave. 26,666; S. D. 10,180). Of these, six adults had the same extremes in range, but an average size of 31,410 square feet.

The ranges of five females of *P. maniculatus* varied from 28,000 to 53,333 square feet (ave. 37,199; S. D. 10,140). All but one of these females were adults. The sizes of home ranges of males and females did not differ significantly. No differences were found when ranges of adult males, or adult females, of both species were compared.

Adjusted Length of Home Range

The adjusted length of the range also can be used as an expression of home range. In this method, one-half the distance to the next trapping station is added to each end of the line drawn between stations at either end of the long axis of the range (Stickel, 1954:2).

The average length of home range for 15 males of *P. truei* was 363 feet (S. D. 105 ft.); for 22 females of this species 326 feet (S. D. 94 ft.); for 14 males of *P. maniculatus* 286 feet long (S. D. 94 ft.); and for four females of this species 347 feet (S. D. 83 ft.). The mean lengths of range of males and

females differed significantly in *P. maniculatus*, but not in *P. truei*. However, no difference was demonstrable in mean sizes of ranges between males, or between females, of the two species.

Distance Between Captures

The distance between captures has been used by several investigators as an index of the extent of home range. More short than long distances tend to be recorded when traps are visited at random, and when inner traps of the range are more strongly favored (Stickel, 1954:10).

TABLE 3—Summary of Data for Estimated Home Ranges of Mice from a Wild Population.

Type of Estimate	Species	Sex	No.	Estimated home range in sq. ft.	± S. D.
Inclusive boundary-strip.....	<i>P. truei</i>	M	16	47,333	19,286
		F	22	40,666	17,566
	<i>P. maniculatus</i>	M	15	34,222	16,000
		F	5	51,333	15,913
Exclusive boundary-strip.....	<i>P. truei</i>	M	16	34,333	13,266
		F	22	27,199	8,820
	<i>P. maniculatus</i>	M	15	26,666	10,180
		F	5	37,199	10,140
Adjusted Length.....	<i>P. truei</i>	M	16	363	105
		F	22	326	94
	<i>P. maniculatus</i>	M	14	286	94
		F	4	347	83

It is important to know approximately how far mice travel in one night. The distances traveled between captures on successive nights were calculated for all mice. Even animals caught most frequently usually were caught only once or twice on successive nights. Data from animals caught less than four times, and hence not usable for calculations of home range, could be used in calculating the distance between captures on successive nights. Thus the data were sampled in a more or less random manner for each species.

The mean distance traveled between captures on successive nights was determined for adult and non-adult animals (juvenile, young and subadult) of both sexes. Adult males of *P. maniculatus* traveled an average of 151.66 feet (n = 24); young males of this species traveled an average of 134.28 feet (n = 7). Adult females of *P. maniculatus* traveled 170.00 feet (n = 4); no data were available for young females.

Adult males of *P. truci* traveled an average of 169.47 feet ($n = 38$); and young males traveled 159.44 feet ($n = 18$). Adult females of this species traveled 155.71 feet between captures ($n = 35$), while young females traveled 140.66 feet ($n = 15$).

The means were tested for differences in the distances traveled between young and adult males and between young and adult females of each species, as well as between males and between females of opposite species. In all cases, there were no demonstrable differences in the distance traveled between captures.

One of the more striking journeys between captures was that of number 59, a juvenal male of *P. maniculatus*, which traveled 1,070 feet between captures on July 16 and 17, 1963. The route between the two capture sites was over the most rugged part of the trapping grid. This datum was excluded from further calculations. The only other animal that approached this distance was a young female *P. truci* that traveled 750 feet between captures.

Figure 3 shows the distribution of distances traveled by mice of each species between successive captures. Since there were no demonstrable differences between age groups or sexes in the distances traveled, these data represent a composite of the ages and sexes of each species. They show 101-125 feet to be the most prevalent of the distances traveled by both species, and 51-75 feet to have a higher percentage of occurrence among *P. maniculatus*. These distances indicate that if an animal was trapped on successive nights, it tended to be trapped within the same unit of the grid. It would have been necessary for an animal to travel 200 feet or more in order to be caught in traps in an adjoining unit of the grid.

The distance between captures also was calculated by the more customary method of averaging the distances between sites of capture, regardless of the time intervening between captures.

Only data from mice caught four or more times were used because these individuals probably had home ranges in the study area, whereas those caught fewer than four times may have been migrants.

The mean distance between captures ($n = 95$) for 15 males and five females of *P. maniculatus* was 161 feet. Sixteen males and 22 females of *P. truci* traveled an average of 143 feet between captures ($n = 248$). For purposes of comparison, these average distances between captures could be considered as radii of the estimated home ranges. When the range for each species is calculated by considering average distance between captures as the radius of the estimated home range, the average range of *P. truci* is 64,210 square feet, and that of *P. maniculatus* is 81,392 square feet. Both of these estimations are larger than those made by the inclusive and exclusive boundary-strip method (Table 3), and smaller than those calculated by using adjusted length of range as the radius.

Since it is known that ranges of some animals tend to be longer than wide (Mohr and Stumpf, 1966), calculations of estimated range based on average distance between captures probably are more accurate than those based on adjusted length of range.

Usually the estimated home ranges were not symmetrical, and did not resemble oblongs or circles in outline. Rather, the ranges tended to follow parts of vegetational zones. Since trapping grids are geometrical in form, there is a tendency among investigators to consider home ranges of animals as conforming to geometrical design. This may or may not be the true situ-

ation; telemetric studies on larger animals indicate that home ranges do not conform to geometrical design. At present there is a poverty of knowledge concerning methods for determining the precise home ranges of small mammals. Telemetry appears to offer an unlimited potential for studies of this kind.

Individuals of *P. truei* and *P. maniculatus* usually do not have mutually exclusive home ranges. When the home ranges for all females or males of one species are drawn on a single map of the trapping grid, almost every one of their ranges overlaps with the range of at least one other mouse. In some instances, the home range of an individual overlaps ranges of several other individuals. In extreme cases an animal's range lies completely within the estimated boundaries of another individual's range. Such an enclosed range

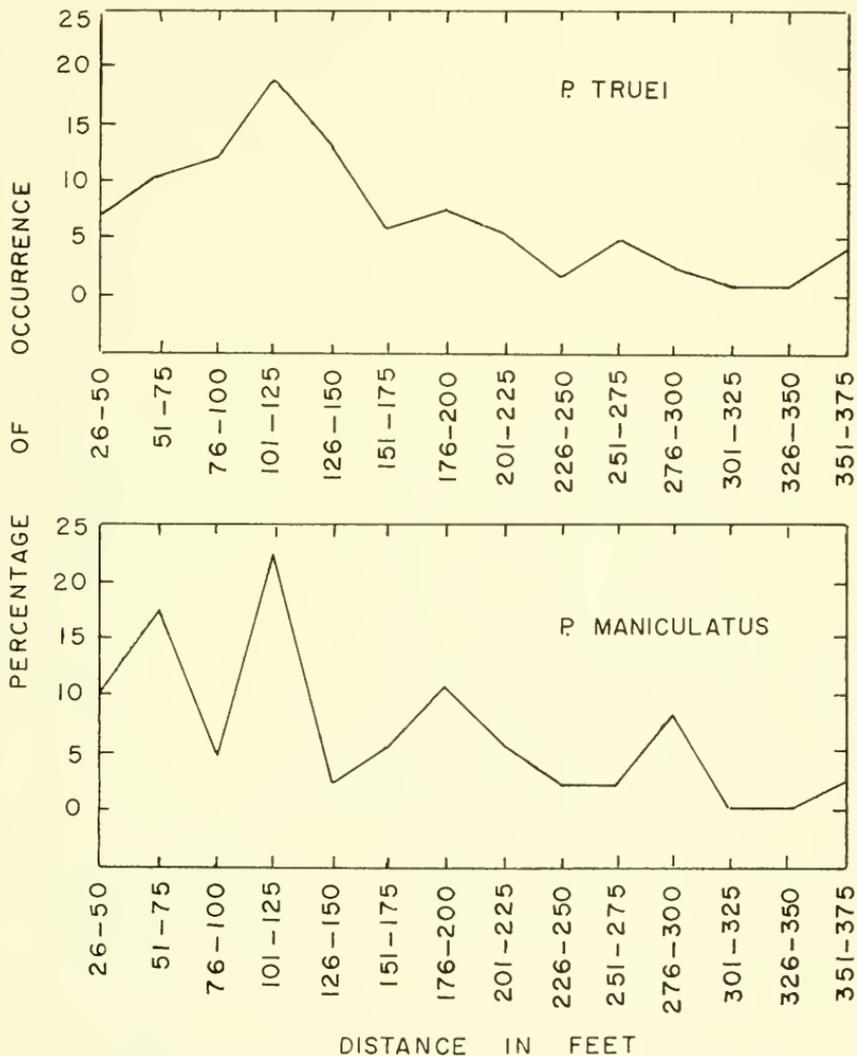


FIG. 3: Graphs showing the distribution of distances between stations at which mice were captured on successive nights in Mesa Verde National Park. Graphs for each species represent records of both males and females.

was always that of a juvenile or of a young animal. However, an adult may have more than half of its range overlapping with that of another adult of the same sex and of the same, or different, species.

In general, the two species tended to be restricted to certain areas of the trapping grid where the respective habitats were more favorable for their needs. Figure 4 shows the parts of the trapping grid utilized by each species. Of course there is overlap in the areas utilized by each species; a few individuals of *P. maniculatus* may be found in what appears to be *P. truei* habitat, and *vice versa*. In such cases, an inspection of the vegetation usually reveals an intermediate type of habitat—for example, an open sagebrush area in pinyon-juniper woodland—that is habitable for either or both species.

The ranges of *P. truei* tend to be clustered in the western half of the trapping grid, whereas the ranges of *P. maniculatus* are clustered in the eastern half of the grid (Fig. 4). The vegetation of the grid and the preferred habitats of each species are discussed in following chapters.

On the basis of the sizes of estimated home ranges, it is possible to compute the approximate number of individuals of each species that occur in each acre of appropriate habitat.

On the basis of an average home range of $30,206 \pm 25,545$ square feet (one standard deviation) for both male and female individuals of *P. truei*, there should be approximately 0.781 to 9.345 individuals of this species per acre of

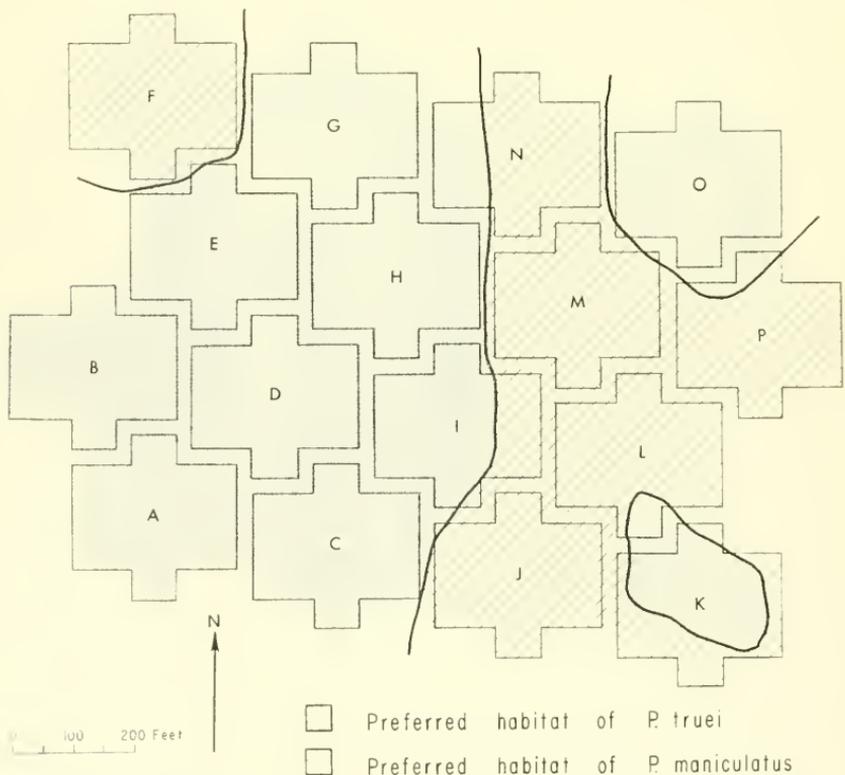


FIG. 4: Diagram of trapping grid south of Far View Ruins, showing the preferred habitats of *P. truei* and *P. maniculatus*.

pinyon-juniper woodland. An average home range of $29,400 \pm 24,570$ square feet for males and females of *P. maniculatus* indicates that the density of this species is between 0.807 and 9.018 animals per acre in mixed shrub or shrub and sagebrush types of vegetation.

Figure 4 shows that approximately 10 of the 16 units of the trapping grid are suitable habitat for *P. truei*; the remaining six units are habitat of *P. maniculatus*. From the preceding calculations of density one could expect to find between seven and 90 individuals of *P. truei*, and between five and 54 individuals of *P. maniculatus* as residents within the 22.95 acres of the trapping grid. The higher estimates of density appear to be large enough to compensate for any overlapping of home ranges.

The calculation of density of each species within the trapping grid is dependent upon the precision with which the home ranges of individuals can be estimated. At this time, home ranges of small rodents can not be measured with great precision, therefore any such calculations are, at best, only approximations. This does not imply that estimations of home range are of little value; however, calculations of density, using home ranges as a basis, tend to amplify the variance inherent in the data. This amplification is reflected in the wide range between low and high limits of the densities for each species within the trapping grid.

In order to check on the accuracy of the above calculations, an estimate of density was made for each species on the basis of trapping data. Trapping records kept for each animal were checked for the year 1963. More data on home ranges were obtained in that year due to higher population densities than in 1964. If an animal was caught four or more times in 1963, it was considered to be a resident; animals caught in both 1963 and 1964 were considered to be residents even if caught fewer than four times. Mice caught three times, with at least a month elapsing between the first and third captures, were considered to be probable residents. Other animals caught three or fewer times were considered to be migrants.

In 1963, 15 individuals of *P. truei* were caught four or more times, or in both years, and considered to be residents; six other mice were classed as probable residents. Of *P. maniculatus*, 18 individuals were classed as residents, and two as probable residents. Thus the trapping data for 1963 indicate that 21 individuals of *P. truei* and 20 of *P. maniculatus* were residents of the trapping grid. These estimates lie well within the estimated limits of density of each species, as calculated from data on home range while taking into account the relative proportions of available habitat for each species within the trapping grid. Analyses of trapping data indicate that the density of each species probably is overestimated by calculations of density based on home range data.

Males and females of both species of *Peromyscus* appeared to be highly individualistic in the amount of area they utilized. Some adult males of *P. truei* covered large areas, whereas others were relatively sedentary. The same was true of young males of *P. truei*, although the younger males tended to have smaller ranges than adult males. Most pregnant or lactating females, of both species, tended to use smaller areas for their daily activities than did non-pregnant or non-lactating females. There were notable exceptions to this generality, for some lactating females had exceptionally large home ranges.

Size of home range apparently was not influenced by the location of an

animal's range within the grid. Far more data would be needed to correlate minor differences in vegetational associations with sizes of ranges in different parts of the grid.

It is surprising that adults of *P. truei* do not have larger home ranges than adults of *P. maniculatus*. *P. truei* is the larger, more robust animal, capable of rapid running and occasional saltatorial bounding; individuals of this species can traverse large areas with ease. The semi-arboreal nature of *P. truei* may explain why individuals of this species do not have larger ranges than individuals of *P. maniculatus*. *P. truei* has a three-dimensional home range, whereas *P. maniculatus* has a range that is two-dimensional only (excluding the relatively minor amount of burrowing done by each species).

VEGETATIONAL ANALYSIS OF HABITATS

Detailed maps of vegetation within the trapping grid were needed to aid in analyzing distribution of mice within the grid. In preparing such maps, I recorded all plants within a 25 foot radius of each trapping station. The dominant and co-dominant plants in the overstory (trees or shrubs) were noted at each station. Next the three most abundant plants other than the dominant and codominants were rated for each station, where possible. Finally a listing was made of all remaining species of plants.

On the basis of this analysis, four vegetational maps were prepared. One shows associations of dominant overstory and understory plants. Individual maps are devoted to the first, second and third most abundant plants in the ground cover within the trapping grid (Figs. 5-8). Approximately seven man-hours were required to analyze each trapping unit, and 112 man hours to analyze the entire grid.

The home range grid encompasses approximately one million square feet. At least four different vegetational stands occur within the grid: 1) pinyon-juniper woodland with various associations in the understory; 2) *Artemisia tridentata* (big sagebrush), or *A. nova* (black sagebrush); 3) *Quercus gambelii* (Gambel oak); and 4) mixed shrubs—*Fendlera rupicola* (fendlerbush), *Amelanchier utahensis* (Utah serviceberry), and *Cercocarpus montanus* (mountain mahogany).

Flora in the ground cover is regulated, at least in part, by the canopy cover; hence different associations of pinyon-juniper woodland and each of the stands mentioned above have different plants, or a different distribution of the same kinds of plants, in their ground cover.

Units A, B, E, and parts of D and G in the western third of the grid are in pinyon-juniper woodland (Fig. 5). A relatively pure understory of *Poa fendleriana* (muttongrass), is typical of such woodland on the middle parts of the mesas. Woodland on the western third of the grid differs somewhat in that, when the area occupied by each plant is considered, *Artemisia tridentata* is codominant there with *Poa fendleriana*. As far as individual plants are concerned, *Poa* far outnumbers *Artemisia*. The next most abundant plants in the ground cover are *Solidago petradoria* (rock goldenrod), *Chrysothamnus depressus* (dwarf rabbitbrush), and *Penstemon liuarioides* (penstemon), in that order.

In unit E there is a large depression, about 200 by 60 feet, created by removal of soil (Fig. 8). *Artemisia nova* grows there, and pioneering plants adapted to early stages of succession are present.

A zone of woodland, where *Artemisia nova* replaces *A. tridentata* as an

As the forest floor begins to slope into the drainage, the ground becomes rocky and shrubs assume more importance in the understory. Most of this shrubby zone is on the slope; on the western side this zone abutts pinyon-juniper woodland, and on the eastern side is bordered by *Artemisia tridentata* in the sandy bottom of the drainage. Shrubs become more abundant and pinyon and juniper trees become less abundant as one approaches the drainage. In the vegetation maps, this brushy zone is delimited on the east by a heavy line passing vertically through the middle of the grid (Figs. 5-8). The co-dominant shrubs in the understory of this zone are *Amelanchier utahensis*, *Artemisia nova* and *Purshia tridentata*. The three most abundant plants on the ground are *Artemisia ludoviciana*, *Chrysothamnus depressus* and *Penstemon linarioides*.

The drainage occupies most of unit N and parts of Units I, J and M. Unit N is at the head of the drainage; the ground slopes rapidly southward and the bottom of the drainage in unit J is approximately 50 feet lower than in unit N. The canopy cover of the drainage is *Artemisia tridentata* (Fig. 5). The same three plants that are most abundant in the ground cover of the slope are also most abundant in the drainage.

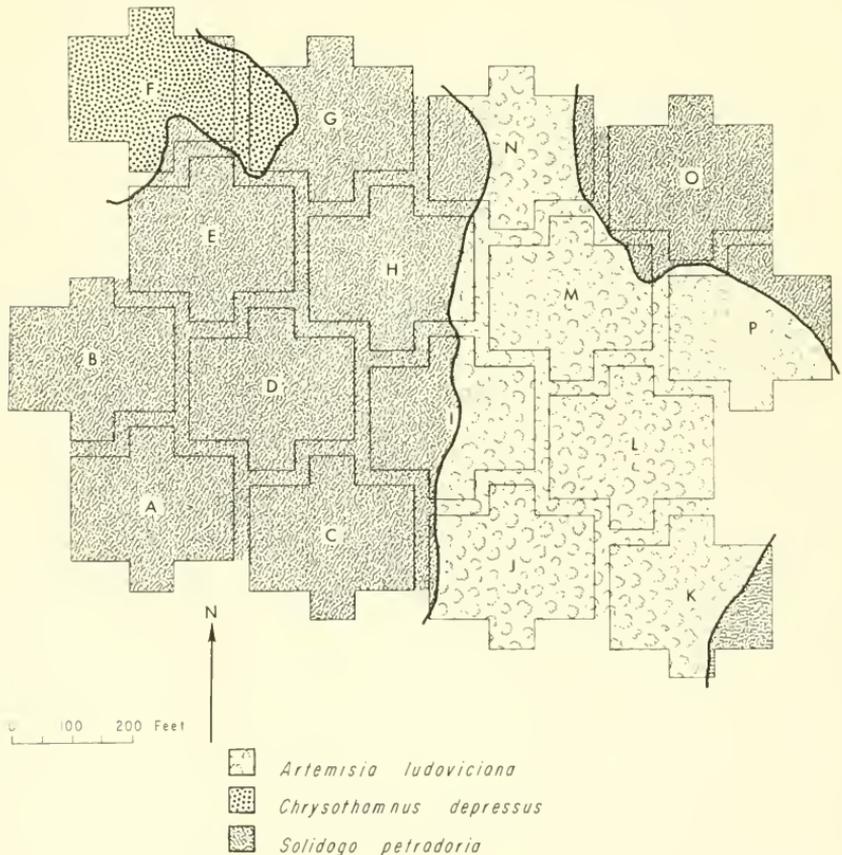


FIG. 6: Diagram showing the most abundant species of plants in the ground cover of the trapping grid south of Far View Ruins.

The eastern slope of the drainage is covered with oak chaparral (*Quercus gambelii*); this zone occupies parts of units J, L, M, and P. *Artemisia ludoviciana*, *Solidago petradoria*, and *Viguiera multiflora* (goldeneye), are the most abundant plants of the ground cover.

Mixed shrubs (*Amelanchier*, *Cercocarpos*, and *Fendlera*) form large islands in the oak chaparral, in units K, L and P. The brushy areas of oak and mixed shrub give way at the top of the slope to pinyon-juniper forest with an understory of *Artemisia nova* and *Purshia tridentata*. The three most abundant plants in the ground cover of the shrub zones are *Solidago petradoria*, *Balsamorhiza sagittata*, and *Comandra umbellata*. The eastern part of unit O has *Amelanchier utahensis* in the understory, in addition to *Artemisia nova* and *Purshia tridentata* (Fig. 5). The northeastern corner of unit O is in pinyon-juniper woodland with an understory of *Cercocarpos montanus*.

There are two relatively pure stands of sagebrush in the grid: one is in unit N, and the other in unit F and part of unit G. As figures 5 to 8 show, unit N has a relatively pure stand of *Artemisia tridentata* (big sagebrush),

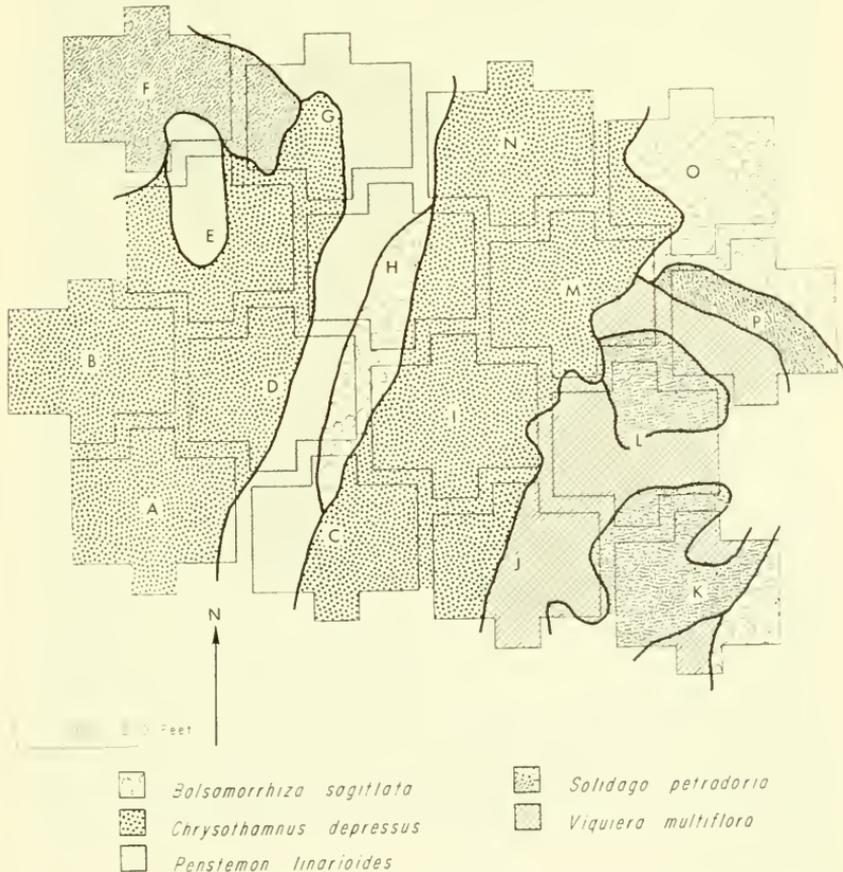


FIG. 7: Diagram showing the second most abundant species of plants in the ground cover of the trapping grid south of Far View Ruins.

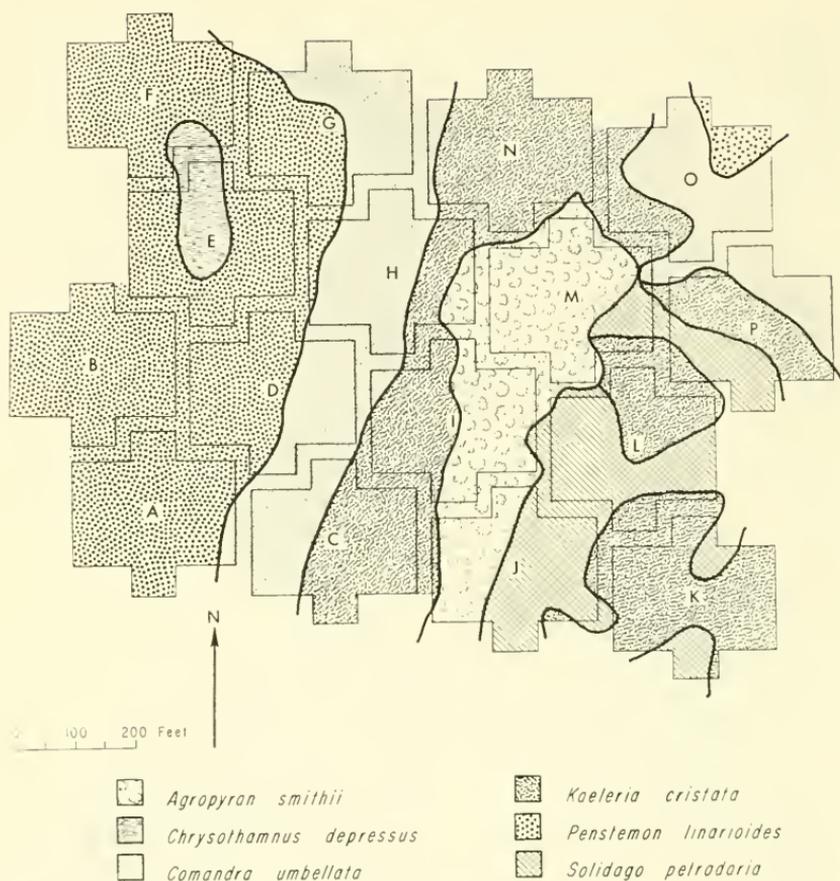


FIG. 8: Diagram showing the third most abundant species of plants in the ground cover of the trapping grid south of Far View Ruins.

with *Artemisia ludoviciana*, *Agropyron smithii* (western wheatgrass), and *Koeleria cristata* (Junegrass), being most abundant in the ground cover. *Artemisia tridentata* and *Artemisia nova* form the overstory in unit F and part of G. The three most abundant plants in the ground cover there are *Chrysothamnus depressus*, *Solidago petradaria*, and *Penstemon linarioides* (Figs. 6-8).

MICROCLIMATES OF DIFFERENT HABITATS

Four microclimatic stations were established in units D, F, L and M of the trapping grid to record air temperatures and relative humidities at ground level. These sites were chosen as being representative of larger topographic or vegetational areas within the grid. Belfort hygrothermographs were installed on June 10, 1964, and were serviced once each week through October 31, 1964, at which time the stations were dismantled. Each station consisted of a shelter 18 by 9 by 11.5 inches, having a false top to minimize heating (Fig. 9). The shelters were painted white. Several rows of holes,

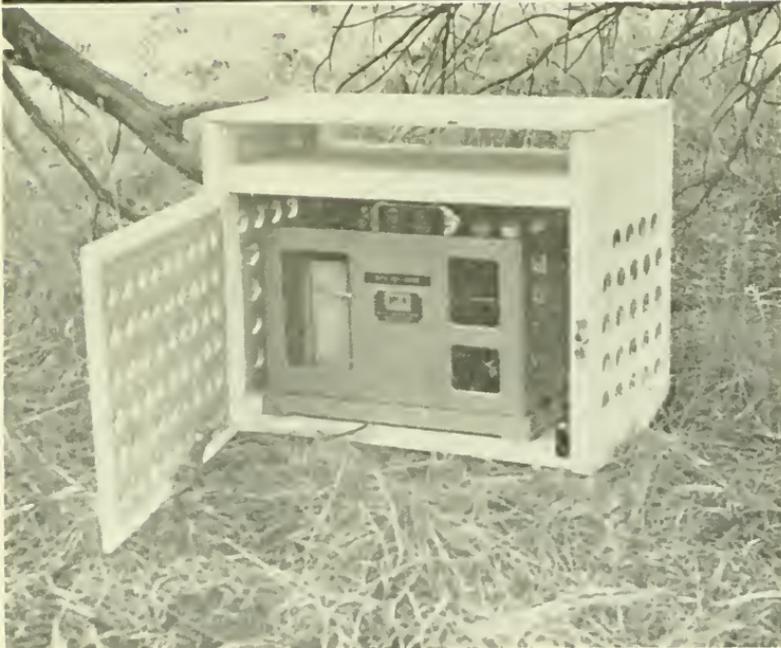
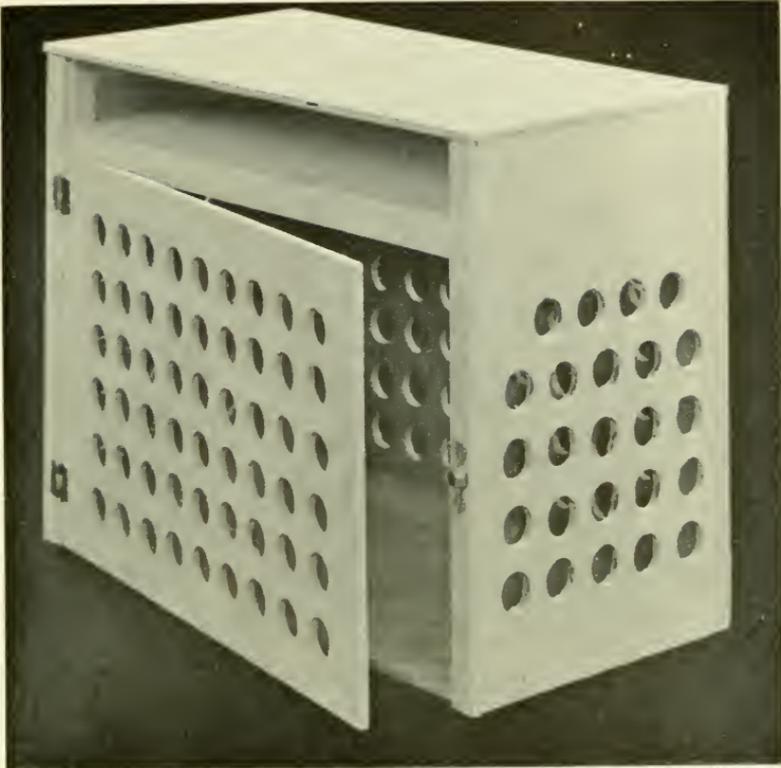


FIG. 9: (above) Photograph of microclimatic shelter built to house hygrothermograph. False top minimizes heating, and ventilation holes are covered with screening. (below) Photograph showing shelter in use.

each one inch in diameter, were drilled in all four sides of each shelter, to provide circulation of air. The holes were covered by brass window screening to prevent entry of insects and rodents. Preliminary tests with several U. S. Weather Bureau maximum and minimum thermometers, suspended one above the other, from the top to the bottom of the shelter, revealed that there was no stratification of air within the shelters. Nevertheless, each shelter was placed so that the sun did not strike the sensing elements of the hygrothermograph inside it.

Accuracy of the hair elements was checked by means of a Bendix-Friez battery driven psychrometer, in periods when humidity conditions were stable (on clear days the relative humidity is at its lowest limits and is "stable" for several hours during early afternoon).

The four microclimatic stations were in the following places: 1) a stand of big sagebrush near Far View Ruins; 2) a pinyon-juniper-muttongrass association; 3) a stand of big sagebrush at the head of a drainage; and 4) a stand of Gambel oak on a southwest-facing slope of the drainage. Table 4 shows monthly averages of maximum and minimum air temperatures and relative humidities at each of the four sites. Vegetation and microclimates of the sites are discussed below.

Far View Sagebrush Site, 7,650 feet elevation

The shelter housing the hygrothermograph was next to the stake of station F4a in the trapping grid (Fig. 10), in a stand of big sagebrush on the flat, middle part of the mesa top, approximately 100 yards southwest of Far View Ruins. The sagebrush extends approximately 200 feet in all directions from the station (Fig. 5). Pinyon pine and Utah juniper trees are encroaching upon this area, and scattered trees are present throughout the sagebrush. This area is one of the habitats of *P. maniculatus*.

Sagebrush tends to provide less shade for the ground than pinyon-juniper woodland, and therefore the surface temperatures of the soil rise rapidly to their daily maximum. In mid-June, air temperatures rise rapidly from 6 A. M. until they reach the daily maximum between 2 and 4 P. M. Shortly after 4 P. M. the air temperatures decrease rapidly and reach the daily low by about 5 A. M.

Relative humidities follow an inverse relationship to air temperatures; when air temperatures are highest, relative humidities approach their lowest values. Thus, on clear days, humidities decrease during the day, reaching a minimum slightly later than air temperatures attain their maximum. Unless it rains, the highest humidities of the day occur between midnight and 6 A. M.

Drainage Site, 7,625 feet elevation

This site was in the bottom of the drainage that runs through the eastern side of the trapping grid, and through parts of units M, N, I, and J. The site was at station M4d on a level bench at the head of the drainage (Fig. 11). Southward from the station the drainage deepens rapidly, and the bottom loses approximately 25 feet in elevation for every 200 feet of linear distance. *P. maniculatus* lives here.

The microclimate of the drainage differs markedly from that of other stations. The major difference is attributable to the topography of the drainage itself. Nocturnal cold air flows from the surrounding mesa top to lower elevations. A lake of cold air forms in the bottom of the drainage; the depth of the lake depends in part upon the depth of the drainage. The same phenomenon occurs in canyons and causes cooler night time temperatures on the floor of canyons than on adjacent mesa tops (Erdman, Douglas, and Marr, in press). Drainage of cold air into lower elevations affects both nocturnal air temperatures and relative humidities. Table 4 shows that maximum air tem-



FIG. 10: (above) Photograph of microclimatic station at the Far View Sagebrush Site, at trapping station F4a in the grid south of Far View Ruins. Dominant vegetation is *Artemisia tridentata*.

FIG. 11: (below) Photograph of microclimatic station at the Drainage Site, in the bottom of a shallow drainage at trapping station M4d of the grid south of Far View Ruins.

peratures in the drainage did not differ appreciably from those at other stations. Mean minimum temperatures, however, were considerably lower in the drainage than at the other sites. This phenomenon is reflected also in the mean air temperatures at this station.

The drainage site had the highest humidities of all stations each month in which data were collected (Table 4). Relative humidities of 90 to 100 per cent were common in the drainage, but occurred at other stations only in rainy periods. For example, in the month of August, 26 of the daily maximum readings were between 95 and 100 per cent at the drainage site, but at the other stations relative humidities were above 95 per cent for an average of only nine nights. Minimum humidities were about the same for all stations, since they are affected by insolation received during the day, and not by the drainage of cold air at night.

Oak Brush Site, 7,640 feet elevation

The station was in an oak thicket at trapping station L4a, 250 feet south and 50 feet east of the drainage site on a southwest-facing slope of about 30 degrees (Fig. 12). The station was on the lower third of the slope, approximately 15 feet higher than M4d, the station in the bottom of the drainage. *P. truei* and *P. maniculatus* occur together in this area.

Air temperatures and relative humidities at this station did not differ appreciably from mean temperatures and humidities at the other stations. The unusual feature is the lack of evidence of cold air drainage. The lake of cold air in the bottom of the drainage apparently is too shallow to reach this station. This site is near the head of the drainage, and the cold, nocturnal air probably moves rapidly down slope into the deeper parts of the canyon, rather than piling up at the shallow head of the drainage.

In spite of the shade afforded the ground by the oak brush, temperatures reached the same maximum values as at the drainage site, owing to the orientation of the slope. South-facing slopes receive more direct insolation throughout the day and throughout the year than north-facing slopes and mesa tops (Geiger, 1965:374). In Mesa Verde, south-facing slopes tend to be more arid; snow melts rapidly, and most of this moisture evaporates. As a consequence, south-facing slopes have less soil moisture and more widely-distributed vegetation than north-facing slopes where snows often persist all winter and melt in spring. (For a detailed discussion of climates on northeast-versus-southwest-facing slopes in Mesa Verde, see Erdman, Douglas, and Marr, in press.)

Pinyon-Juniper-Muttongrass Site, 7,600 feet elevation

The station was in the trapping grid at D5b (Fig. 13). The pinyon-juniper woodland surrounding this site resembles much of the woodland on the middle part of the mesa. The forest floor is well shaded by the coniferous canopy, and muttongrass is the dominant plant in the ground cover. *P. truei* lives in this habitat.

The climate at this site is moderate. Shade from the canopy greatly moderates the maximum air temperatures during the day; minimum air temperatures, however, are about the same as at the other stations (Table 4). Mean temperatures are somewhat lower at this site than at the others because of the lower maximum temperatures. Relative humidities do not differ markedly from those at other stations.

Figure 14 shows hygrothermograph traces at all stations for a typical week. An interesting phenomenon is illustrated by several of these traces. By about midnight, air temperatures have cooled to within a few degrees of their nightly low. At this time, heat is given up by the surface of the ground in sufficient quantities to elevate the air temperature at ground level. This release of re-radiated energy lasts from one to several hours, then air temperatures drop to the nightly low just before sunrise. A depression in the percentage of rel-

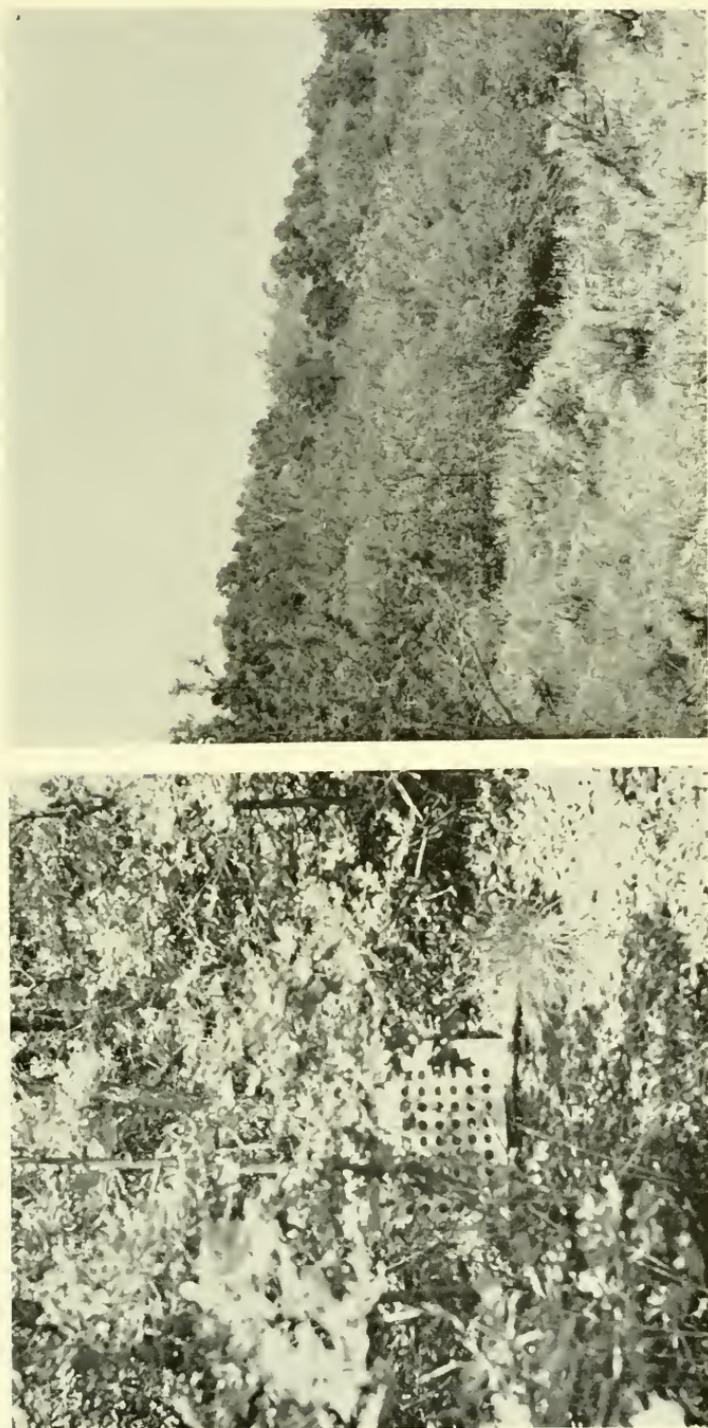


FIG. 12: (left) Photograph of microclimatic station at the Oak Brush Site, at trapping station L4a of the grid south of Fat View Ruins. (right) General view of the stand of Gambel oak in unit L. of the trapping grid.



FIG. 13: Photograph of microclimatic station at the Pinyon-Juniper-Mutton-grass Site, at trapping station D5b of the grid south of Far View Ruins. Grass in the foreground is muttongrass, *Poa fendleriana*.

ative humidity accompanies this surge of warmer air. On some nights winds apparently disturb, or mix, the layers of air at ground level. On such nights the reradiation of energy is not apparent in the traces of the thermographs. Reradiation of energy is restricted to ground level, and traces of hygrothermographs in standard Weather Bureau shelters, approximately four feet above the ground surface, at other sites on the mesa top did not record it.

The instruments used in this study were unmodified Belfort hygrothermographs containing as sensing units a hair element for relative humidity and a Bourdon tube for air temperatures. The hair element, especially, does not register changes in humidity at precisely ground level; rather, it reflects changes in the layer of air from about ground level to about a foot above. Thus data from these instruments give only approximations of the conditions under which mice live while they are on the ground.

Climatic conditions greatly influence trapping success. Larger numbers of mice generally were caught on nights when humidities were higher than average. Rain in part of the evening almost invariably resulted in more mice of each species being caught. This was probably due to increased metabolism, by the mice, to keep warm. Apparently the mice began foraging as soon as the rains subsided; mice were always dry when caught after a rain. Few mice were caught if rains continued throughout the night and into the daylight hours.

Nights of high trapping success usually were associated with days having solar insolation below the average. Insolation was measured with a recording phrheliometer at a regional weather station (M2) on the middle of Chapin

TABLE 4—Monthly Averages of Daily Means for Maximum, Minimum, and Mean Air Temperatures and relative Humidities at Four Sites in Mesa Verde National Park, Colorado.

Site	Maximum Temps.			Minimum R. H.		
	J	A	S	J	A	S
Far View Sagebrush.....	89	86	77	68	82	88
Drainage.....	86	85	78	87	93	96
Oak Brush.....	86	82	76	57	80	80
Pinyon-Juniper-Poa.....	75	74	66	59	82	88
	Minimum Temps.			Minimum R. H.		
	J	A	S	J	A	S
Far View Sagebrush.....	42	53	42	18	25	29
Drainage.....	36	48	38	21	27	29
Oak Brush.....	42	52	42	19	30	31
Pinyon-Juniper-Poa.....	44	51	42	22	30	32
	Mean Temps.			Mean R. H.		
	J	A	S	J	A	S
Far View Sagebrush.....	66	72	60	43	54	48
Drainage.....	61	70	58	54	60	62
Oak Brush.....	64	70	59	38	55	56
Pinyon-Juniper-Poa.....	60	67	54	41	55	60

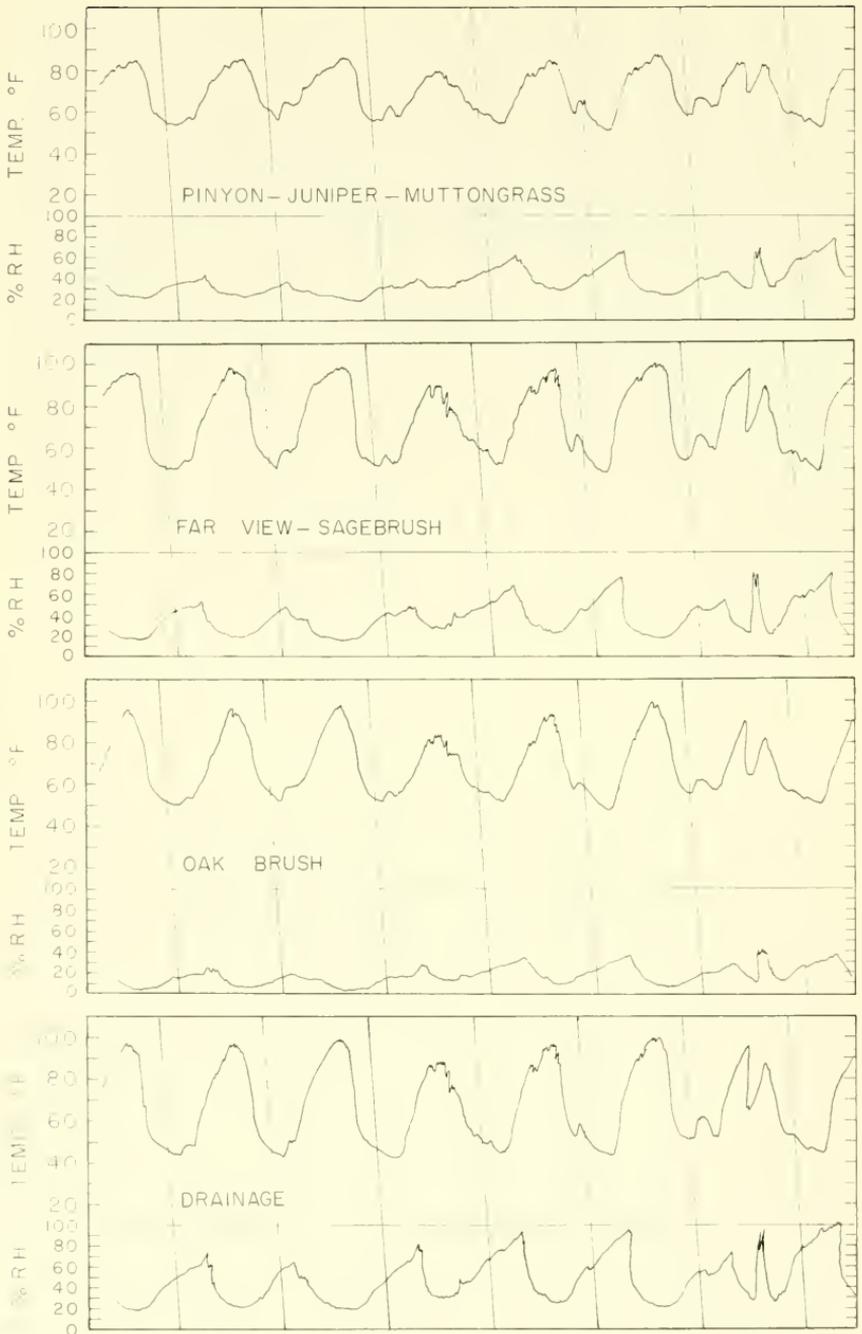


FIG. 14: Diagram of hygrothermograph traces showing daily progressions of air temperatures and relative humidities at each of four microclimatic stations, from the morning of July 1 through the morning of July 8, 1964. Slanting vertical lines on each chart designate midnight (2400 hrs.) of each day.

Mesa, at an elevation of 7,150 feet (Erdman, Douglas, and Marr, in press). This station was approximately one mile south of the trapping grid; isolation at this site would have been essentially the same as that received by the trapping grid. Below-average isolation for one day indicates cloudy conditions, which are accompanied by increased humidity, but may or may not be accompanied by precipitation. Trapping on nights preceded and followed by days of average or above average isolation with average humidities—indicative of clear days and clear moonlit nights—did not yield appreciably higher catches of mice than other nights. Hence there was no evidence that mice tended to avoid, or to seek out, traps on clear moonlit nights.

On cold, humid nights in autumn numerous mice caught in Sherman live traps succumbed from exposure, even though nesting material (kapok or cotton) and food were in the traps. Occasionally mice succumbed to heat when traps were inadvertently exposed to too much sunlight. Apparently little heat is required to kill individuals of either species. Traps in which animals died due to excessive heat usually were not hot to the touch; in most instances the traps were checked before 9:00 A.M., several hours before the sun caused maximum heating. Such individuals may have licked the fur of their chests in an attempt to lower their body temperatures. Although mice characteristically salivate before succumbing from heat, these individuals had moist fur over the entire chest and upper parts of the front legs, indicating licking. Mice killed by exposure to heat or cold usually were juveniles or young; subadult and adult individuals of both species were more tolerant. Older animals would be expected to have better homeostatic controls than younger individuals.

HABITAT PREFERENCE

In Mesa Verde *P. truei* and *P. maniculatus* occur together only at the fringes of the pinyon-juniper woodland, where ecotonal areas provide less than optimum habitats for both species. Almost all individuals of *P. truei* occur only in pinyon-juniper woodland, whereas *P. maniculatus* occurs only in more open habitats, such as grassy meadows and stands of sagebrush.

Pinyon mice were abundant in a variety of associations within the pinyon-juniper woodland. The highest population densities were in pinyon-juniper woodland having an understory of mixed shrubs. In such an association, *Poa fendleriana* usually is the dominant grass in the ground cover. *P. truei* was especially abundant along brushy slopes where mixed shrubs (*Amelanchier*, *Cercocarpus* and *Fendlera*) were codominant with pinyon pines and Utah junipers. The pinyon-juniper-mixed shrub area west of Far View Ruins was almost optimum habitat for *P. truei*.

P. truei was abundant on the rocky ridge of Wetherill Mesa near Mug House; the pinyon-juniper woodland here has a *Cercocarpus* understory, and appears to provide close to optimum conditions for this species.

Not all associations of the pinyon-juniper woodland support large numbers of *P. truei*. Pinyon-juniper woodland having a ground cover of *Poa fendleriana*, and no shrubs, supports few mice; the woodland on Wetherill Mesa near Long House is an example. Juniper-pinyon woodland having a *Purshia tridentata* understory also supports only a few mice. Such areas occur on the southern

ends of the mesas and are characterized by widely-spaced trees and little ground cover—a reflection of the relatively low amounts of precipitation received by the southern end of the park.

P. truei was not found in grasslands on Navajo Hill, or in meadows at the southern end of Moccasin Mesa. The old burned areas on the northern end of Wetherill Mesa and on Morfield Ridge now support numerous grasses and shrubs, but *P. truei* appears not to live there.

P. truei tends to avoid stands of sagebrush, or grasslands, lacking pinyon or juniper trees. *P. truei* may venture into such areas while feeding. This species is found in thickets of Gambel oak and in areas with an overstory of mixed shrubs only when a living pinyon-juniper canopy is present, or when a woodland adjoins these areas.

Rocky terrain apparently is not a requirement for *P. truei*, since much of the pinyon-juniper woodland that is free of rocks supports large numbers. Optimum habitat, however, had a rocky floor. In such places, rocks probably are of secondary importance, whereas the shrubs and other plants growing on rocky soils are important for food and cover. Rocks likely provide additional nesting sites, and allow a larger population to live in an area than might otherwise be possible.

In Mesa Verde the deer mouse, *P. maniculatus*, prefers open areas having dense stands of grasses, or brushy areas adjoining open terrain. This species lives in stands of big sagebrush; in grassy areas having an oak-chaparral or mixed-shrub-overstory; and in grasslands without shrubs, such as on the southern end of Moccasin Mesa. Pure stands of sagebrush did not support large numbers of mice unless there was additional cover nearby in the form of shrubs or oak brush.

Optimum habitats for *P. maniculatus* were on Navajo Hill, in the burned areas on Morfield Ridge, on the northern end of Wetherill Mesa, and in the grassy areas near the entrance of the park. The trapping areas in the first three mentioned had heavy growths of grass and an overstory of shrubs.

Some individuals of *P. maniculatus* ventured into pinyon-juniper woodland and entered traps. Such animals usually were found in places having a heavy understory of sagebrush, or in disturbed places within the woodland.

P. maniculatus, but not *P. truei*, was taken in the arid pinyon-juniper-bitterbrush stand on the southern end of Wetherill Mesa. *P. maniculatus* also was present, in about equal numbers with *P. truei*, in a pinyon-juniper-muttongrass stand north of Long House. Both of these localities supported only a few mice.

P. maniculatus is found more frequently in pinyon-juniper woodland when the population density is high, and when such woodlands adjoin grasslands or sagebrush areas. As mentioned earlier, *P. truei* and *P. maniculatus* occur together in ecotonal areas between the forest and grassy or brushy areas. In Mesa Verde the deer mouse inhabits exposed grassy areas that have mostly shrubs in the open canopy.

P. maniculatus is the first to colonize areas that have been burned; this species invades such areas as soon as primary successional vegetation becomes established. It can be stated that in general, *P. maniculatus* will be found in the harsher, more arid habitats. If the habitat is so inhospitable that only a few mice can survive there, *P. maniculatus* will be present. *P. truei* apparently requires the more moderate conditions found in the pinyon-juniper forest, and this species does not venture far from the edge of the forest.

NESTING AND NEST CONSTRUCTION

Ten individuals of *P. truei* and three of *P. maniculatus* were followed to their nesting places. Photographs were taken of the nesting sites before and after uncovering. Plants or other materials used in their construction and any commensal arthropods present were saved and later identified.

Nests of *P. truei* usually were associated with juniper trees. Dead branches and trunks of juniper trees decay from the inside, and the resulting hollows are favored sites for the nests. Pinyon pine trees tend to decay from the outside and were not used as nesting sites by *P. truei*. Nests of *P. truei* were found in hollow trunks and branches of otherwise healthy juniper trees, and in hollow logs lying on the ground. The heartwood apparently rots rapidly in juniper trees, but the sapwood remains intact for many years—even after the tree is lying on the ground. For example, a part of the pinyon-juniper woodland on the southern end of Chapin Mesa was burned in 1858, and the hollow trunks of junipers were still standing in 1966. Almost all of the pinyon pine trees that were killed by that fire have since decayed; their former presence is verified only by the crumbling remnants of their trunks that lie on the ground throughout the burned area.

The following accounts illustrate the preferences of the two species of mice in selection of nesting sites:

No. 105, *P. truei*, adult. On July 22, 1964, after being released from a trap, this female ran to a serviceberry bush 10 feet south of station 14d, preened herself, ate a berry from the bush, and disappeared under a large rock at the base of the bush. Subsequent excavation revealed a large nest composed of grasses (*Poa fendleriana*, *Sitanion hystrix*, *Agropyron smithii*, *Koeleria cristata*), and a few leaves of serviceberry. There were three entrances to the nest, one on each side of the rock.

This mouse was captured again on August 12, 1964, released and followed to a hollow juniper log 15 feet south of station C7b, and 245 feet from the above nest. This log was dismantled, but no nest was found. A large number of chewed juniper seeds around the log indicated that this mouse, or others, had frequented the area.

On August 20, 1964, this female was followed to a large juniper log 20 feet northeast of station 14b. A small nest of shredded juniper bark was found inside the log, and there were numerous nuts of pinyon pine and seeds of Utah juniper that had been gnawed open. This site was about 320 feet from that at C7b, and about 240 feet from station 14d (Fig. 15).

No. 118, *P. truei*, young. On August 29, 1963, this male ran into a hollow branch of a partly dead juniper tree 15 feet south of station C5d. Part of this branch had been sawed off at some earlier time, and a hole about one-and-a-half inches in diameter was present in the center of the remaining part. The branch was not dissected, but probing revealed that the hole extended far into the branch and enlarged as it approached the trunk.

No. 177, *P. truei*, adult. This lactating female ran into the hollow trunk of a juniper 10 feet north of station C7a. Both lateral branches of the main trunk were rotten and hollow, but the tree appeared to be healthy. Chewed juniper seeds were present in the trunks and around the base of the tree.

This female later ran to a juniper log 30 feet north of station N4d. Apparently there was no permanent nest at this site (Fig. 15).

No. 178, *P. truei*, adult. This female ran into a hollow juniper tree 10 feet south of station H3c. Hundreds of old juniper seeds, with their embryos chewed out, were present at the base of the tree. The tree was not cut down.

No. 238, *P. truei*, adult. This male ran into a dead juniper log 10 feet south of station O4b. Chewed juniper seeds were present on the ground, but no nest was found in the log.

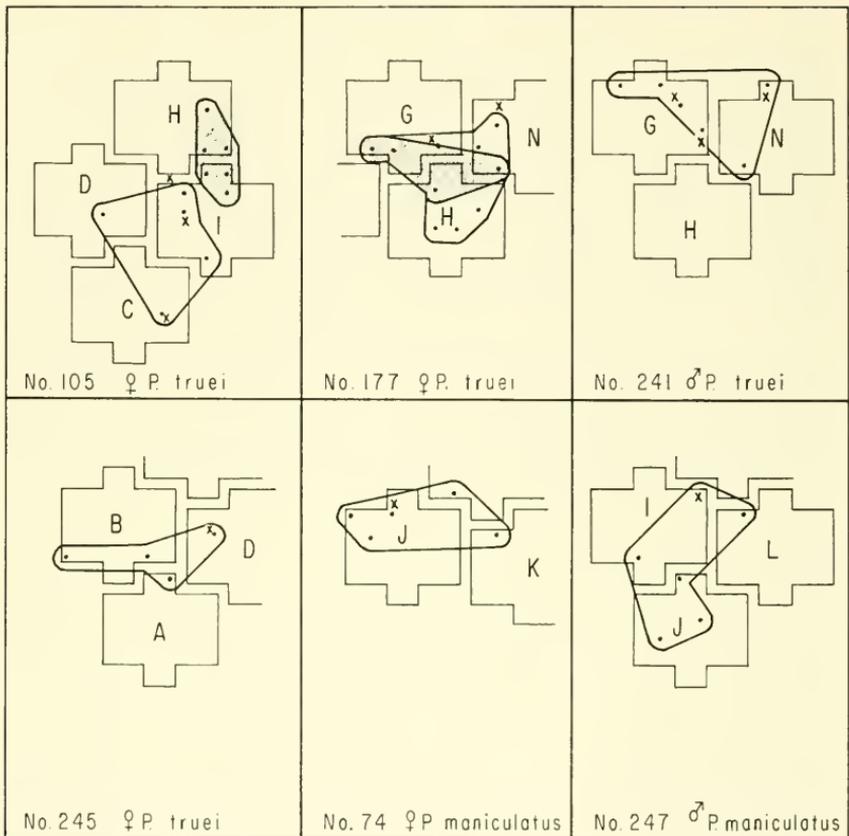


FIG. 15: Diagrams showing estimated home ranges of six individuals of two species of *Peromyscus*, and location of these ranges in the trapping grid. Nesting or hiding places are described in the text, and are indicated on each diagram by an X. Shaded areas represent home ranges estimated from trapping records for 1963; outlined, unshaded areas represent estimated home ranges for 1964.

No. 241, *P. truei*, adult. This male ran into a small hole at the base of a juniper tree 25 feet south of station G7c. The hole was at the fork of the tree, four inches above the ground, and led to a large subterranean chamber in the basal part of the trunk.

This male later ran into a dead juniper log lying on the ground 20 feet southwest of station N3b. No nest was found in the log.

After another capture, this mouse ran to a small juniper log 40 feet southeast of station G3d. There was a nest of shredded juniper bark and many juniper seeds inside the log (Figs. 15-17).

No. 245, *P. truei*, adult. This female ran into a large, hollow juniper log 20 feet northwest of station D4d. No nest was seen, but chewed juniper seeds were noted in and around the log (Fig. 15).

No. 251, *P. truei*, juvenile. This female ran into a dead juniper log beside station P4b. Chewed cones of pinyon pine and chewed juniper seeds were on the ground. A small nest of shredded juniper bark, and a few leaves of serviceberry, were found inside the log. Chewed pinyon nuts and juniper seeds also were present in the nest.

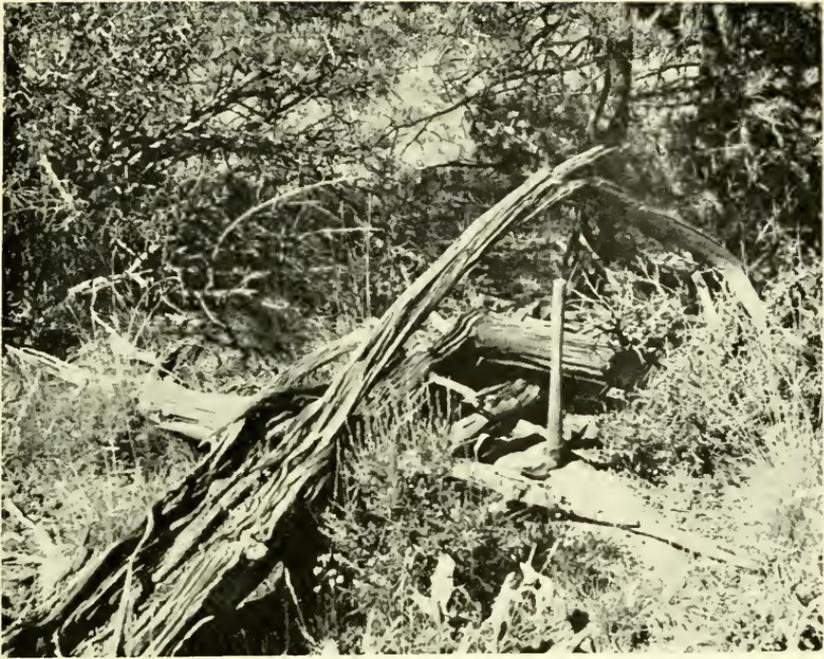


FIG. 16: (above) Photograph of juniper log at station G3d, which contained the nest of *P. truei* # 241.

FIG. 17: (below) Photograph of dissected juniper log at station G3d, showing the nest of *P. truei* # 241, at end of mattock handle. The nest of shredded juniper bark contained chewed seeds of juniper trees.

No. 267, *P. truei*, juvenile. This male ran into a fallen juniper log 40 feet southwest of station P7a and then disappeared into a hole leading under an adjacent rock. Dissection of the log revealed many chewed juniper seeds inside and beneath the log, but no nest. I did not overturn the large rock or excavate under it.

No. 268, *P. truei*, adult. This pregnant and lactating female ran into a hollow branch of a party-dead juniper tree 10 feet south of station O7d. The limb and base of the tree were hollow, and there were large numbers of chewed juniper seeds nearby. Because of time limitations, the branch was not dissected.

No. 74, *P. maniculatus*, juvenile. This female ran into a small circular hole in the ground 13 feet north of station J3a. Excavation revealed that this hole led into the abandoned tunnel of a pocket gopher (*Thomomys bottae*). The tunnel was followed for about four feet, but no nest was found and the tunnel led under a thicket of oak brush which made further excavation impractical (Fig. 15.)

No. 247, *P. maniculatus*, adult. This male was followed to a large nest situated at the base of a stump and under a juniper log lying beside the stump, five feet from station 12c. This large nest was built on the ground and was constructed of grasses (*Poa fendleriana*, *Stipa commata*, and *Koeleria cristata*), and contained a few leaves of Gambel oak. It was the largest nest found. Chewed pinyon nuts were in the nest. (Fig. 15).

No. 276, *P. maniculatus*, juvenile. This male ran into a small hole at the base of a dead juniper tree 40 feet north of station O2c. It would have been necessary to cut the tree down to uncover the nest, and this was not deemed to be worthwhile.

The preceding accounts indicate that, in Mesa Verde, nests of *P. truei* usually are associated with hollow juniper logs or branches. In one instance a nest of *P. truei* was found on the ground, under a rock. Shredded juniper bark, and, in one case, grasses were the materials most commonly used for nest building.

Individuals of *P. maniculatus* did not build nests in trees. One nest was found under a stump and adjacent log. Another site was in the abandoned tunnel of a pocket gopher, and a third was under a large rock. The only nest that was unquestionably built by a *P. maniculatus* was constructed of grasses and a few leaves.

It seems unlikely that competition for nesting sites between the two species of *Peromyscus* affects the local distribution of each species. The analysis of nesting sites suggests that *P. truei* is restricted, in Mesa Verde, by the availability of fallen logs, hollow branches, or hollow trunks of juniper trees. My observations lead me to think that within the pinyon-juniper woodland there is a surplus of nesting sites for individuals of *P. truei*. Many juniper trees have dead branches, and hollow juniper logs are abundant throughout the forest. It is inconceivable to me that the population of *P. truei* could reach densities sufficient to saturate every nesting site available to them in the trapping grid.

Sagebrush areas, or brushy zones adjacent to the pinyon-juniper woodland usually do not contain juniper logs; when hollow juniper trees or logs are not available, *P. truei* is not found as resident of such areas. As mentioned earlier, individuals of *P. truei* may venture into such areas to feed if they are adjacent to pinyon-juniper woodland.

An individual of *P. truei* may have more than one nest within its home range (for example Nos. 105 and 241 cited above). Each mouse probably has refuges, each containing a nest, strategically located in its home range. Thus, if a mouse is chased by a predator, or by another mouse, it need not

return to its main nest, but can seek refuge in one of its secondary nests. These secondary nests were small and were invariably constructed from shredded juniper bark. Some of these nests were little more than a scant handful of shredded bark that formed a platform to sit upon. Other nests were larger and ball-shaped, with one opening on the side. All of the secondary nests that were found were inside hollow juniper logs. The bark used in construction of the nests had, in each case, been transported from nearby living trees. The logs had previously lost their bark through decay.

The evidence indicates that these secondary refuges are prepared with considerable care. Not only is the bark transported for some distance, but it is shredded into a soft mass of fibers. When a mouse first establishes itself in a new area, perhaps it begins several such nests before settling upon the most favorable site. The less desirable sites, if still within the animal's range, are then available (barring competition by a new inhabitant) for outlying refuges.

My data do not indicate whether individuals of *P. maniculatus* use a similar arrangement of nests within their home ranges. The population of *P. maniculatus* was sparse in the trapping grid, and the habitat these mice occupied was such as to make following them extremely difficult.

In captivity, both species constructed nests that were indistinguishable to me, when the mice were given cotton, kapok, or pieces of burlap as building material. The cotton or kapok was used directly, but the burlap was shredded into a fine mass of fluffy fibers. The burlap seemed to me to be the best building material, for it maintained its shape best.

Both species constructed nests that resembled inverted bowls. Solitary mice naturally built smaller nests than those built by females with young.

The entrance to the closed nests varied; often the female would bolt through the side of the nest where there was no opening. Sometimes the mice would exit and enter through the top of the nest. In some cases it appeared that the entire nest was closed; probably the occupant had closed the entrance. Such a closed nest would have the advantage of greatly moderating the microenvironment within the nest, and would allow the animal within to remain comfortable with a minimum expenditure of energy. The larger nests found in the trapping grid resembled those built by captives. Nests built of grasses were always larger than those built of juniper bark. Juniper bark is as easily worked into nests as are grasses, in my judgment. Therefore, difficulty of construction of nests from this material probably does not account for the smaller size of the nests composed of bark. I think the difference in insulating characteristics between the two materials probably accounts for the difference in size of the nests.

REPRODUCTION

In Mesa Verde, *Peromyscus* reproduces from April through September. Reproduction is greatly reduced in the autumn, and most females complete reproduction before October.

Ten of the 20 females of *P. maniculatus*, taken in May, contained embryos; five others were lactating. Lactating and pregnant females were collected on May 5, 1962, indicating that reproduction in some females began in early April. In September, 15 of 34 females were pregnant or lactating, whereas in October only two out of 15 females of *P. maniculatus* were reproducing. Only

one female of *P. maniculatus* was found to contain embryos in October. This large adult was taken on October 3, 1963, and had six embryos, each five millimeters long. She probably would have produced a litter later in October, and would have been nursing into November. A report of October breeding in north-central Colorado described nine of 23 females of *P. maniculatus* as being in a reproductive state; seven were lactating and one was pregnant between October 26 and 31, 1952 (Beidleman, 1954:118).

In the Museum of Natural History, the University of Kansas, there are 35 females of *P. maniculatus* more than 144 millimeters in total length taken from Mesa Verde in November, 1957 (Anderson, 1961:53). None of these contained embryos, and no pregnant females have been taken from the park in November.

P. truei and *P. maniculatus* reproduce at about the same time. A female of *P. truei* prepared as a specimen on May 10, 1964, contained four embryos, each 20 millimeters long, indicating a breeding time in mid-April. Svihla (1932:19) reported the gestation period for non-lactating *P. truei* to be 25 to 27 days and for lactating individuals, 40 days. Lactation tends to increase the gestation period of other *Peromyscus* by about five days (Asdell, 1964:266). The gestation period of nine non-lactating females of *P. m. rufinous* was reported by Svihla to be 23 to 24 days. Lactation increased the length of the period of gestation in this subspecies to between 23 and 32 days (mean for seven females 26.57 ± 0.73 , Svihla, 1932:19).

Females of *P. truei* were observed in various stages of reproduction from June through September. Ten of the 20 females of *P. truei* taken in September were reproducing; four contained embryos and the other six were lactating. In October, only one of 17 females caught in snap traps was lactating. Lactating females were caught in live-traps as late as October 23, although most females had ceased reproduction by then. No pregnant or lactating females were observed in November.

In *P. maniculatus*, puberty has been placed at 32 to 35 days for females weighing 13 grams, and in males at from 40 to 45 days, at weights of 15 to 16 grams (Jameson, 1953:45). In *P. truei*, the weight of the testes is reported to rise in March and diminish through September, with accessory organs following the same cycle (Asdell, 1964:267). Young of *P. truei* nurse for about one month, although some litters may not be weaned until 40 days of age. Young of *P. maniculatus* are weaned between 22 and 37 days of age (Svihla, 1932:30).

Twenty-six pregnant females of *P. maniculatus*, taken in the breeding seasons of 1961-1964, contained from one to eight embryos each; the mean was 4.65 ± 1.67 . Other investigators have found similar mean values in this species (Asdell, 1964:266).

Thirteen females of *P. truei* taken in the breeding seasons of 1961-1964, contained from three to six embryos each; the mean was $4.0 \pm .912$. Svihla (1932:25) reported litter sizes, at birth, of two to five and a mean of 2.84, in 19 litters. Other investigators have reported litter sizes of one to five with a mean of 3.4, and one to six with a mean of 3.6 (Asdell, 1964:268). Apparently *P. truei* does not have more than six young per litter.

In captivity, females of both species began reproduction in early February. These captives had been kept for several months at a temperature of 21 degrees Centigrade, and on a daily photoperiod of 15 hours. Some captive males had enlarged, scrotal testes in January; the extended photoperiod and warm tem-

perature probably influenced the breeding condition. In both species testes of wild males caught in autumn after late September and on through the winter were abdominal, except for one male of *P. maniculatus* which had enlarged, scrotal testes on October 15.

Dates at which different animals arrived at breeding condition varied, in part owing to subadults (young of the year) appearing in the catch from early summer to late autumn. Some adult females appeared to be pregnant or lactating throughout much of the summer and early autumn, whereas other females, that were caught a number of times, apparently reproduced only once in the summer.

Some females may fail to breed even though they are mature enough to do so. One female of *P. truei* captured eight times (August 30 to September 20) was a juvenile when first caught, and was classed as young (in postjuvener molt) on September 10. She did not reproduce in her first breeding season, unless she did so after September 20, which is unlikely. Another female of *P. truei* was an adult when first caught, and was caught 12 times (August 21 to October 25). At no time were her mammae enlarged and she was not lactating or pregnant. It is improbable that she reproduced earlier in the season, for teats of mice that have reproduced earlier usually are enlarged to such a degree that previous parturition is clearly indicated. It was surprising to catch a female, of any age, 12 times in two months without sign of reproductive activity.

Only one female of *P. maniculatus* did not show reproductive activity. She was a juvenile on July 19 when first caught; a subadult on August 28 when caught the third time, and an adult on October 23 when caught the fifth time.

Burt reported a rest period of a month or more in the summer, in Michigan, during which many females of *P. leucopus* did not reproduce. They began to breed again in late summer at about the time when young of the year began reproducing (Burt, 1940:17, 19). Abundant mast was correlated with reproductivity in autumn, according to Jameson (1953:54), who thought that "food is a basic determinant of the autumn reproduction" of *P. leucopus*.

Little has been written about the length of time males remain in breeding condition. Difficulties in determining breeding condition are many. Fertility customarily is determined by sectioning testes and noting the presence or absence, and relative abundance, of sperm. This procedure necessarily sacrifices the individual and indicates the breeding condition at only one moment and for only the individuals sacrificed. My observations of males caught a number of times in live traps shed some light on the breeding condition of males, but the investigator is likely to err in extrapolating physiological data from morphology when he notes whether the testes are abdominal or scrotal and whether they are enlarged or small. It was assumed that testes that have not descended, and that lie within the abdominal cavity, are not capable of producing viable sperm. This is the condition in most juveniles, and in all males during winter. As the breeding condition is attained, testes descend into the scrotum. Soon the testes and their accessory organs enlarge and are readily apparent.

Howard (1950:320) reported that numerous males of *P. leucopus* sired litters when their testes appeared to be abdominal, and therefore questioned whether the criterion of descended testes is valid as an indicator of breeding condition. My captive males of *P. maniculatus* and *P. truei* did not sire litters when their testes were abdominal, even though such males were left with

adult females for as long as four to five months (August through December). Captive pairs of both species yielded no evidence of reproductive activity until January when, as mentioned earlier, some of the males had scrotal testes. Young were born first in early February, although their parents had been confined together since the preceding August. Jameson reported the testes of fecund males of *P. maniculatus* as almost always 8.0 millimeters or larger (Jameson, 1953:50). Testes that are at least partly scrotal must be considered as being capable of producing motile sperm, even though this may not be the case for all individuals.

Toward the beginning and end of the breeding season the testes and accessory organs of wild mice were small and probably produced few if any sperm. At these times some males apparently were so frightened by being handled that the testes were retracted into the inguinal canals. It would have been easy to consider such males as having abdominal testes when in fact they did not. In such cases the scrotum usually was noticeably enlarged; it was found also that in many cases the testes returned to the scrotal position if the mouse was held gently for a few minutes. Careful handling of animals was found to prevent, or at least retard, retraction of the testes. Retraction of the testes from the scrotum was not a problem at the height of the breeding season when the testes were engorged.

I had originally assumed that all adult males would be fertile throughout the breeding season, and that any males with abdominal testes would be subadults or young of the year. This assumption was an oversimplification; all adult males did not reach breeding condition at the same time of year. My data do not support a firm conclusion, for it is difficult to follow non-captive individuals throughout a breeding season, owing to sporadic appearance of animals in traps. Nevertheless, observations of mice that were trapped a number of times indicated the following:

- 1) Some adult males that had abdominal testes in the middle of July reached breeding condition as late as late August and even late September.

- 2) Some juvenal males had scrotal testes at the time their postjuvinal molt was just beginning to be apparent on their sides. Most juvenal males did not have scrotal testes, and many juveniles that appeared repeatedly in traps from mid-July through late October did not attain breeding condition. A mouse that was a juvenile in mid-July must have been born in mid-June.

- 3) Apparently animals born early in the breeding season may reproduce later in that season, whereas those born later in the breeding season tend not to breed until the following year.

Possibly cooler evening temperatures in July and August, due to the relatively larger amounts of precipitation in those months, inhibit reproductive development of late-born young. Most plants have ceased vegetative growth and have produced seeds by this time; but the interrelationships between growing seasons, climatic conditions, and reproductive physiology are unknown.

Only one adult of each species had scrotal testes after late September; the *P. truei* had scrotal testes on October 24, 1963, and the *P. maniculatus* had scrotal testes on October 15 of that year.

GROWTH

Growth of captive *P. maniculatus* and *P. truei* is discussed in several reports. One of the most complete is that of McCabe and Blanchard (1950) on *P. m. gambelii* and *P. t. gilberti* in California. A detailed discussion of the dentition in *P. truei* and wear of the teeth in different age groups is given by Hoffmeister (1951). Molt in these species has been considered by a number of authors (Collins, 1918; McCabe and Blanchard, 1950; Hoffmeister, 1951; Anderson, 1961). The report by McCabe and Blanchard is valuable because molt is compared between the two species from the first to the twenty-first week of postnatal development.

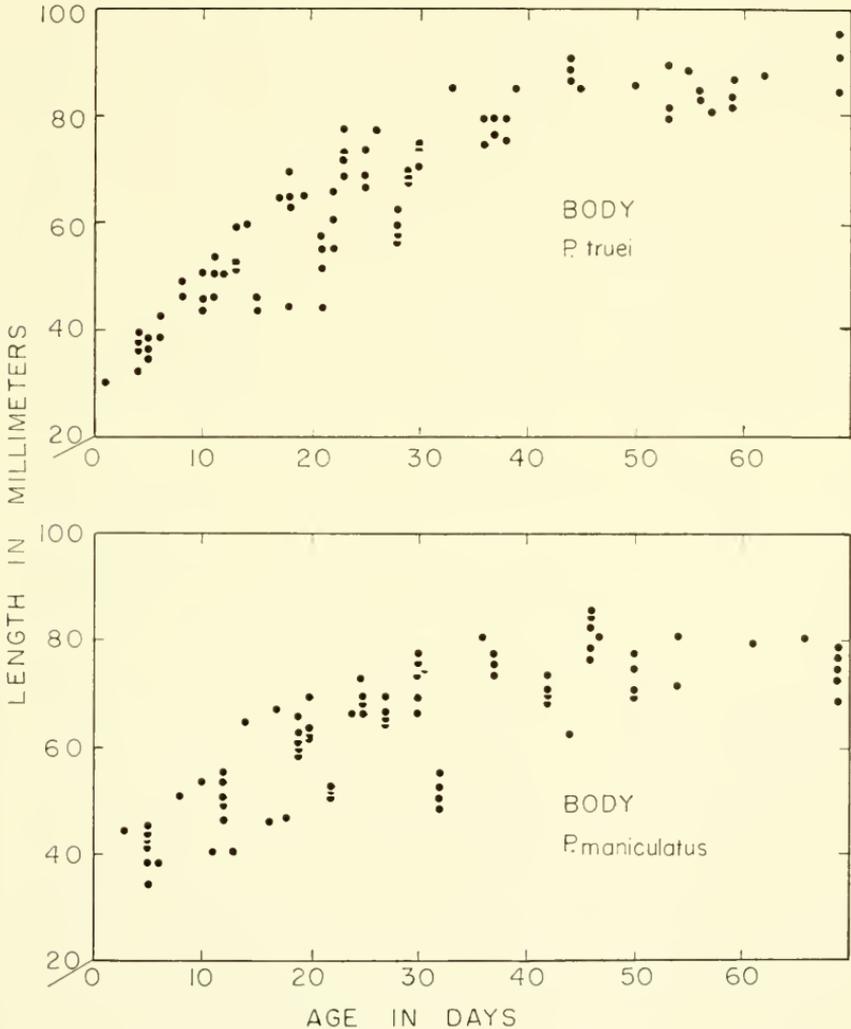


FIG. 18: Scatter diagram of postnatal growth of captive mice, showing increase in length of bodies from birth to 70 days of age. The records for *P. truei* represent 11 individuals of five litters; those for *P. maniculatus* represent 17 individuals of four litters.

The thoroughness of the above-mentioned studies is readily apparent to those who have worked with mice of the genus *Peromyscus*. Nevertheless, the ecology of local populations of *P. maniculatus* and *P. truei* as reported for the San Francisco Bay area (McCabe and Blanchard, 1950) has little relationship to the ecology of mice of other subspecies of these species, in southwestern Colorado. Indeed, the preferred habitats, and to some extent the behavior, differ strikingly in Colorado and California.

Figures 18 and 19 show that some litters grow appreciably faster than

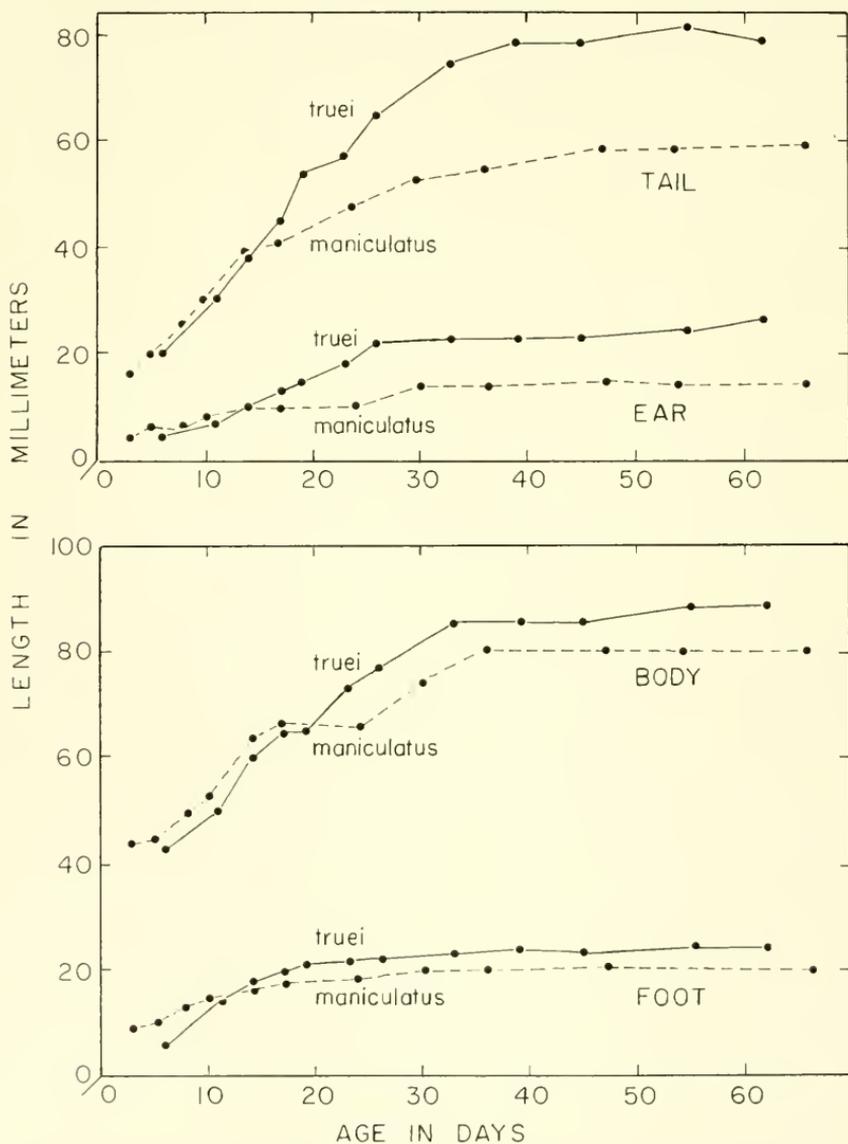


FIG. 19: Graphs showing postnatal growth of solitary captive individuals of *P. truei* and *P. maniculatus*, representing the only young in each of two litters.

others, but the end results are about the same. Since the young were measured at irregular intervals, statistical procedures for calculating confidence limits of the curves were not applicable.

Solitary young reared by one female of each species, attained maximum size more rapidly than animals having litter mates (Fig. 19). Nevertheless, solitary individuals and individuals from litters all reach essentially the same size 50 days after birth.

The gestation time of *P. truei* is several days longer than that of *P. maniculatus*, and the young of *truei* are fewer and heavier than those of *maniculatus*. As would be expected, *truei* remains in the nest longer and nurses longer than *maniculatus*.

Young of each species grow rapidly for the first month, and attain, in that time, the largest percentage of their adult size; they grow rapidly up to sometime between the thirtieth and fiftieth days. Thereafter the rate of growth diminishes and the animals begin to gain weight rather than continuing to extend the lengths of the body and appendages.

Figure 19 reveals that the appendages of young *maniculatus* attain most of their length about a week earlier than those of *truei*. Young *truei* acquire mobility and coordination somewhat later than young *maniculatus*, but both species are seemingly equal in these respects by about the end of the second week.

Length of gestation period, number and size of embryos, amount of time spent in the nest, and time required for bodily growth are all of major importance in determining the relative success of *truei* and *maniculatus*. These parameters will be considered further in the discussion.

PARENTAL BEHAVIOR

In the laboratory, pregnant females were supplied with either kapok, cotton, or a piece of burlap with which to make a nest. The kapok or cotton was used directly by the mice in constructing a hollow, compact, moundlike nest. When burlap was used for nest building, the female first completely frayed the cloth by chewing it into a fluffy mass of fibers.

When the top of a nest was opened to inspect young, the female would attempt to pull the nesting material back into shape by means of forefeet and teeth. The mother's defensive posture was to cover the young with her body, often lying over them and facing upward, toward the investigator. In this semi-recumbent position, the female would attack the investigator's fingers with her forefeet and teeth. Often the female would stand bipedally and use the forefeet and teeth to mount the attack. If at this time a young chanced to wander away from the mother, she would quickly pick it up and place it in the nest at her feet.

When disturbed, females of both species, but especially *P. maniculatus*, often dove headlong under their nest or into the wood shavings on the floor of the cage. This type of retreat was most often used when young were nursing. Time is required even by the mother to disengage nursing young, and this mode of escape is the most expedient. The mother disengaged nursing young by licking around their faces and pushing with her paws.

Nursing females of both species tolerated the male parent in the nest. A male and female often sat side by side in the nest and by means of their bodies participated in covering the young. Males were not observed to attempt any

defense of the nest, or of the young. Females were tolerant of older young in the nest when another litter was born and was being nursed. In one nest, a female of *P. truei* gave birth to a litter of three when her older litter was 29 days old. The three older young continued to nurse until they were 37 days old, at which time they were removed from the cage. The female appeared tolerant of this nursing by members of the older litter, but appeared to give preference to the wants of the younger offspring.

One female of *P. truei* lost or killed all but one young of her litter; at about the same time, a *P. maniculatus* and all but one of her young inexplicably died. Since the remaining young *maniculatus*, a male, was just weaned and was considered expendable, I placed him in the cage with the female *truei* and her 33-day-old, male offspring. The reaction to the newcomer was unexpected. The female immediately covered the *P. maniculatus* and her own young and prepared to defend them against me. Later, when the *P. maniculatus* was disturbed, he had only to emit a squeak and the female *truei* would run to cover and protect him. When the young male of *P. truei* was 69 days old the female kept him out of the nest, but still kept the male *maniculatus* in the nest with her. Although the female was somewhat antagonistic to her own young, she did not injure him, but only kept him out of the nest. The male *truei* was left in the cage with his mother and the *P. maniculatus* from September 23 to December 10. None of the mice had any apparent cuts on the ears or tail to indicate fighting. As much as seven months after the *P. maniculatus* was introduced into the cage, the female *truei* continued to cover him with her body whenever there was a disturbance. The male *maniculatus* not only tolerated this attention, but ran under the female *truei* when frightened. "Adoption" of young of another species has been reported for a number of animals, but, without further evidence, it is not possible to postulate that such adoptions occur between species of *Peromyscus* in nature.

Young males are tolerated by their mothers after weaning. One young male *maniculatus* was left in the cage with his mother from the time of his birth in autumn until late February of the following year. A litter was born on February 24. A young male *P. truei* was also left in the cage with his mother until he had acquired most of his postjuvinal pelage; the female and male usually sat together in the cage.

Females of both species sometimes eat their young when the young die shortly after birth. One female of each species killed three of her four young, and ate their brains and viscera. In one of these cases, the female, of *P. maniculatus*, also died; the female of *P. truei* was the same one that adopted the surviving *P. maniculatus*. The female *truei* continued to nurse her one remaining young for at least several days after killing three of his litter mates. A reason for this cannibalism might have been that I had fed these mice for several weeks on a mixture of grains low in protein content. Inadequacy of this diet for nursing females may have caused them to become cannibalistic. The feed of all captives was changed to Purina Laboratory Chow after the young were killed.

Transportation of Young

Females of both species transported their young either by dragging them collectively while the young were attached to mammae, or by carrying them one at a time in the mouth. Since mice of the subgenus *Peromyscus* have three

pairs of nipples, they probably transport only six young collectively. Svihla (1932:13) has stated that both pectoral and inguinal teats are used in transporting young, in contrast to Seton's reputed assertion that only inguinal nipples were used. But Svihla neglected to cite Seton's complete statement. Seton (1920:137) recorded a litter of three as using only the inguinal mammae, but on the following page recorded the use of both inguinal and pectoral mammae by another litter of four. My findings agree with those of Svihla. Nursing females of both species were removed periodically from cages by lifting them by the tail. The young would hang onto the mammae and the female would clutch the young to her with all four feet. Young two weeks old or older crawled behind the mother while nursing.

The method of transporting young in the mouth has been mentioned by Seton (1920:136) and described by Lang (1925) and Hall (1928:256). These authors report that the mother picks the young up in her paws, and places it ventral-side up in her mouth, with her incisors around it. The young are not picked up by the skin on the nape of the neck, as are the juveniles of dogs and cats. I have found that females of both species of *Peromyscus* carry their young ventral-side up in their mouth while the young are small, and sometimes when the young are older. Generally, when females of *P. truei* moved young weighing more than 10 grams, the female grasped the young from the dorsal side, across the thorax just posterior to the shoulders, and held them with the incisors more or less around the animal. Perhaps this method was used with older young because of the observed tendency of the larger young to resist being turned over and grasped from the ventral side, and because their increased weight would have made it difficult, if not impossible, for the mother to pick them up with her paws. The young rarely resisted the efforts of the mother to move them by this method; when grasped across the thorax by the mother, the young would remain limp until released. Some females of *P. truei* would drag almost fully grown young back into the nest in this manner. I have not observed older young of a comparable age to be moved by females of *P. maniculatus*. The females of *P. maniculatus* appear to be somewhat less concerned than those of *P. truei* for the welfare of their young once they are mobile and close to being weaned.

The following listing describes changes in postnatal development of young, of each species, from birth to nine weeks of age.

P. truei

FIRST WEEK: At birth, young are helpless, red overall, small with wrinkled skin. Pinna of ear folded over and closed; eyes closed; digits not separated from rest of foot.

Redness diminished by fourth day.

Hair apparent by fifth day; dorsal one-half or two-thirds of body more darkly pigmented than venter by fourth day.

Young squeak loudly and suck; sometimes crawl, but drag hind legs.

P. maniculatus

At birth, young are helpless, red overall, smaller than *P. truei*, skin wrinkled. Ear, eyes, and digits as in *P. truei*.

Redness decreases and disappears by fourth day.

Hair apparent by fourth day; body bicolored by end of week.

Young squeak loudly; sucking more pronounced than in *P. truei*; may crawl, but drag hind legs.

SECOND WEEK: Appreciable increase in size; head about 60 percent larger than at birth, by 14th day, and still large in proportion to body.

Toes on hind foot separated more from foot.

Body well haired by end of week; dorsum dark gray, venter whitish; tail bicolored in most, but not haired.

Pinna of ear unfolded and open by end of week.

Through day 10, use hind legs to push, but by end of week use legs to crawl; difficult to hold, squirm but do not bite.

Walk behind mother while nursing; agile.

As in *P. truei*.

As in *P. truei*, but somewhat more advanced.

Body well haired by end of week; dorsum dark gray with brownish tint; venter whitish; tail bicolored in most, but not haired.

As in *P. truei*, but development somewhat more advanced.

Crawl well by end of week; difficult to hold, squirm but do not bite; agile.

THIRD WEEK: Eyes open on 16th to 21st day.

Gray pelage of dorsum brownish. Apparently there is a molt line progressing posteriorly from nose; the molt line has moved to shoulder region by end of week; pelage anterior to line browner, grayer posterior to it.

Tail haired and weakly bicolored in some individuals by end of week.

Young walk and jump well; squirm but rarely bite.

Eyes open on 16th to 20th day, partly open earlier.

Pelage of dorsum brownish; molt line across shoulders progressing posteriorly; browner anterior to line, grayer posterior to it.

Tail haired and bicolored in all individuals.

Young walk and jump well; fight and bite when handled.

FOURTH WEEK: Begin to eat solid foods at 23-29 days, but also nurse.

Molt line about $\frac{3}{4}$ inch posterior to head. Juvenal pelage completed by end of week. Some young have brownish hair on front legs.

Young roll over on backs and use feet to ward off litter mates that are dropped into nest, or into container, with them.

Some young eat grain by 24th day; others continue to nurse.

Juvenal pelage complete; no sign of postjuvenal molt.

As in *P. truei*; also, all jump well, and fight fiercely when handled.

FIFTH WEEK: Young weaned on 30th to 40th day; some nurse beyond 30th day if female is lactating.

Juvenal pelage complete and no postjuvenal molt apparent on dorsum.

All young weaned before or by end of week; none observed to nurse beyond 30th day, even if female is lactating.

Juvenal pelage complete; postjuvenal pelage not apparent on most, but probably present on all, and concealed under juvenal pelage.

SIXTH WEEK: Postjuvenile pelage apparent in most individuals under juvenile pelage, especially along lateral line.

Postjuvenile molt apparent in most young; almost complete in some, except above tail and on flanks.

SEVENTH WEEK: Postjuvenile pelage apparent in most young; in some the molt line has progressed well up on the sides, but not to mid-dorsum.

Postjuvenile pelage apparent in all young; less distinct molt line than in *P. truei*.

EIGHTH WEEK: All individuals growing; total lengths of 156-170 millimeters; weight 17-22 grams.

Growth completed in some individuals; those in larger litters have total lengths of 128-144 millimeters; weight 14-17 grams.

NINTH WEEK: Testes partly scrotal in one male on 59th day.

"Scrotum in season usually large, vaginae open, evidence of coitus common." (McCabe and Blanchard, 1950:39).

New brown pelage encroaching on saddle and on hind legs; postjuvenile molt completed in some individuals by eleventh week.

Postjuvenile molt completed in some individuals by end of week. New pelage tends to be concealed under juvenile pelage longer than in *P. truei*.

CHANGES OWING TO INCREASE IN AGE

Increase in length of limb bones, changes in proportion of bones in the skull, eruption and degree of wear of teeth, and changes in pelage can be used to ascertain relative age. Different investigators might choose different limits for the three categories young, subadult, and adult. Museum specimens were assigned to one of five age groups listed below mostly on the basis of tooth wear, essentially as described by Hoffmeister (1951:1).

Juvenile: M3 just breaking through bony covering of jaw or showing no wear whatsoever.

Young: M3 worn smooth except for labial cusps, and M1 and M2 showing little or no wear.

Subadult: M3 worn smooth; labial cusp may persist, but is well worn; M1 and M2 having lingual cusps worn, but not smooth; labial cusps showing little wear.

Adult: Lingual cusps worn smooth and labial cusps showing considerable wear; labial cusp of M3 may persist.

Old: Cusps worn smooth; not more than one re-entrant angle per tooth discernible, frequently none.

For live animals examined in the field, criteria based on pelage and breeding condition were used, as follows:

Juvenile: Only gray, juvenile pelage present.

Young: Subadult pelage apparent on lateral line or on sides; body usually smaller than in adults.

Subadults: Subadult pelage having mostly replaced juvenile pelage; mice often as large as adults; testes of males often abdominal in breeding season; gray juvenile pelage may persist on head of some individuals.

Adult: Adult pelage present; body usually largest of all animals in population; females may have enlarged mammae from nursing previous litters; testes of males usually scrotal in breeding season; gray pelage may be present on head of some individuals.

Old individuals in the field could not be distinguished from adults; hence any animals that appeared older, or more developed, than subadults were classified as adults.

In *P. truei*, subadult pelage appears first on the lateral line or on the flanks; new pelage is ochraceous and contrasts markedly with the gray juvenal coat. In *P. maniculatus*, the subadult pelage contrasts less with the juvenal coat; the new pelage progresses from anterior to posterior over the body in the same manner as in *truei*, but replaces the juvenal coat in a less distinct manner than in *truei*. As a result, contrast often is lacking between juvenal and subadult pelages in *maniculatus* making it difficult to assign an individual to one of these two age categories when examined in the field. In museum specimens, the subadult pelage is much more noticeable because it can be compared with the pelages of other specimens. The subadult pelage in *P. maniculatus* is duller than the adult pelage: In *P. truei* the subadult and adult pelages appear to have an equal sheen.

In early winter, the post-juvenal pelage acquired by young individuals of *P. truei* was thick and luxuriant and indistinguishable from the winter pelage of adults. My observations lead me to conclude that individuals born late in the breeding season molt from juvenal summer pelage directly into winter adult pelage. Technically, this new coat is the post-juvenal one, yet it cannot be distinguished as such after the molt is completed.

ANOMALIES AND INJURIES

Anatomical anomalies were rare in the individuals of *Peromyscus* that I examined. When anomalies were found they were striking, principally because of their low rate of occurrence.

One female of *P. truei*, born in captivity, had a congenital defect of the pinna of the right ear, noted on the fifteenth day after birth. Closer examination then and later revealed that the pinna was normal in all respects except that the tip was missing. The tip showed no evidence of injury. When the mouse was subadult, this defective pinna was approximately half as long as the normal pinna. The topmost part of the defective pinna was somewhat more constricted in circumference than the normal one.

On September 11, 1963, a subadult male of *P. truei* was captured that had five functional toes on its right front foot, the only one of more than 175 individuals caught and handled in the field that exhibited polydactyly. The front foot was examined closely in the field, but it could not be determined how or where the extra bones of the sixth toe articulated. *Peromyscus* normally has four full-sized toes on each front foot, and a small inner toe hardly more than an enlarged tubercle, having no nail.

A few mice of both species had broken toes or claws torn off. Such injuries were more common on toes of the hind foot. In several instances the toes were shortened, as if by marking, although the animals concerned had been

marked earlier by clipping toes other than the injured toes. The reason for these injuries is not apparent, although they could have been caused by fighting, or from having been caught in doors of Sherman live traps.

Toes of several mice were swollen and inflamed due to small glochids of cacti that were stuck in them. Apparently the mice had stepped on the glochids by chance, for I found no evidence that *Peromyscus* of either species eats cacti.

One *P. truei* had a broken tail; three other individuals had tails about one-half normal length. One *P. maniculatus* had a shortened tail. Some of these injuries probably were caused by the Sherman live traps; several individuals of *P. truei* were released after having been caught by the tail by the spring-loaded door of these traps.

On October 17, 1963, an adult *P. truei* had a bleeding penis; when this mouse was recaptured on October 25, the injury was healed.

Losses Attributed to Exposure in Traps

Observations of wild mice caught in live traps suggest that metabolic maturity is reached later than physical and reproductive maturity. In such trapping, it became apparent that juvenal and young mice suffered from exposure to cold and to heat much more than did subadult or adult mice. Although traps were carefully shaded and ample nesting material and food provided, some mice died in the traps. An overwhelming majority of these mice were juveniles and young.

Traps were checked in the morning, both in the summer and autumn, yet mice died in traps that were barely warm to the touch, in summer, and cool to the touch in autumn. Older mice frequently were found in traps that were warm, or even hot, to the touch; yet the older mice rarely died in such traps. Apparently the tolerance of adults is much greater to heating and chilling. Greater bulk and perhaps longer pelage in adults might provide sufficiently better insulation to account for this difference.

Occasionally juvenal mice were found in traps in a sluggish and weakened condition, especially in autumn when nights were cool. In such cases the mice were either cupped in the hands and warmed until lively enough to fend for themselves, or, if especially weakened, were taken to the laboratory. None of such animals that were returned to the laboratory lived for more than two weeks. Most of those released in the field did not reappear in the traps.

I conclude that juvenal and young mice placed under stress by overheating or cooling die immediately or live only a few days. Subadult and adult animals tolerate more extreme conditions of overheating or cooling, presumably because they are able to regulate their internal temperature better, by either losing or retaining heat more effectively.

Mice found dead in overheated traps had salivated heavily, and may also have licked the fur on their chests to increase heat dissipation. One such adult, of *P. truei*, had a wet chest when he was taken from a warm trap; when released, this mouse ran to a nearby plant of *Comandra umbellata*, and ate a few of the succulent leaves before running off. This individual was trapped several times later in the summer, and apparently suffered no ill effects from the exposure.

Dental Anomalies

Abnormalities in the formation and occlusion, or decay of teeth, are relatively rare in wild mammals. Of all bodily structures, the teeth apparently are under the most rigid genetic controls; they form early in the embryo and follow rigidly specified patterns in their ontogeny. Apparently any deviation from the normal pattern of tooth formation is quickly selected against. All specimens of *P. m. rufinus* and *P. t. truei* in the collection of the Museum of Natural History at the University of Kansas, and in my collection, were examined for dental anomalies. A total of 317 specimens of *P. m. rufinus* and 54 specimens of *P. t. truei* were examined. The following specimens were found to have abnormalities:

K. U. 69361, *P. maniculatus*, adult: Small bundles of plant fibers are lodged between all upper teeth and have penetrated the maxilla anterior to the left M1. The maxillary bone is eroded away from the roots of all teeth. The anteriormost roots of both lower first molars are almost completely exposed, because the dentary has been abraded away.

K. U. 76041, *P. maniculatus*, young: A piece of plant fiber is wedged between the left M2 and M3. The maxillary bone has eroded away from around the roots of M3, indicating the presence of an abscess in this area.

K. U. 69362, *P. maniculatus*, adult: All teeth in the lower right tooth-row are greatly worn, especially on the lingual side. The labial half of the right M1 is all that remains; decay is apparent both in the crown and roots on the lingual side of this tooth.

K. U. 69397, *P. maniculatus*, old: The maxillae have eroded away from around the anterior roots of each first upper molar, leaving these roots unsupported.

C. L. D. 231, *P. maniculatus*, old: The teeth in this female are greatly worn; re-entrant angles are not visible in any teeth. A circular hole, 0.1 millimeter in diameter, exists in the dentine immediately over (when viewed from the underside of the skull) the posterior root of the right M1. The crowns of the teeth are greatly reduced in height, and the dentine is thin.

Anomalies in the Skull

Wormian bones and other abnormalities in the roofing bones are noted, as follows:

K. U. 76090, *P. maniculatus*, young: The interparietal is divided; the divided suture is in line with the suture between the parietals. The interparietal is 7.8 millimeters long.

K. U. 76091, *P. maniculatus*, young: A wormian bone, 0.5 millimeter by 0.2 millimeter, lies between the anterior border of the interparietal and the posterior border of the left parietal, at a point midway between the center line of the skull and the posterolateral border of the parietal bone.

C. L. D. 248, *P. maniculatus*, adult: An oval wormian bone, 1.1 millimeters long and 0.6 millimeter wide, lies between the parietals at their posterior margin; the long axis of the bone is parallel to the long axis of the skull.

C. L. D. 246, *P. maniculatus*, juvenal: The interparietal is divided equally by a suture. An oval wormian bone, 0.3 millimeter long and 0.1 millimeter wide, lies between the frontals, midway between the anterior and posterior borders of these bones.

C. L. D. 656, *P. maniculatus*, young: A small, rounded wormian bone lies between the right parietal and interparietal, lateral to the posterior junction of the suture between the parietals. This bone extends anteriorly into the parietal bone from the suture of the interparietal and parietal. This bone is 0.7 millimeter wide, and extends 0.6 millimeter into the parietal.

C. L. D. 662, *P. maniculatus*, subadult: An elongated, diamond shaped wormian bone closes the suture between the parietal bones. This bone is 2.3 millimeters long and 0.8 millimeter wide.

K. U. 34735, *P. truei*, old: The anterior one-quarter of the left parietal bone

is slightly depressed; and the posterior one-third of the left frontal and anterior one-quarter of the left parietal are thin and sculptured. This malformation of the roofing bones posterior to the orbit probably is not the result of a break, for the orbital part of the frontal bone is normal. The frontal-parietal sutures are in the normal positions on both sides of the skull.

The above-mentioned anomalies do not appear to be correlated with age or locality at which the specimens were taken. Apparently such anomalies are present throughout the population, but in a small percentage of specimens.

FOOD HABITS

Mice of the genus *Peromyscus* are known to eat a wide variety of plants and arthropods, and to be highly opportunistic in selection of food (Cogshall, 1928; Hamilton, 1941; Williams, 1955, 1959a; Jameson, 1952; Johnson, 1962). In order to determine possible food preferences, captive mice of both species were fed plants indigenous to Mesa Verde. Entire plants were used whenever possible; available seeds also were offered (Tables 5, 6). All feeding experiments were replicated with at least six different individuals in order to minimize the trends resulting from individual preferences or dislikes. The mice of each species tended to be consistent in their feeding.

The plant species listed in Tables 5 and 6 were those that were eaten or rejected by a majority of the individuals tested.

Plant material eaten by *P. maniculatus* and refused by *P. truei* included only the leaves and stem of *Vigniera multiflora*. Plant material eaten by *P. truei* and refused by *P. maniculatus* included the leaves of *Calochortus gunnisonii* and the leaves and stem of *Erigeron speciosus*.

Plant material eaten by captives of both species included *Calochortus gunni-*

TABLE 5—Plants, or Parts of Plants, Eaten by Captive Individuals of *P. truei* in Mesa Verde National Park, Colorado. O = not eaten, + = eaten, — = not offered.

Species of Plant	Leaves	Stem	Flower	Seeds
<i>Amelanchier utahensis</i>	—	—	—	+
<i>Calochortus gunnisonii</i>	+	+	—	+
<i>Chaenactis douglasii</i>	0	0	—	—
<i>Chrysothamnus depressus</i>	0	0	0	—
<i>Chrysothamnus nauseosus</i>	+	0	0	—
<i>Comandra umbellata</i>	+	+	—	—
<i>Erigeron speciosus</i>	+	+	—	—
<i>Eriogonum alatum</i>	—	—	—	+
<i>Juniperus osteosperma</i>	—	—	—	+
<i>Lupinus caudatus</i>	0	0	+	—
<i>Lithospermum ruderales</i>	0	0	—	0
<i>Mellilotus alba</i>	+	+	+	+
<i>Mellilotus officinalis</i>	+	+	+	—
<i>Orthocarpus purpureo-albus</i>	+	+	+	+
<i>Pedicularis centranthera</i>	+	+	—	—
<i>Penstemon linarioides</i>	+	+	—	+
<i>Pinus edulis</i>	—	—	—	+
<i>Polygonum sawatchense</i>	+	+	—	0
<i>Solidago petradoria</i>	0	0	0	—
<i>Vigniera multiflora</i>	0	0	0	0

sonii—stem and seeds; *Comandra umbellata*—leaves and stem; *Eriogonum alatum*—seeds; *Penstemon linarioides*—leaves and stem; *Pinus edulis*—seeds; and *Juniperus osteosperma*—seeds.

Plant materials refused by both species of mice included the leaves and stem of *Chaenactis douglasii*, the leaves, stem and seeds of *Lithospermum rudale*, and the leaves, stem and flowers of *Solidago petradoria*.

Cricetine rodents chew plant and animal foods thoroughly; contents of their stomachs appear as finely-particulate fragments. These fragments invariably contain pieces of epidermis from ingested plants. Due to the presence of cutin in the cell walls, epidermis is last to be digested.

Microscopic analysis of plant epidermis is useful in helping to determine food habits of various animals (Dusi, 1949; Williams, 1955, 1959a; Brusven and Mulkern, 1960; Johnson, 1962). The microscopic analysis of stomach contents provides a practical method of determining which plants are eaten by rodents. Contents of stomachs and intestines were removed from mice caught in snap traps, and from preserved specimens. The contents were placed on a piece of bolting silk, washed thoroughly with running water, stained with iron-hematoxylin and mounted on slides, or stored in 70 per cent ethanol (Williams, 1959a; Douglas, 1965).

TABLE 6—Plants, or Parts of Plants, Eaten by Captive Individuals of *P. maniculatus* in Mesa Verde National Park, Colorado. O = not eaten, + = eaten, — = not offered.

Species of Plant	Leaves	Stem	Flower	Seeds
<i>Artemisia ludoviciana</i>	0	0	—	—
<i>Calochortus gunnisonii</i>	0	+	—	+
<i>Chaenactis douglasii</i>	0	0	—	—
<i>Comandra umbellata</i>	+	+	—	—
<i>Erigeron speciosus</i>	0	0	—	—
<i>Eriogonum alatum</i>	—	—	—	+
<i>Juniperus osteosperma</i>	—	—	—	+
<i>Lappula redowskii</i>	0	0	—	+
<i>Lithospermum rudale</i>	0	0	—	0
<i>Orthocarpus purpureo-albus</i>	0	0	+	+
<i>Penstemon linarioides</i>	+	+	+	+
<i>Pinus edulis</i>	—	—	—	+
<i>Purshia tridentata</i>	+	+	—	—
<i>Sitanion hystrix</i>	0	0	—	0
<i>Solidago petradoria</i>	0	0	0	—
<i>Sphaeralcea coccinea</i>	+	+	—	+
<i>Stipa comata</i>	0	0	—	+
<i>Viguiera multiflora</i>	+	+	—	—

In order to analyze these epidermal fragments, a collection of plants was made within the park. Slides of the epidermis of these plants were prepared and analyzed for diagnostic characters (Douglas, 1965:197-199). Features such as the stomatal arrangement in relation to subsidiary cells; the types of trichomes, scales and glands; the cellular inclusions such as starch grains, mucilage and resins are of taxonomic value (Metcalfe and Chalk, 1950). The configuration of the anticlinal cell walls is useful in separating species that are similar in other respects (Douglas, 1965:199).

The following species of plants, and other food items, were identified in the stomach or intestinal contents of *Peromyscus maniculatus*:

<i>Agropyron smithii</i>	<i>Penstemon linarioides</i>
<i>Artemisia</i> sp.	<i>Phlox hoodii</i>
<i>Eriogonum umbellatum</i>	<i>Stipa comata</i>
<i>Lupinus ammophilus</i>	Arachnid legs

Stomach and intestinal contents of *P. truei* contained the following food items:

<i>Artemisia nova</i>	<i>Eriogonum</i> sp.
<i>Artemisia</i> sp.	<i>Gutierrezia sarothrae</i>
<i>Penstemon</i> cf. <i>barbatus</i>	<i>Yucca</i> sp.
<i>Penstemon</i> cf. <i>linarioides</i>	Chitin
<i>Poa fendleriana</i>	Feathers
Arachnid legs	

Many of the plants eaten by the mice had large numbers of crystals in the epidermis. Druses were the most abundant, but raphid crystals also were seen. Every slide contained at least one species of plant which contained druses. Such crystals are composed mostly of calcium oxalate (Esau, 1960: 41). In Mesa Verde, families of plants having crystals include: Boraginaceae, Chenopodiaceae, Compositae, Cruciferae, Leguminosae, Liliaceae, Malvaceae, Onagraceae, Rosaceae, and Saxifragaceae. Calcium oxalate is a highly insoluble compound and is innocuous if it passes through the gastro-intestinal tract without being absorbed. In rates of the genus *Neotoma*, some calcium oxalate passes through the intestines unchanged, but large amounts of calcium are absorbed through the intestine. The urine of pack rats is creamy in color and contains calcium carbonate. It is not understood how these rats metabolize the highly toxic oxalic acid, when converting calcium oxalate to calcium carbonate (Schmidt-Nielsen, 1964:147-148). Apparently calcium oxalate passes through the intestine unchanged in both species of *Peromyscus*, for their urine is clear and yellowish.

Although both species of mice appear to prefer plants having soft leaves, some plants having coarse leaves also are eaten. Many of the slides contained isolated sclerids. The stomach contents of one individual of *P. truei* contained a small fragment of the epidermis of *Yucca*. This fragment may have come from a young shoot. It is unlikely that *Peromyscus* would eat the larger, coarser leaves of *Yucca*.

Pinyon and juniper nuts were found in nests of all mice. Captive mice were especially fond of pinyon nuts, and these probably provide a substantial part of the diet of *Peromyscus* in the autumn and early winter. The winter staple of *P. truei* appears to be juniper seeds. Nesting sites of this mouse often could be located by the mounds of discarded seeds lying nearby.

Both species eat pinyon and juniper seeds; since *P. truei* lives in the forest, it has better access to these foods than does *P. maniculatus*. Mice remove the embryos of juniper seeds by chewing a small hole in the larger end of the seed. The seed coats of juniper are extremely hard, and a considerable amount of effort must be expended to remove the embryo. Captives discarded the resinous and pithy, outer layers of juniper berries. Individuals of *P. truei* are adept climbers. Since many juniper berries remain on branches throughout the winter, the ability of these mice to forage in the trees would be especially advantageous when snow covers the ground.

WATER CONSUMPTION

Peromyscus maniculatus is ubiquitous, occurring in habitats ranging from mesic boreal forests to arid southwestern deserts. Most subspecies of *P. maniculatus* live in moderately mesic or near-mesic environments, but a few have adapted to arid conditions. It has been assumed that the success of *P. maniculatus* in inhabiting such diverse habitats is associated with its adaptability to different kinds of food and varying amount of available water (Williams, 1959b:606).

Throughout its range *P. maniculatus* coexists with one or more other species of *Peromyscus* that are more restricted in distribution. *Peromyscus truei* is one such species.

Both species live under xeric or near-xeric conditions, for the climate of Mesa Verde is semiarid. Other than a few widely-scattered springs, there are no sources of free water on the top of the Mesa Verde land mass; thus animals inhabiting the park must rely upon moisture in the plants and other foods they eat, or upon dew.

Several investigators have studied water consumption in mice of the genus *Peromyscus* (Table 7). Dice (1922) did so for the prairie deer mouse, *P. m. bairdii*, and the forest deer mouse, *P. leucopus noveboracensis*, under varying environmental conditions. He found that both species drank about the same amounts of water per gram of body weight, and that food and water requirements did not differ sufficiently to be the bases for the habitat differences between these species. Neither of his samples was from an arid environment. Chew (1951) studied water consumption in *P. leucopus*, and recently reviewed the literature on water metabolism of mammals (Chew, 1965). In his studies of five subspecies of two species of *Peromyscus*, Ross (1930) found significant differences in water consumption between species but not between subspecies within a species. One of the subspecies of *P. maniculatus* tested was from a desert region, whereas the other two were from mesic areas along the coast of California.

Lindeborg (1952) was the first to measure water consumption of both *P. m. rufinus* and *P. t. truei*, the species and subspecies with which my experiments are concerned. Lindeborg also tested the ability of five races of *Peromyscus* to survive reduced water rations. Unfortunately, the subspecies chosen for these experiments did not include *P. t. truei* or *P. m. rufinus*. Lindeborg (1952:25) found that the "amounts of water consumed by various species of *Peromyscus* from different habitats within the same climatic region were not conclusively different." However, he did find significant differences between some subspecies from different geographical areas. For example, he found no significant difference in water consumption between *P. m. bairdii* from Michigan and either *P. m. blandus* or *P. m. rufinus* from New Mexico, but he found a highly significant difference between *P. l. noveboracensis* from Michigan and *P. l. tornillo* from New Mexico. Lindeborg also found that the subspecies of *Peromyscus* that consumed the least water, and that were best able to survive a reduced water ration, were those from the more xeric climatic areas.

Some mammals may be able to change their diets in times of water stress, and thereby compensate for a shortage of water. At such times, *Dipodomys* selects foods with high percentages of carbohydrates and conserves water by reducing the amounts of nitrogenous wastes to be excreted (Schmidt-Nielsen *et al.*, 1948).

Williams (1959b) found that *P. m. osgoodi* from Colorado drank more water on a diet rich in protein than on one rich in carbohydrates. But, her mice on a high carbohydrate diet used less than a normal amount of water for a period of only five weeks; at the end of the five weeks they were drinking about as much as they had been when on the control diet of laboratory chow. Likewise, mice adjusted to the high protein diet by consuming more water; but by the end of the fifth week their daily water consumption approximated the amount drunk when fed on laboratory chow. Because of these results, Williams questioned the validity of the assumption that *P. maniculatus* is able to inhabit a diversity of habitats because of its adaptability with respect to food and water requirements.

I conducted a series of experiments on water and food consumption by individuals of *P. truei* and *P. maniculatus*. It was thought that if there were differences in water or food consumption, or both, knowledge of them might help to explain the obvious differences in habitat preferences of these two species in Mesa Verde National Park.

In August of 1965, 30 individuals of *P. truei* and *P. maniculatus* were trapped in Mesa Verde National Park at elevations of 7000-8400 feet, and transported to Lawrence, Kansas, where the experiments were carried out.

Mice were housed in individual metal cages (10 x 7.5 x 5 inches), having removable tops of wire mesh, and an externally-mounted water bottle that had a drop-type spout extending into the cage. Cages were on one of five shelves of a movable tier of shelving, and were rotated randomly, from one shelf to another, each week. A layer of dry wood shavings covered the bottom of each cage. A control cage was similarly equipped.

The mice were kept in a room in which temperature and photoperiod were controlled. The ambient air temperature of this room was 20 to 23 degrees Centigrade throughout the experiments, and averaged 21 degrees. Humidity was not controlled, but remained low throughout the experiments. The room was illuminated for eight hours each day, from about 9 a. m. to 5 p. m.

The animals were fed at least once a week, at which time all remaining food was weighed and discarded, and the remaining water was measured. Tap water was used in all of the experiments. The cages were cleaned each week. Each time the cages containing mice were handled, the control cage was handled in the same way. The amount of evaporation was determined each week by measuring the water remaining in the bottle of the control cage.

Water and food consumption of individuals of *P. maniculatus* and *P. truei* were measured when the mice were fed diets of differing protein content. To my knowledge, the only other study in which water consumption was measured for mice of the genus *Peromyscus* on diets of different protein contents was by Williams (1959b). Because of the limited number of animals available, it was decided that the best results could be obtained by placing all individuals on the same diet for a predetermined number of weeks, then on a second diet for a certain period, and so on.

Each mouse was weighed at the beginning, at the mid-point, and at the end of each experiment. The mice were weighed on the same days, at times when they were inactive. Because weights of individual mice differ, water and food consumption was calculated on the basis of the amount consumed per gram of body weight per day. All foods were air-dry and contained a negligible amount of water.

First, food and water consumption was measured for nine individuals of each species on a diet of Purina Laboratory Chow. This chow contains not less than 23 per cent protein and 4.5 per cent fat, and about 57 per cent carbohydrate. Since the mice had been maintained on this diet for several months prior to the experiments, food and water consumption was measured for a period of only two weeks. Individuals of *P. truei* consumed more total water and more water per gram of body weight than individuals of *P. maniculatus* (Table 7).

Next, 10 mice of each species were placed on a diet of Purina Hog Chow for a period of four weeks. This chow contains not less than 36 per cent protein and one per cent fat, and about 42 per cent carbohydrate. Both species increased their daily water consumption immediately after being placed on this diet (tables 7 and 11). On the high protein diet, *P. truei* again consumed much more water than did *P. maniculatus* (tables 7 and 9).

The tendency of both species to eat more of the hog chow than they ate when fed standard laboratory chow may reflect a higher palatability of the hog chow. Both species consumed similar amounts of food per gram of body weight, on each of the diets (Table 7). The larger *P. truei* requires more

TABLE 7—Food and Water Consumption of *Peromyscus maniculatus* and *P. truei* When Fed Diets of Different Protein Content. Food and Water Consumption Are Determined for the Grams, or Milliliters, Consumed per Gram of Body Weight per Day; Daily Totals Are also Given.

<i>Peromyscus maniculatus rufinus</i>							
Diet per cent protein	No. mice	Food /gram /day ± S. D.	Total grams /day	Water /gram /day ± S. D.	Total water /day		
Lab Chow 23...	9	.201 .074	4.455	.262 .183	5.751		
Hog Chow 36..	10	.238 .060	5.232	.496 .186	10.749		
Corn 11.....	11	.149 .044	3.144	.174 .012	3.696		

<i>Peromyscus truei truei</i>							
Diet per cent protein	No. mice	Food /gram /day ± S. D.	Total grams /day	Water /gram /day ± S. D.	Total water /day		
Lab Chow 23...	10	.216 .070	6.353	.373 .119	10.880		
Hog Chow 36..	10	.230 .079	6.966	.653 .189	19.571		
Corn 11.....	10	.158 .010	4.318	.332 .016	9.034		

grams of food per day than the smaller *P. maniculatus*, but this slight difference in food consumption probably has no effect on the distribution of these species within Mesa Verde.

The results obtained with the low protein diet were strikingly different from those of the first two experiments. In this experiment the same groups of mice were placed on a diet of whole, shelled corn for a period of six weeks. The corn contained less than 11 per cent protein, about three per cent fat, and about 80 per cent carbohydrate.

By the end of the first week, on the low protein diet, all mice had reduced their water intake by about half the amount used per day on the high protein diet (Table 7). There was not a statistically significant difference, for either species, between the average amounts of water drunk in the first and in the sixth weeks of the experiment.

The data in Table 7 show that on all three diets, individuals of *P. maniculatus* drank less water per gram of body weight than individuals of *P. truei*. Variation in water consumption was high; some individuals of *P. maniculatus* that drank more than the average amount for the species, consumed as much water as some individuals of *P. truei* that drank less than the average amount. In general, individuals of *P. maniculatus* drank about half as much water each day as individuals of *P. truei*. Individuals of both species were consistent in their day-to-day consumption.

Table 8 shows average water consumption for several species of *Peromyscus* as reported in the literature, and as determined in my study. It is difficult to compare my results with most of the data in the literature, because of a lack of information as to protein, fat, carbohydrate, and mineral contents of foods used in other studies. Lindeborg (1952) and Dice (1922) fed mice on a

TABLE 8—Amounts of Mean Daily Water Consumption as Reported in the Literature for Species of *Peromyscus*. Figures in Parentheses are Means; Those Not in Parentheses Are Extremes.

	Mean daily ml./gm. wt./day	Water consumption total ml. per day	Temperature	Humidity	Per cent dietary protein	Investigator
<i>P. m. rufinus</i> ...	(.262) .124-.699	(5.70) 2.71-15.07	20-23	low	23	Douglas
<i>P. m. rufinus</i> ...	(.101)	(2.39)	20-25	24-47	Lindeborg, 1952
<i>P. m. osgoodi</i>16-.25	3.2-4.3	18-22	10-20	23	Williams, 1959
<i>P. m. bairdii</i> ...	(.126) .082-.177	(1.74) 1.12-2.72	21	25-68	Dice, 1922
<i>P. m. bairdii</i>124-.182	(2.37-3.17)	20-25	24-47	Lindeborg, 1952
<i>P. t. truei</i>	(.372) .224-.561	(10.80) 7.0-16.92	20-23	low	23	Douglas
<i>P. t. truei</i>	(.085)	(2.77)	20-25	24-47	Lindeborg, 1952
<i>P. l. nov</i>057-.117	1.36-2.29	21	25-68	Dice, 1922
<i>P. l. nov</i>	(5.36)	18	62.5	Chew, 1951

mixture of rolled oats, meat scraps, dry skimmed milk, wheat germ, etc. described by Dice (1934). Their data on water consumption in *P. maniculatus* indicate that this mixture probably is lower in protein content than Purina Laboratory Chow, that was used in my experiments and those of Williams' (tables 8 and 9).

The amount of dietary protein consumed under natural conditions is not known for most wild animals. One index of the minimum amount of protein necessary is the amount required for an animal to maintain its weight. At best, this can be only an approximation of the required amount, for other factors, such as stress, disease, change in tissues during oestrus or gonadal descent, and changes in constituents of the diet other than protein, would all be expected to affect the body weight (Chew, 1965: 145-147).

The data in Table 7 show that both species vary their food intake with changes in diet. Table 10 shows weight changes that took place in individual mice when fed each of the three diets. A change in weight of one gram cannot be considered as important, for the weight of an individual mouse fluctuates depending upon when he last drank, ate, defecated or urinated.

The only significant changes in weight occurred when mice were fed low protein food (Table 10). Individuals of *P. truei* lost 15.72 per cent and individuals of *P. maniculatus* lost 10.03 per cent of their total body weights on this diet. This indicates that food having a protein content of more than 10 per cent but less than 23 per cent is required for maintenance of weight in these animals.

Although knowledge of the amount of water consumed, *ad libitum*, by adult mice is valuable information, maintenance of the population depends upon reproduction and dispersal of young individuals. My trapping data indicate that only two to three per cent of the adults live long enough to breed in consecutive breeding seasons. In spring, the breeding population is composed largely of mice that were juveniles or subadults during the latter parts of the breeding season. Therefore, the critical time for the population may well be the time when the season's young are being produced. Any unfavorable circumstances, such as a shortage of food or water, that would affect pregnant or lactating females would be of primary importance to the integrity of the population.

One would assume that pregnant and lactating females require more water

TABLE 9—A Comparison of Mean Daily Water Consumption of Mice on High Protein Diets. Numbers in Parentheses Are Average Values; All Others Are Ranges of Values.

Species	Mean daily H ₂ O consumption		Temperature	Relative humidity	Investigator
	cc./gm. wt.	Total cc.			
<i>P. m. osgoodi</i>	(0.27-0.54)	(4.6-9.3)	18-22 C	10-20	Williams, 1959
<i>P. m. rufinus</i>	(0.496) 0.186-0.764	(10.74) 4.54-16.57	20-23 C	low	Douglas
<i>P. t. truei</i>	(0.653) 0.429-1.031	(19.57) 13.28-30.28	20-23 C	low	Douglas

than non-pregnant females. One might also assume that juveniles require different amounts of water and food than adults. Juveniles have less dense pelage than adults, and probably are affected more by their immediate environment because of their relatively poor insulation. Juveniles might also be in an unfavorable situation insofar as water conservation is concerned, because they are actively growing, and in most cases, acquiring new pelage; it is well known that these are times of stress for the individual.

Lindeborg (1950:76) found that 15 days before parturition, pregnant and non-pregnant females of *P. m. bairdii* drank about the same amounts of water, that females consumed more water after the young were born and until they were weaned, and that water consumption increased with an increase in weight in young, growing individuals. He found that in the later stages of pregnancy, females of *P. m. bairdii* required 36 per cent more water than non-breeding females; at 14 days after parturition, nursing females required 111 per cent more water than non-breeding females, and at weaning time, 158 per cent more water. Dice (1922:35) reported a 217 per cent increase in drinking of

TABLE 10—Weights of Mice at Start and Finish of Experiments, Showing Changes in Weight and Mean Weights, and Means of Changes in Weight (mean delta).

Peromyscus truei truei

No.	Lab Chow			Hog Chow			Corn		
	Start	End	Δ	Start	End	Δ	Start	End	Δ
1.....	31.0	31.3	0.3	31.3	32.3	1.0	32.3	29.0	3.3
5.....	31.1	30.5	0.6	30.5	32.8	2.3	32.8	28.7	4.1
6.....	27.6	27.1	0.5	27.1	29.5	2.4	29.5	27.3	2.2
7.....	28.0	26.3	1.7	26.3	27.5	1.2	27.5	22.2	5.3
13.....	25.8	30.6	4.8	30.6	27.0	3.6	27.0	22.2	4.8
14.....	26.9	30.7	3.8	30.7	31.4	0.7	31.4	27.3	4.1
15.....	25.4	29.4	4.0	29.4	29.8	0.4	29.8	24.0	5.8
16.....	33.0	32.9	0.1	32.9	30.5	2.4	30.5	26.0	4.5
19.....	37.6	38.1	0.5	38.1	31.8	6.3	31.8	22.0	9.8
20.....	23.5	25.8	2.3	25.8	26.2	0.4	26.2	22.9	3.1
Ȳ.....	28.9	30.2	1.8	30.2	29.8	2.0	29.8	25.2	4.7

Peromyscus maniculatus rufinus

No.	Lab Chow			Hog Chow			Corn		
	Start	End	Δ	Start	End	Δ	Start	End	Δ
2.....	23.0	20.7	2.3	20.7	21.1	0.4	21.1	18.6	2.5
3.....	22.7	23.1	0.4	23.1	23.8	0.7	23.8	20.7	3.1
4.....	22.0	21.1	0.9	21.1	21.8	0.7	21.8	21.3	0.5
8.....	26.3	28.1	1.8	28.1	15.8	2.3	25.8	23.8	2.0
9.....	21.5	24.0	2.5	24.0	25.1	1.1	25.1	21.8	3.3
10.....							22.5	20.0	2.5
11.....	21.0	22.1	1.1	22.1	20.8	1.3	20.8	19.0	1.8
12.....	22.3	23.2	0.9	23.2	21.3	1.9	21.3	20.4	0.9
17.....	18.9	20.0	1.1	20.0	19.2	0.8	19.2	19.4	0.2
18.....	17.0	17.5	0.5	17.5	19.5	2.0	19.5	17.3	2.2
21.....	18.9	18.1	0.8	18.1	20.2	2.1	20.2	17.3	2.9
Ȳ.....	21.4	21.8	1.2	21.8	21.8	1.3	21.9	19.9	2.2

P. m. bairdii before parturition, and 171 per cent increase while nursing.

Several females of both species were bred prior to the start of the experiments described herein. As a consequence, it was possible to determine water and food consumption for lactating females of each species, and later, for their litters. Pregnant and lactating females, and newly-weaned litters, were fed laboratory chow throughout this experiment. The litters were separated from their mothers as soon as the young were observed to be eating, or no later than 33 days after birth.

Table 11 shows the amounts of water and food consumed by two females of each species while they were either in the later stages of pregnancy, or were nursing. Although the data in Table 11 do not cover the full developmental time of the litters involved, it is obvious that both lactating females of *P. truei* and one female of *P. maniculatus* consumed more water than the average for their species (Table 7). Water and food consumption was measured for both females of *P. truei* while they were nursing. The female that gave birth to litter A was left in the cage with the male for several days after the litter was born, resulting in another litter being born about 27 days after the first. Therefore, the record of this female represents an extreme case of stress (probably a common occurrence in nature) in which a female is nursing one litter while she is pregnant with a second.

The record of the female of *P. truei* that gave birth to litter B is the most complete, including data from the fifth day after parturition until the young were weaned on the thirty-third day after parturition. The record of the female of *P. maniculatus* that gave birth to litter C covers the last 10 days of nursing before the young were weaned. After being separated from her litter, this female drank more than the average amounts of water, on both high and low protein diets. Although the food and water were lost several times for the female of *P. maniculatus* with litter D, the period of time covered by the 14 days when water and food consumption were measured includes times just prior to parturition and to weaning of the young.

TABLE 11—Water and Food Consumed by Nursing Females of *P. truei* and *P. maniculatus*. Consumption Is Calculated on the Basis of Amount (Milliliters or Grams) Consumed per Gram of Body Weight per Day, as well as Total Amounts Used per Day.

Female	Water used	No. days	Average weight	ml. H ₂ O gm./day	Total water day	No. in litter
<i>P. truei</i> (A).....	447	17	33.00	.796	26.29	3
<i>P. truei</i> (B).....	676	28	32.70	.738	24.14	3
<i>P. maniculatus</i> (C).....	191	10	19.45	.983	19.10	5
<i>P. maniculatus</i> (D).....	133	14	24.35	.224	5.46	6
Female	Food used	No. days	Average weight	gms. food gm./day	Total food day	No. in litter
<i>P. truei</i> (A).....	214.7	26	33.00	.250	8.26	3
<i>P. truei</i> (B).....	120.5	24	32.70	.153	5.02	3
<i>P. maniculatus</i> (C).....	47.8	10	19.45	.246	4.78	5
<i>P. maniculatus</i> (D).....	180.1	21	27.42	.312	8.58	6

It is interesting that the female of *P. maniculatus* with litter C used much more than the average amount of water for the species, and even more per gram of body weight than lactating females of *P. truei*. Conversely, water consumption of the female with litter D was within one standard deviation of the mean for all adults of *P. maniculatus*. I infer that at least some lactating females of *P. maniculatus* are better adapted to aridity than are some lactating females of *P. truei*.

Table 11 also shows food consumption of the four females discussed above. All females, with the exception of the female with litter D, consumed amounts of food that lie within one standard deviation of the means for their species. The female with litter D had the most young, consumed the most food but drank the least water of the four females. Later, when separated from her litter and placed on the low protein diet, this female drank only .046 milliliters of water per gram of body weight per day. This figure is less than one-third of the average amount (.174) for this species (Table 7).

The records of water and food consumption for litters A, C, and D are given in Table 12; the mice in litter B persisted in placing wood shavings in the opening of the spout on their water bottle, causing loss of the water. The data show that mice in all three litters had an average water and food consumption within one standard deviation of the mean for adults of their respective species (Tables 7 and 12). It is interesting that juveniles of both species require no more food and water per gram of body weight than adults. This indicates that if a young animal survives the rigors of postnatal life until it is weaned, it is then at no disadvantage as far as food and water consumption are concerned. This would be greatly advantageous to the species, as a population, for the young could disperse immediately upon weaning, and go into any areas that would be habitable for adults of the species.

The young of pregnant and lactating females are the animals in the population most likely to be affected by a deficient supply of water. Drought could reduce the water content of the vegetation to such a level that pregnant

TABLE 12—Food and Water Consumed by Young Mice in Litters, After Weaning. Consumption Is Calculated on the Basis of the Amount (Milliliters or Grams) Consumed per Gram of Litter Weight per Day; Total Amounts Are Shown and Can Be Divided by Litter Size for Average Individual Consumption. Litter Sizes Are as Follows: A=3; C=5; D=6.

Litter	Total water used	Total corrected	No. days	Average total weight	ml. H ₂ O/gm./day	Total water /day
<i>P. truei</i> (A).....	1207	1120	57	58.30	.337	19.64
<i>P. maniculatus</i> (C).....	1427	1340	57	76.14	.308	23.50
<i>P. maniculatus</i> (D).....	700	670	31	58.80	.367	21.61

Litter	Total food used	No. days	Average total weight	Gms. /gms. wt. /day	Total food /day
<i>P. truei</i> (A).....	651.2	50	58.30	.223	13.02
<i>P. maniculatus</i> (C).....	743.8	57	76.14	.171	13.04
<i>P. maniculatus</i> (D).....	471.1	31	58.80	.258	15.19

or lactating females might find it difficult, if not impossible, to raise litters successfully. If such a drought persisted throughout an entire breeding season, the next year's population would be reduced in numbers, for even under normal climatic conditions it is almost exclusively the juveniles that survive from one breeding season to the next. If such a hypothetical drought occurred, lactating females of *P. truei* would be in a more critical position than lactating females of *P. maniculatus*.

In order to determine how much water was available to mice in the peak of the breeding season, samples of the three most common plants in the study area were collected each week for analysis of their moisture content. Plants were placed in separate plastic bags that were sealed in the field. About a dozen plants of each species were used in each determination. Only the new tender shoots of the plants were collected, for it was assumed that mice would eat these in preference to the tougher basal portions of the plants. The plants were taken immediately to the laboratory and were weighed in the bag. Then the bag was opened and it and the contents placed in an incubator at 85 degrees Fahrenheit for a period of at least 72 hours. About 48 hours were required to dry the plants to a constant weight. The dried plants were weighed and their percentages of moisture were determined. Plants lose some water upon being placed in a closed bag; small drops of water appear immediately on the inner surface of the bag. Therefore, the bag must be weighed at the same time as the plants and the weight of the dried bag must be subtracted later.

The three kinds of plants chosen were among the most widely distributed species in the study area, and all three grow close to the ground, within reach of mice. Stems and leaves of two of the plants, *Comandra umbellata* and *Penstemon linarioides*, were readily eaten by captive animals. Mice also were observed to eat leaves of *Comandra* after being released from metal live traps. The third species, *Solidago petradoria*, differs from the other two in having a short woody stem that branches at ground level. The more succulent shoots arise from this woody stem. The leaves of *Solidago* are coarse and were not eaten by captive mice. Nevertheless, this species was chosen because it is widely distributed and has the growth form of several other species of plants in the area.

The graph in Figure 20 shows that *Comandra* contains the highest percentage of water through most of the summer. Water content of both *Penstemon* and *Comandra* was greatly reduced in the dry period that occurred in early July. *Solidago* maintained a relatively constant percentage of moisture; perhaps its woody stem serves for water storage. The rains of July and August increased the percentage of moisture in the plants, but not to the extent expected. Neither *Solidago* nor *Comandra* reached the levels of hydration of early June. All plants were collected at or about 11 a. m. At night, when mice are active, these plants would be expected to contain a higher percentage of water than in the daytime.

The data in Figure 20 indicate that mice probably are not endangered by water shortages in most years. The average percentage of moisture in the plants studied was as follows: *Comandra umbellata* 62.33 per cent; *Solidago petradoria* 53.0 per cent; *Penstemon linarioides* 49.28 per cent. If a mouse were to eat ten grams of plant material containing 50 per cent moisture, it would provide him with five grams of food and five grams of water, both of which exceed the minimum daily needs for non-pregnant adults of either species.

The data indicate that there are sufficient differences in water consumption between *P. maniculatus* and *P. truei* to account for their habitat preferences in Mesa Verde National Park. In years having average precipitation, water present in the vegetation has the potential for providing enough moisture for the needs of both species. Extended drought would affect individuals of *P. truei* more adversely than individuals of *P. maniculatus*.

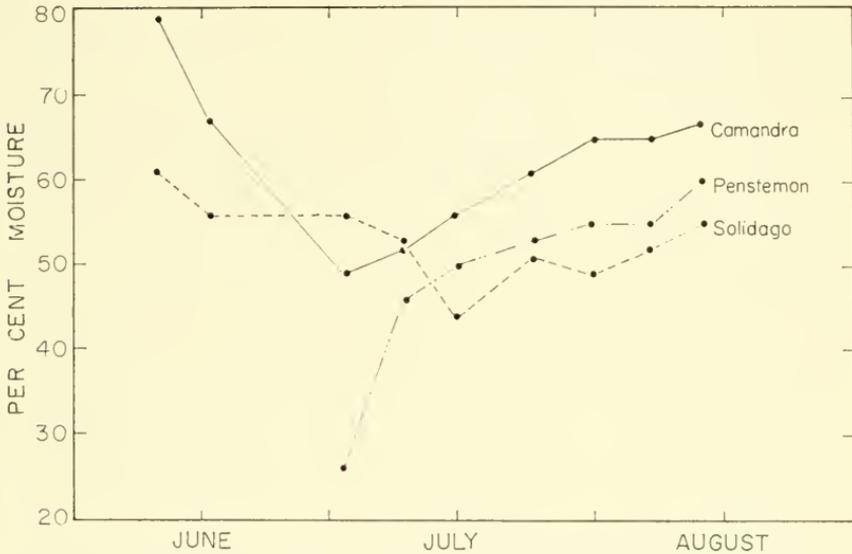


FIG. 20: Graph showing percentages of moisture contained during the summer of 1964, by three abundant and widely-distributed species of plants in Mesa Verde National Park, Colorado.

PARASITISM

Ectoparasites were collected by placing specimens of *Peromyscus* in separate plastic bags soon after death, adding cotton saturated with carbon tetrachloride, closing the bag for about five minutes, then brushing the fur of the specimen above a sheet of white paper. The ectoparasites were sorted and sent to specialists for identification. Endoparasites were saved when stomach and intestinal contents were examined. Larvae of botflies were collected from mice in the autumn of 1962, placed in sand in containers, and kept over winter until they hatched. Eyelids of alcoholic specimens were inspected for mites by an authority on these organisms.

In 1961, the incidence of parasitism by botflies was the highest for the period 1960-1966. *P. maniculatus* was more heavily infected with warbles than was *P. truei*. In 84 individuals of *P. maniculatus* taken in September 1961, from Morfield Ridge, 32.1 per cent had warbles. The average number of warbles per animal was 1.24, and it was not uncommon to find two or three warbles per mouse. Sixty-nine per cent of the warbles were in the third instar stage, and the rest were in the second instar stage. Warble infestation was higher in the first half of September (40 per cent of mice infected) than in the second half of the month (30 per cent infected), but a larger percentage of the warbles were found (69 per cent) in the second half of the month.

In October 1961, 12.9 per cent of 62 *P. truei* were infected with warbles. The average number of warbles per infected mouse was 1.37. Seventy-three per cent of the warbles were in the third-instar stage; the rest were in the second-instar stage. Warble infestation was higher in the first half of October (16 per cent of the mice infected) than in the second half of the month (5.5 per cent infected). These mice were collected from several localities on Chapin Mesa, in pinyon-juniper woodland.

In Mesa Verde the greatest incidence of infestations is in late September and early October. This agrees with the finding of other investigators (Sealander, 1961:58).

Sealander (1961) investigated hematological values in deer mice infected with botflies, and found that infected mice had significantly lower concentrations of hemoglobin than non-infected mice. Myiasis, associated with infection by *Cuterebra*, is likely to lead to a lowering of the physiological resistance of a segment of the population, and perhaps to a subsequent decline in the population (Sealander, 1961:60).

Mice infected by warbles were less agile than non-infected mice. Other investigators also have reported awkwardness in locomotion in infected mice (Scott and Snead, 1942:95; Sealander, 1961:58). Test and Test (1943:507) noted that parasitized mice did not appear to be emaciated, and this was also true of parasitized mice at Mesa Verde. Healed wounds, where warbles had emerged, were apparent on a number of mice. The warbles, and wounds, usually were found on the flanks and backs of the mice. The large, third-instar larvae weighed about one gram apiece; there is little doubt that such large larvae induce trauma in their hosts.

The highest rate of infestation by botflies occurred in 1961, the year in which the population density of *P. maniculatus* was near its peak. The population of this species was reduced considerably in 1962, and remained low through 1964. In 1965, the density of *P. maniculatus* appeared to be increasing. Other investigators have reported that increased incidence of *Cuterebra* infestation in deer mice coincides with lower population densities and with a downward trend in the population (Scott and Snead, 1942:95; Wilson, 1945). My data indicate that this may not be the situation in Mesa Verde.

The intestines or stomachs of almost all individuals of *P. maniculatus* contained parasites. Endoparasites were less abundant in individuals of *P. truei*. This heavier infestation of *P. maniculatus* by tapeworms, roundworms, and spiny-headed worms probably reflects the larger proportion of insects eaten by *P. maniculatus* than by *P. truei*.

The most common endoparasite encountered was the nematode, *Mastophorus numidica* Seurat, 1914; it was found in the stomachs of many individuals of both species of *Peromyscus*. This nematode has been reported from *Felis ocreata* in Algeria, *Bitis arietans* in the Congo, and from the following mammals in the United States: *Canis latrans*, *Peromyscus crinitus*, *P. gossypinus*, *P. maniculatus*, *P. truei*, *Onychomys leucogaster*, *Dipodomys ordii*, *Reithrodontomys megalotis*, and *Eutamias minimus*.

Individuals of *P. maniculatus* obtained on the northern end of Wetherill Mesa in May and June of 1962 had numerous ectoparasites. At this time, the population of *P. maniculatus* was high, but on a downward trend.

My data and observations lead me to conclude that individuals of *P. manicu-*

latus are more heavily parasitized by both botflies and endoparasites than are individuals of *P. truei*. The reasons for this unequal amount of parasitism in two species of mice occurring in the same general area remain obscure.

The kinds of endoparasites and ectoparasites collected from *P. maniculatus* and from *P. truei* are listed below (m = present in *P. maniculatus*, t = present in *P. truei*).

ACARINA: Ixodidae: *Dermaacentor andersoni* mt, *Ixodes angustus* mt, *Ixodes spinipalpis* m. Laelaptidae: *Androlaelaps glasgovi* m. Myobiidae: *Blarinobia* sp. m. Trombiculidae: *Euschoengastia lanei* mt, *Euschoengastia criceticola* m, *Euschoengastia dicipiens* t, *Euschoengastia peromysci* m, *Leewenhockia americana* m, *Trombicula loomisi* m.

DIPTERA: Cuterebridae: *Cuterebra cyaneella* mt.

SIPHONAPTERA: *Callistopsyllus deuterus* m, *Catallagia dicipiens* m, *Epeptedia stanfordi* mt, *Malaraeus sinomus* mt, *Malaraeus telchiumum* mt, *Megarthroglossus proeus* mt, *Monopsyllus wagneri wagneri* mt, *Orchopeus leucopus* mt, *Peromyscopsylla hesperomys adelpha* mt, *Phalacropsylla allos* t, *Rhadinopsylla sectilis goodi* t, *Stenistomera macrodactyla* m, *Stenoponia (ponera or americana)* mt.

CESTODA: *Choanotaenia* sp. m, *Hymenolepis* sp. t.

NEMATODA: *Mastophorus numidica* mt, *Syphacia obvelata* mt, *Trichuris stansburyi* t.

ACANTHOCEPHALA: *Mouiliformis clarki* mt.

PREDATION

In order to determine the relative numbers of each species of *Peromyscus* that were taken on a seasonal basis by predators, scats of coyotes and foxes were collected from trails and roads at least twice each month, from September 1963 through August 1964. Scats were identified, labeled and dried; all bones and samples of hair were later removed from each scat. Scats that were intermediate in size between the droppings of foxes and coyotes, and that could not be identified readily in the field, were not collected. Bones from the scats were identified to species, and hair was identified to genus or species by comparing color patterns or cuticular patterns with samples from known mammals. More than 200 impression slides and whole mounts of guard hair and underfur were prepared.

Seven individuals of *P. truei* and three individuals of *P. maniculatus* were represented in 114 coyote scats (Table 13). Both species of *Peromyscus* comprised only 3.9 per cent of the 253 items of food represented in the 114 scats. Rabbits, *Sylvilagus* sp. and mule deer, *Odocoileus hemionus* were the major food items of coyotes. Mice of the genus *Peromyscus* apparently were preyed upon mostly in autumn (September through November), when mouse populations were near their yearly peaks.

Foxes also prey upon *Peromyscus* in the park. One *P. truei* was represented in the 16 scats of foxes that were analyzed. This individual was taken in the winter quarter (December through February).

The bobcat may be an important predator upon *Peromyscus* in this region, but few scats of this animal were found. Since these could not be assigned to

TABLE 13—Food Present in 114 Coyote Scats Collected at Mesa Verde National Park each Month from September 1963 through August 1964.

Food Item	Number of occurrences	Percentage of total items
<i>Sylvilagus</i> sp.	32	12.65
<i>Spermophilus variegatus</i>	5	1.97
<i>Eutamias</i> sp.	12	4.74
<i>Reithrodontomys megalotis</i>	4	1.58
<i>Peromyscus boylii</i>	2	0.79
<i>Peromyscus maniculatus</i>	3	1.18
<i>Peromyscus truei</i>	7	2.76
<i>Neotoma cinerea</i>	2	0.79
<i>Neotoma mexicana</i>	9	3.56
<i>Neotoma albigula</i>	5	1.97
<i>Neotoma</i> sp.	3	1.18
<i>Microtus longicaudus</i>	1	0.39
<i>Microtus mexicanus</i>	11	4.34
<i>Microtus montanus</i>	1	0.39
<i>Microtus</i> sp.	1	0.39
<i>Odocoileus hemionus</i>	59	23.32
Grass	34	13.44
Juniper berries	23	9.09
Pinyon needles	14	5.53
Pinyon nuts	1	0.39
Arthropods	7	2.76
Juniper needles	3	1.18
Rodent or Lagomorph bones	5	1.97
<i>Sceloporus</i> sp.	1	0.39
Unidentified fruit	2	0.79
Rocks	3	1.18
Paper	4	1.58
Soil	3	1.18
Feathers	5	1.97
Total	253	

a specific month, they were not saved for analysis. Anderson (1961:58) believed that bobcats and gray foxes were the most abundant predators in the park. My observations over a period of two years led me to conclude that coyotes were more abundant than foxes and that foxes were, in turn, more abundant than bobcats.

Hawks, owls and eagles live in the park. Red-tailed hawks were seen frequently in the burned area on the northern end of Wetherill Mesa. Both hawks and owls probably prey upon *Peromyscus* in Mesa Verde, for they are well-known predators upon mice and small rodents in other areas. I tried to find owl and hawk nests that were occupied, but located only nests that were abandoned or impossible to reach.

Captive gopher snakes, *Pituophis melanoleucus*, ate adults of both species of *Peromyscus*. Gopher snakes probably are the most abundant snake in the park; they feed mostly on mice and other rodents. Fur of *Peromyscus* was found in the stomach of a striped whipsnake, *Masticophis taeniatus* (Douglas, 1966:734).

DISCUSSION

Five species of *Peromyscus* inhabit Mesa Verde National Park (Anderson, 1961). Two of these species, *P. crinitus* and *P. difficilis* are rare, and none was taken in more than 14,000 trap nights. Several individuals of *P. boylii* were taken in live traps, but this species could not be regarded as common. The two remaining species, *P. truei* and *P. maniculatus*, are the most abundant species in the park. Comparison of the habitats and life-cycles of these two forms and analyses of their interrelationships have been the objectives of this study.

The distribution of *P. truei* in the park is regulated by the presence of living pinyon-juniper woodland where logs and hollow trees of *Juniperus osteosperma* provide nesting and hiding places, and where seeds of juniper trees and nuts of pinyon trees provide food. Several other investigators have reported *P. truei* to be associated with trees, but apparently these findings have not assumed the importance they warrant in understanding the ecology of this species. Bailey (1931:152) observed an individual of *P. truei* nesting in a tree on Conchas Creek, New Mexico, and thought that this species might be more arboreal than was generally supposed. The type specimen of *P. t. truei* was taken by Shufeldt from a "nest protruding from an opening in the dead and hollow trunk of a small pinon, at least 2 feet above the ground . . . The nest, composed of the fine fibers of the inner bark of the pinon, was soon pulled out, and its owner dislodged. . . ." (Shufeldt, 1885:403). Individuals of *P. truei* usually build nests in trees, or in hollow logs, and are therefore more abundant in pinyon-juniper woodland where there are many such nesting sites.

Rocks and stones are not necessary in the habitat of *P. truei*, although this species was most abundant where there was stony soil. The coincidence of rock or stones and a high density of *P. truei* is thought to be explainable in terms of vegetation. Stony soils support mixed shrubs as well as pinyon and juniper trees; the additional cover and source of food probably allow a greater abundance of *P. truei* than would be possible without the shrubs. Secondarily, the rock provides nesting sites for more mice.

Stands of mixed shrubs, lacking a pinyon-juniper canopy, do not support *P. truei*. Its absence was noteworthy on Navajo Hill and on the northern end of Wetherill Mesa where only *P. maniculatus* lived among the mixed shrubs and grassland. On the Mesa Verde, pinyon and juniper trees must be present in order for *P. truei* to

live in an area; and, these trees must be alive. Dead pinyons and junipers still stand in the burned part of Morfield Ridge, but no *P. truei* were found there.

Although a few individuals of *P. truei* were taken in stands of sagebrush adjacent to pinyon-juniper woodlands, this species does not ordinarily venture far from the forest.

P. maniculatus lives almost everywhere in Mesa Verde: the preferred habitats are open and grassy with an overstory of mixed shrubs. Individuals of *P. maniculatus* venture into ecotonal areas lying between grasslands and pinyon-juniper forest, or between sagebrush and pinyon-juniper forest. *P. maniculatus* is found also in disturbed areas and in stands of sagebrush that occur in clearings of the pinyon-juniper woodland. In such areas, *P. maniculatus* and *P. truei* are sympatric; their home ranges overlap and any interspecific competition that might occur would be expected in these places.

The ability of *P. maniculatus* to live in many different habitats is correlated in part with its ability to build nests in a variety of sites. Whereas *P. truei* usually builds nests only in dead branches or logs, *P. maniculatus* builds nests in such varied places as spaces under rocks, at the bases of rotten trees, and in abandoned tunnels of pocket gophers. This adaptability is advantageous for the dispersal of young individuals and the movement of adults into new areas.

Nesting sites have important bearing on survival of the young. In Mesa Verde the rainy season occurs in July and August, while both species of *Peromyscus* are reproducing. It is reasonable to assume that young animals that remain dry survive better than those that become wet and chilled. The nestling young of *P. truei* are in a more favorable position to remain dry and warm than are nestling young of *P. maniculatus*.

Captives of each species differed in the amounts of water consumed per gram of body weight. Individuals of *P. truei* consumed more water per gram of body weight than individuals of *P. maniculatus*. Animals may drink more water than they require when allowed to drink *ad libitum*, but Lindeborg (1952) has shown that species which consume less water when it is not restricted also fare better on a reduced ration. *P. maniculatus* appears to be better adapted to aridity than *P. truei*. The preferred habitats of each species are in accord with these findings.

Within the trapping grid, the most moderate microenvironment, in terms of temperature and humidity, was in the pinyon-juniper

forest, where *P. truei* lives. The temperature extremes were wider in the microenvironments of a thicket of oak brush and of two different stands of sagebrush, where *P. maniculatus* lives, than in the forest. *P. maniculatus* tends to live in the harsher, more arid parts of Mesa Verde. Because of its propensity to build nests under things, or in the ground, and because of its ability to use less water per gram of body weight, *P. maniculatus* is better adapted to withstand harsh environments than is *P. truei*.

P. truei may be restricted to the pinyon-juniper woodland because of its need for more mesic conditions. Still, Mesa Verde is semi-arid and there are few permanent sources of water available for animals. The primary source of moisture for rodents must be their food. Analysis of the percentages of moisture contained in the three most common plants in the trapping grid showed that *P. truei* could obtain the required moisture by eating about ten grams of these plants daily; individuals of *P. maniculatus* would need to eat less in order to satisfy their water needs.

Individuals of *P. truei* died more frequently in warm live-traps than did individuals of *P. maniculatus*. This indicates that *P. truei* can tolerate less desiccation, or a narrower range of temperatures, than can *P. maniculatus*.

Both species of mice eat some of the same plants, but these plants occur widely. *P. truei* seems to rely more upon the nuts of pinyons and the seeds of junipers than does *P. maniculatus*. Mounds of discarded juniper seeds were associated with all nesting sites of *P. truei*. Bailey (1931:153) also noticed the fondness of this species for pine nuts and juniper seeds. Apparently, the availability of these foods is one of the major factors affecting the distribution of *P. truei*. However, this is not the only factor, as is shown by the presence of *P. maniculatus* but lack of *P. truei* in a juniper-pinyon association with an understory of bitterbrush. This habitat was seemingly too arid for *P. truei*.

Factors Affecting Population Densities

The production of young, and success in rearing them, is essential to continuity of any population. *P. maniculatus* is favored in this respect, because the females produce more young and wean them sooner than do females of *P. truei*. In addition, lactating females of *P. maniculatus* require significantly less water than do females of *P. truei*. Since young mice of both species require no more water per gram of body weight than do adults, the young can disperse into any area that is habitable by their species. *P. maniculatus* probably is affected less by prolonged drought than is *P. truei*.

Since lactating females require the most water of any animal in the population, they are the weakest link in the system. Females of *Peromyscus* are known to reabsorb embryos when conditions are unfavorable for continued pregnancy. If prolonged drought occurred in the reproductive season, and desiccated the vegetation upon which the mice depend for moisture, the populations should diminish the following year. Lactating females of *P. truei* would be affected more seriously by a shortage of water than would lactating females of *P. maniculatus*.

Of two species, the one producing the more young probably would be subjected to more parasitism and predation than the species producing fewer young. A favorable season for botflies, *Cuterebra* sp., revealed that *P. maniculatus* has a higher incidence of parasitism by these flies than has *P. truei*; possibly the adult flies concentrate in the open, grassy areas where *P. maniculatus* is more abundant, rather than in the woodlands where *P. truei* lives. Perhaps the lower parasitism of *P. truei* by warbles is related to the physiology of this species of mouse. Near Boulder, Colorado, the incidence of infection by warbles is lower in *P. difficilis*, a species closely related to *P. truei*, than in *P. maniculatus* (V. Keen, personal communication).

Although predation by carnivores would be expected to be higher on *P. maniculatus*, because this species does not climb, my data show that more individuals of *P. truei* were taken by coyotes. I lack confidence in these findings, suspecting that another sample might indicate the reverse. Birds of prey probably catch more individuals of *P. maniculatus*, because this species lives in more open habitats. My data do not warrant firm conclusions regarding predation.

The length of time females must care for their young influences the rate at which individuals can be added to the population. Females of *P. truei* nurse their young longer and keep them in the nest longer than do females of *P. maniculatus*. Although this may enhance the chances of survival of young of *P. truei*, it also reduces the number of litters that each female can have in each breeding season. Females of *P. maniculatus* can produce more young per litter, and each female probably can produce more litters per year than females of *P. truei*.

Captives of *P. truei* were tolerant of other individuals of the same species, even when kept in close confinement. However, when there was slight shortage of food or water they killed their litter mates, or females killed their young. Only a short period of

time was necessary for one mouse to dispatch all others in the litter. The attacked mice were bitten through the head before being eaten; the brains and viscera were the first parts consumed. The population might be decimated rapidly if drought forced this species to cannibalism. When the supply of food or water was restored, the captive mice resumed their tolerant nature.

In captivity, *P. maniculatus* is amazingly tolerant of close confinement with members of the same species; individuals did not tend to kill their litter mates, or their young, even during shortage of food and water. This tolerance, especially under stressful conditions, probably enables *P. maniculatus* to persist in relatively unfavorable areas.

Adaptations to Environment

Each of the two species of *Peromyscus* illustrates one or more adaptations to its environment. *P. truei* is adapted to climbing by possession of long toes, a long tail, and large hind feet. The tail is used as a counterbalance when climbing (Horner, 1954). When frightened, individuals of *P. truei* often ran across the ground in a semi-saltatorial fashion, bounding over clumps of grass that were as much as 18 inches high. Such individuals usually ran to the nearest tree and climbed to branches 10 to 20 feet above the ground.

Large eyes are characteristic of the *truei* group of mice, and may be an adaptation to a semiarboreal mode of life. A similar adaptation is shared by some other arboreal mammals, and of arboreal snakes. The large eyes of *P. truei* in comparison to those of *P. maniculatus*, probably increase the field of vision, and permit the animal to look downward as well as in other directions.

The above-mentioned adaptations of *P. truei* permit these graceful mice to use their environment effectively. By climbing, this species can nest above-ground in the hollow branches of trees, and can rear its young in a comparatively safe setting. The ability to climb also permits vertical as well as horizontal use of a limited habitat. Because of the three-dimensional nature of the home range of *truei*, its range is actually larger than that of *maniculatus* although the standard trapping procedures makes the home range of the two appear to be about the same size. Finally, trees may offer safety from predators, and a source of food that probably is the winter staple of this species.

Peromyscus maniculatus has adapted differently to its environment. Small size of body and appendages permit this species to use a variety of nesting sites and hiding places even though it is

restricted, by its anatomy, to life on the ground. The tail and hind feet are shorter than in *P. truei*, and *P. maniculatus* is an inefficient climber. I have placed individuals in bushes, and found that many walk off into space from a height of several feet. Perhaps the relative smallness of their eyes accounts for their seeming lack of awareness of how high they are above the ground.

When frightened, individuals of *P. maniculatus* ran rapidly in a zig-zag path and dove into the nearest cover. Mice, released from live traps, often stuck their heads under leaves, leaving their bodies exposed. This species tends to hide as rapidly as possible, and remain motionless. This tactic would not be of much value as an escape from carnivores, but it could be effective against birds of prey.

In Mesa Verde, *P. maniculatus* inhabits the more arid, open areas. When the population is dense, individuals of this species are found also in pinyon-juniper woodland. Apparently *P. maniculatus* prefers the grassy areas and the thickets of oak brush. Although such habitats have harsh climatic conditions, they offer innumerable hiding places, and thus have great advantage for a species confined to the ground.

The low requirements of water per gram of body weight, the ability to eat diversified foods, the use of varied habitats, the high fecundity, and the ability to use any nook for retreat or nesting make *P. maniculatus* a successful inhabitant of most parts of Mesa Verde, and indeed, of most of North America.

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INTRODUCTION

The tree frogs of the *Hyla rubra* group are abundant and form a conspicuous element of the Neotropical frog fauna. Representatives of the group occur from lowland México to Argentina; the greatest diversity is reached in the lowlands of southeastern Brazil (Cochran, 1955). The group apparently originated in South America; the endemic Central American species evolved from stocks that invaded Middle America after the closure of the Colombian Portal in the late Pliocene.

Dunn (1933) partially defined the *rubra* group as it occurs in Central America. Cope (1865, 1876, 1887), Brocchi (1881), Boulenger (1882), Günther (1901), Noble (1918), Kellogg (1932), Dunn and Emlen (1932), Stuart (1935), and Gaige (1936) dealt with the Middle American species now considered to make up the *rubra* group. More recently, Taylor (1952, 1958), Fouquette (1958), Starrett (1960), and Duellman (1960, 1963, 1966a) studied aspects of the taxonomy and biology of the species of this group. The five species of the *rubra* group in Central America have received ten different names. One species, *Hyla staufferi*, has received five names (two subspecies are recognized herein). *Hyla boulengeri* was named in the genus *Scytopsis*, but the type species of *Scytopsis* is a member of the genus *Phrynohyas* Fitzinger, 1843 (Duellman, 1956.)

Little has been published concerning the ecology, life history, osteology, and mating calls of the Middle American species of this group. The purpose of the present report is to describe the species occurring in Middle America and to comment on their distributions, ecology, cranial osteology, and mating calls, and in so doing provide evidence for the evolutionary history of the species inhabiting Middle America.

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I am indebted to the Ford Foundation-Universidad de Oriente (Venezuela) Science Project for a scholarship which enabled me to study for two years at The University of Kansas, foster institution of the project. I have benefited by being able to work in the Museum of Natural History at The University of Kansas and I am grateful to Dr. E. Raymond Hall, Director, for providing space and equipment.

I gratefully acknowledge the assistance and advice of Dr. William E. Duellman, who suggested and directed this work, made available specimens under his care and gave much of his time in reading the manuscript and suggesting improvements. I am grateful to Dr. Frank B. Cross who critically read the manuscript and made many editorial suggestions. I am indebted to Linda Trueb for assistance with the osteological aspects of this study; she helped to clarify many confusing points. I am grateful to Charles W. Myers for making available his field notes on these frogs in Panamá, to Arthur C. Echternacht for reading part of the manuscript, and to John D. Lynch for many suggestions and helpful criticisms. The illustrations were executed by David M. Dennis.

Materials and Methods

For the purposes of the present study I examined 1383 preserved specimens, 50 skeletons, and 9 lots of tadpoles. External characteristics used in the analysis of variation are those currently employed in the study of anuran systematics. Twelve measurements and six proportions were taken in the manner described by Duellman (1956). Only the most important references are given in the synonymies, except those of the two subspecies of *Hyla staufferi*, which are more nearly complete. The taxonomic history of each frog is discussed under *Remarks* in each account. The cranial osteology was studied by using skeletons and cleared and stained specimens of all species. Developmental stages of tadpoles were determined from Gosner's (1960) table. Personal field work in Central America in the summer of 1966 provided an opportunity to make observations on the ecology, calling sites, and color in life; these data were supplemented by field notes from, and discussions with, Dr. William E. Duellman and Charles W. Myers.

The mating calls of the frogs were recorded in the field on Magnemite and Uher Tape Recorders by Dr. Duellman in the course of his work on the hylid frogs of Middle America—supported by grants from the National Science Foundation (G-9827 and GB-1441). These recordings, plus those borrowed from other institutions, provided 50 tapes for analysis of the mating calls. The calls were analyzed on a Vibralyzer (Kay Electric Company).

THE HYLEA RUBRA GROUP

Definition.—The species forming the group are small to moderate-sized tree frogs (maximum snout-vent length of males of various species 20-49 mm.), distinguished from other groups in the genus *Hyla* as follows: Brown, grayish brown, or yellowish tan above; thighs plain, marbled with dark brown, or having vertical bands; vocal sac single, median, subgular; snout flat, protruding, rounded or pointed; webbing between fingers reduced or absent; web between first and second toes reduced to fringe on second toe, rest

of toes about half webbed; tarsal fold reduced or absent; shanks robust; inner metatarsal tubercle larger than outer; prevomerine teeth on transverse ridges between small to large sized choanae; skull generally longer than wide; nasals large (length more than 40 per cent total length of skull) and having pointed maxillary processes; maxillary bearing small ventromedial palatine process; quadratojugal slender, always joined to maxillary by bony suture; auditory region of proötic slender and short; delicate spatulate columella ventral to crista parotica, broad basally, compressed anterolaterally, slightly rounded distally; anterior arm of squamosal extending about half distance to maxillary; sphenethmoid wider than long; frontoparietal fontanelle present or absent; prevomerine, premaxillary, and maxillary teeth present; prevomer with two lateral processes forming incomplete bony margin to internal nares; tadpoles having pointed xiphicercal tail, snout short, rounded; 2/3 tooth rows; dorsal fin deeper than ventral fin; sinistral spiracle; short dextral anal tube not reaching edge of ventral fin; mating calls consisting of single long note or series of short notes.

Composition.—This group contains about 24 currently recognized species, most of which occur in Brazil. Only five species—*boulengeri*, *elaeochroa*, *foliamorta*, *rubra*, and *staufferi* with two subspecies—occur in Central America. *Hyla boulengeri* and *rubra* are widespread in South America, and *foliamorta* occurs in Colombia, whereas the other species are known only from Middle America.

Distribution.—The species of the *Hyla rubra* group range from the lowlands of northern Argentina and Bolivia to southern Tamaulipas and Guerrero, México.

Comments.—In Central America two subgroups of species can be recognized. *Hyla boulengeri* and *H. foliamorta* are distinctive in the large size of adults (snout-vent lengths 41-49 mm.); both have prominent bars on the thighs, a well-defined interorbital triangular mark, blotches or spots dorsally, and large choanae. *Hyla elaeochroa*, *H. rubra*, and *H. staufferi* are smaller (snout-vent lengths 29-40 mm.); they have the thighs weakly barred or vermiculate anteriorly and posteriorly or unmarked, an ill-defined interorbital triangular mark, linear markings dorsally, and small choanae.

Key to Species and Subspecies

- | | |
|---|---|
| 1. Larger frogs (males to 49 mm. snout-vent length); thighs strongly barred; supratympanic fold black; dorsum blotched or spotted | 2 |
| Smaller frogs (males to 40 mm. snout-vent length); thighs weakly barred or plain; supratympanic fold pale brown; dorsum usually having linear pattern | 3 |

2. Dorsum tuberculate; snout subacuminate; vocal sac flecked with brown; tarsal fold rudimentary; web absent between fingers; black spots absent in scapular region *H. Boulengeri*
 Dorsum smooth; snout pointed; vocal sac dark gray; tarsal fold absent; trace of web between fingers; two or more elongate dark spots in scapular region *H. foliamorta*
3. Snout-vent length more than 30 mm.; tympanum $\frac{3}{4}$ to $\frac{1}{2}$ diameter of eye; prevomerine elevations about size of choanae 4
 Snout-vent length less than 30 mm.; tympanum less than $\frac{1}{2}$ diameter of eye; prevomerine elevations smaller than choanae 5
4. Thighs mottled posteriorly; discs on fingers about $\frac{1}{2}$ size of tympanum; faint dark line from nostril to eye *H. rubra*
 Thighs faintly barred or plain posteriorly; discs on fingers about size of tympanum; distinct dark line from nostril to eye *H. elaeochroa*
5. Dorsum brown with irregular dorsolateral stripes and interrupted paravertebral stripes; two transverse bars on shanks; interorbital bar present *H. staufferi staufferi*
 Dorsum gray with complete dorsolateral and paravertebral stripes; longitudinal stripe on shank; interorbital bar absent *H. staufferi altae*

Key to Known Tadpoles

1. Entire lower beak black; beaks moderate-sized, serrate; dorsal fin high, extending to middle of back 2
 No more than half of lower beak black; beaks small, finely serrate; dorsal fin lower, barely extending onto body 3
2. Papillae present only laterally *H. Boulengeri*
 Papillae present laterally and ventrally *H. foliamorta*
3. Distinct brown stripe from nostril to eye; two stripes below eye, *H. elaeochroa*
 Faint stripe from nostril to eye; no stripe below eye *H. staufferi*

ACCOUNTS OF SPECIES AND SUBSPECIES

Hyla Boulengeri (Cope)

Scytotis Boulengeri Cope, Bull. U. S. Natl. Mus., 32:12, December 1, 1887 [Holotype.—USNM 13974, from "Nicaragua"; J. A. McNeil, collector].

Hyla Boulengeri: Günther, Biologia Centrali-Americana, Reptilia and Batrachia, p. 267, June 1901. Noble, Bull. Amer. Mus. Nat. Hist., 38:339, June 1918. Taylor, Univ. Kansas Sci. Bull., 35:856, July 1, 1952.

Diagnosis.—Size large (δ to 49 mm., ♀ to 53 mm.); skull as long as wide; frontoparietal fontanelle present; snout subacuminate; canthus not pronounced; choanae large; tongue cordiform, slightly longer than broad; interorbital triangle tubercular; skin on dorsum tuberculate; tarsal fold reduced or absent; thighs, shanks, and tarsi boldly barred with dark brown and pale yellow-green in life.

Description.—Head flattened, longer than wide; snout projecting beyond lower lip; loreal region oblique; canthus not pronounced; length of eye less than interorbital distance; tympanum large, about 70 per cent of diameter of eye; interorbital triangle distinct; arms short; fingers lacking web; palmar tubercle tripartite; subarticular tubercles distinct; long tubercle on base of first finger; discs truncate; legs long; tarsal fold reduced or absent; inner metatarsal

tubercle rounded, larger than outer, both elevated; subarticular tubercles distinct; one phalanx free of web on second, third, and fifth toes, three free on fourth toe (Fig. 1A and B); skin tuberculate on dorsum, less so on flanks; skin of belly granular, that on chest and throat weakly granular; tongue cordiform, longer than wide, free and notched behind; vocal slits large, lateral to tongue.

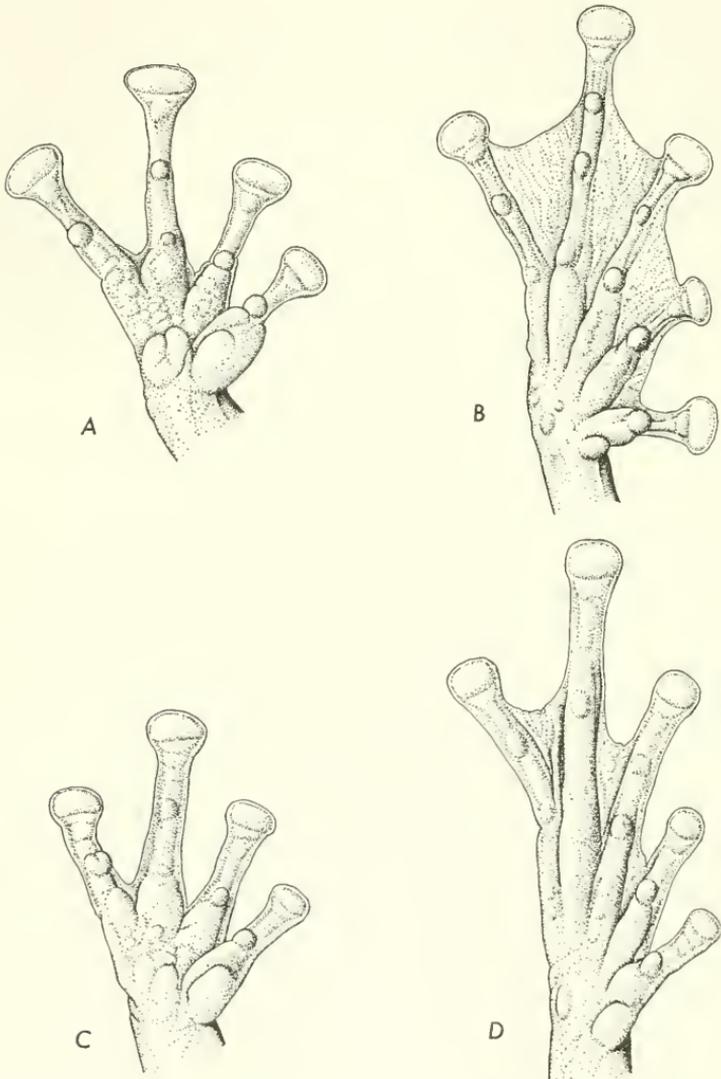


Fig. 1. A and B.—Hand and foot of *Hyla boulengeri* (KU 102173), $\times 3$. C and D.—Hand and foot of *Hyla s. staufferi* (KU 57790), $\times 6$

In life, dorsum tan or brown with dark spots on snout, head, and scapular region; interorbital triangle and blotch posteriorly on dorsum dark brown;

flanks pale green; groin pale green or orange, mottled with dark brown; thighs tan or brown above with dark transverse bars on anterior and posterior surfaces; spaces between bars green or orange; inner surfaces of shanks and outer surfaces of tarsi brown and orange; foot brown above; forelimbs brown and pale green above, weakly barred; belly creamy white with scattered brown spots; vocal sac creamy white flecked with brown; lower jaw brown with white spots on lips (Pl. 1A).

In preservative, head and dorsum dark brown with triangular spot between eyes; dark spots on head and scapular region and dark brown blotch posteriorly on dorsum; flanks creamy white with brown spots; groin creamy white mottled with dark brown; thighs brown above with dark brown transverse bars on anterior and posterior surfaces; inner surfaces of shanks and outer surfaces of tarsi barred with pale brown; dorsal surface of foot mottled brown and creamy white; ventral surface of foot and toes pale brown; forelimbs faintly barred with pale brown; belly white with a few pale brown spots; vocal sac flecked with pale brown; lower jaw marked with small white spots on lips.

Variation.—Geographic variation is evident in the snout-vent length, tibia length, and foot length, all in relation to snout-vent length, and the relative size of the tympanum to the eye (Table 1). The largest specimens are from the humid Pacific lowlands of Costa Rica; individuals from the Caribbean lowlands of Costa Rica, Canal Zone, and South America are smaller. A general trend for increase in size extends from South America to the Pacific lowlands of Costa Rica.

Most variation in color does not seem to be correlated with geography; color variation is nearly as great within a given population as between separated populations. However, most specimens from Rincón de Osa, Puntarenas Province, Costa Rica, are dusky brown, but a few are darker. In comparison with specimens from the Caribbean lowlands of Central America, specimens from the Pacific slopes in Costa Rica have a darker interorbital triangle. In some specimens from the latter area rugosities are present on the borders of the interorbital triangle, on the snout, on the upper eyelid, and on the heel. Specimens from the Caribbean lowlands are less tuberculate, and most individuals from there lack rugosities on the tarsus. Living individuals from Puerto Viejo, Heredia Province, Costa Rica, and from the Canal Zone, Panamá, are brown above with a metallic green tint. Rugosities are present on the posterior edges of the forelimbs in some specimens from throughout the range. In most respects, specimens from the Canal Zone resemble those from the Caribbean lowlands of Costa Rica more than they resemble those from the Pacific lowlands of Costa Rica, but some individuals from the Canal Zone are less metallic above and have small white spots dorsally on the body, head, and limbs.

A moderate amount of color change from night to day has been noted. At night, a male from Puerto Viejo, Heredia Province, Costa Rica, was grayish tan above with slightly darker markings; the flanks were pale yellowish green. By day, the dorsum was brown with darker markings, and the throat was pale gray with white flecks; the rest of the venter was creamy white. The groin was pale green with black mottling; the anterior and posterior surfaces of the thighs and inner edges of the tarsi were greenish yellow with black bars.

TABLE 1.—Geographic Variation in Size and Proportions in Males of *Hyla boulengeri*.
(Means in parentheses below observed ranges.)

Locality	N	Snout-vent length (mm.)	Tibia length/ snout-vent	Tympanum/ eye	Foot length/ snout-vent
Costa Rica: Tilarán.....	23	37.4-48.7 (43.8)	0.52-0.58 (0.55)	0.62-0.76 (0.71)	0.39-0.45 (0.42)
Costa Rica: Rincón de Osa.....	10	41.4-46.1 (44.0)	0.54-0.60 (0.57)	0.63-0.80 (0.74)	0.40-0.45 (0.43)
Costa Rica: Alajuela Province...	13	35.6-43.1 (39.8)	0.55-0.60 (0.57)	0.63-p.78 (0.69)	0.41-0.46 (0.44)
Costa Rica: Puerto Viejo.....	25	37.5-42.9 (41.6)	0.51-0.62 (0.55)	0.63-0.79 (0.71)	0.38-0.46 (0.43)
Costa Rica: Suretka.....	9	38.7-42.0 (41.0)	0.56-0.58 (0.56)	0.53-0.72 (0.62)	0.35-0.45 (0.42)
Panamá: Canal Zone.....	16	36.7-42.9 (39.0)	0.52-0.58 (0.54)	0.70-0.78 (0.74)	0.40-0.44 (0.42)
Venezuela: Santomé.....	4	35.5-40.9 (38.5)	0.45-0.48 (0.46)	0.63-0.67 (0.65)	0.36-0.40 (0.38)

TABLE 2.—Comparison of Mating Calls in the *Hyla rubra* Group.
(Means in parentheses below observed ranges.)

Species	N	Notes per call group	Duration of note (sec.)	Pulses per second	Fundamental frequency (cps)	Major frequencies (cps)	
						Lower	Upper
<i>H. boulengeri</i>	8	1	0.24-0.47 (0.35)	80-120 (101)	70-74 (71)	1400-1820 (1611)	2520-3182 (2840)
<i>H. foliamorla</i>	7	1	0.23-1.86 (0.69)	50-60 (51)	52-61 (56)	912-1026 (918)	2736-3477 (3055)
<i>H. etaeochroa</i>	15	2-95 (49)	0.12-0.24 (0.17)	40-50 (42)	48-65 (57)	1254-1586 (1499)	2562-3477 (2911)
<i>H. s. staufferi</i>	18	2-77 (23)	0.13-0.23 (0.18)	100-130 (120)	96-130 (106)	1582-1872 (1743)	1962-3744 (3056)
<i>H. s. altae</i>	7	2-22 (11)	0.14-0.18 (0.15)	110-130 (120)	104-117 (112)	1853-2106 (2008)	3379-4056 (3775)

Cranial Osteology.—The skull of *Hyla boulengeri* is as long as it is wide, and is flat; the premaxillary is small and bears 13 to 17 teeth (mean for 6 specimens, 14.9). The alary processes of the premaxillaries are widely separated, concave posteriorly, and vertical. Ventrally, the premaxillary is connected to the prevomer by bony tissues. The maxillary is slender and bears 70 to 91 teeth (mean for 6 specimens 78.1). The pars facialis of the maxillary is laterally convex and about four times as high as the pars dentalis.

The nasal is large (its length about 40 per cent of total length of skull), and pointed anteriorly and posteriorly in dorsal view. The nasals are separated anteromedially by the cartilaginous septum nasi. One or two protuberances are present on the midlateral concavity of the nasal. Posteriorly, the nasal overlaps the sphenethmoid and articulates with the palatine. Dorsally the sphenethmoid is large, pentagonal, and completely ossified. The frontoparietal is elongate, smooth, and bears a small supraorbital process on the anterior edge of the orbit. A keyhole-shaped frontoparietal fontanelle is present; the fontanelle is narrow anteriorly and wide posteriorly.

The bony part of the proötic is separated dorsally from the squamosal by the cartilaginous crista parotica. The squamosal is small, its anterior arm slender and pointed. The posterior arm of the squamosal is pointed terminally and articulates with the proötic medially.

The prevomer is large and elongate. Anteriorly the prevomer is connected to the maxillary-premaxillary articulation; posteriorly, the prevomer is separated from the sphenethmoid by cartilage. Each prevomer bears six to nine teeth. The palatine is present and edentate. The anterior end of the parasphenoid is broad (less pointed than in *Hyla foliamorta*). The pterygoid is slender and well developed.

Natural History.—*Hyla boulengeri* inhabits humid lowland tropical forests and breeds in temporary ponds. Claspings pairs and gravid females were observed at Puerto Viejo, Heredia Province, Costa Rica, on June 21, 1966. Males were calling from depressions in decaying logs and stumps, in forked stems, and from leaves of broad-leafed plants near the pond. Males were observed in late July and early August calling from *Calathea* and *Heliconia* leaves at the edge of a pond in the wet forest of the Osa Peninsula. William E. Duellman informed me that he collected calling males in January at El Real, Darién, and in March at Almirante, Bocas del Toro, Panamá. Taylor (1952) found calling males in June at Turrialba, Cartago Province, Costa Rica, and Dunn (1931a) observed males calling in July, November, and December in Panamá. Gravid females have been found from April to August. Breeding activities of *Hyla boulengeri* always seem to be associated with temporary ponds; in Central America breeding apparently takes place throughout most of the year.

The mating call of *Hyla boulengeri* consists of one short, moderately low-pitched note. Each note has a duration of 0.24 to 0.47 second and is repeated at intervals of one second to several minutes. The notes have 80 to 120 pulses per second, a fundamental frequency of about 70 cycles per second, and a dominant frequency of 2,840 cycles per second (Table 2, Pl. 3A).

The eggs are deposited in a mass in the water. No information is available concerning early development. Tadpoles in advanced stages of development were found in a temporary pond at Rincón de Osa, Puntarenas Province, Costa

Rica. The pond was about 10 cm. deep, had a muddy bottom and lacked vegetation. Three recently metamorphosed young were found in mid-August, 1966, on grass at the edge of another temporary pond in the forest.

Tadpoles—Twelve tadpoles are available. These were collected at Rincón de Osa, Puntarenas Province, Costa Rica. The maximum size represented is 34.0 mm., total length (stage 42 of development).

A typical tadpole in stage 36 of development (KU 104295) has a body length of 12.0 mm., tail length of 20.0 mm., and total length of 32.0 mm. Other characters are as follows: depth of tail equal to length of body; body deeper than wide; distance between eye and nostril equal to that between nostril and tip of snout; mouth anteroventral, upper and lower lips bare; papillae present laterally; tooth rows 2/3; upper rows about equal in length; first upper row slightly, and second upper row widely, interrupted medially; lower rows about equal in length, shorter than upper rows; third lower row containing 5-10 large teeth; beak strong, serrate; spiracle nearer anus than eye; anal aperture not extending to border of ventral fin; caudal musculature slender posteriorly, extending to tip of pointed tail; dorsal fin extending to middle of body, slightly deeper than ventral fin; posterior three fourths of tail spotted; rest of tail and body gray-brown or transparent; hindlimbs flecked or spotted with brown (Table 3, Fig. 2A and 3A).

TABLE 3.—Sizes of Tadpoles of *Hyla Boulengeri* in Relation to Developmental Stages. (Means in parentheses below observed ranges; measurements in mm.)

Stage	N	Body length	Tail length	Total length
30.....	1	11.0	22.2	33.2
35.....	1	11.0	12.0	23.0
36.....	3	9.5-12.0 (11.2)	20.0-21.5 (20.5)	31.0-32.0 (31.7)
38.....	2	11.5	22.0	33.5
42.....	2	10.5-13.0 (11.8)	21.0-22.0 (21.5)	32.5-34.0 (33.3)
44.....	2	14.0-15.0 (14.5)	8.0-15.0 (12.5)	22.0-30.0 (26.0)
46.....	1	15.0	15.0

A recently metamorphosed young has a snout-vent length of 15 mm.; the head is as long as wide, the eyes are prominent; the limbs are weakly barred; the skin is rugose above and granular below. The venter is immaculate; the dorsum and limbs are gray-brown in preservative (pale green in life). The interorbital space, supratympanic fold, and scapular region are darker than the rest of the body; the fingers lack webbing; the webbing on the foot is the same as in adults; small metatarsal tubercles are present, but the tarsal fold is absent.

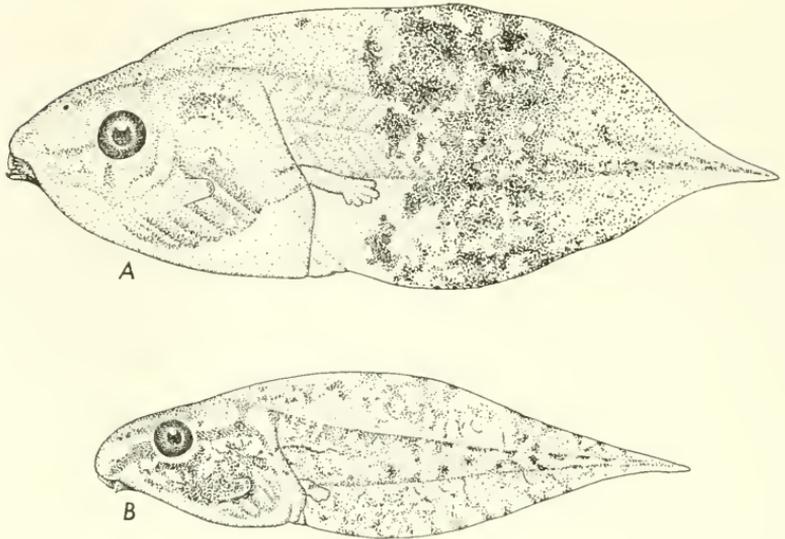


Fig. 2. Tadpoles of (A) *Hyla boulengeri* (KU 104295) and (B) *Hyla elaeochroa* (KU 104134), $\times 3$.

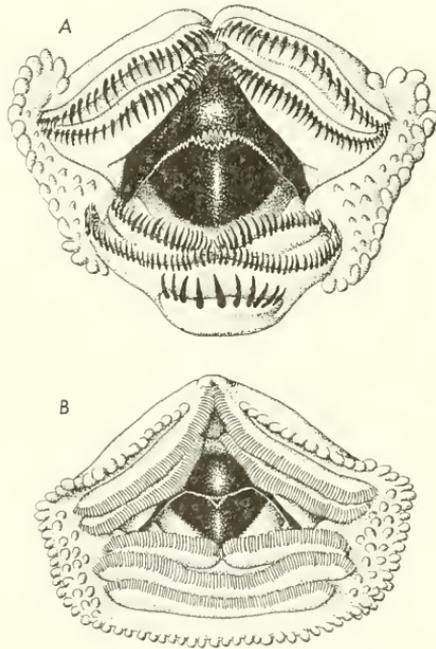


Fig. 3. Mouthparts of tadpoles of (A) *Hyla boulengeri* (KU 104295) and (B) *Hyla elaeochroa* (KU 104134), $\times 25$.

Remarks.—Cope (1887:12) described *Scytotis boulengeri* from Nicaragua. Günther (1901:267) placed *boulengeri* in the genus *Hyla*, and stated that Cope possibly placed *boulengeri* in the genus *Scytotis* on the supposition that it had an accumulation of "sebaceous glands" above the tympanum. Noble (1918:339) redescribed *Hyla boulengeri* on the basis of three specimens from Zelaya Province, Nicaragua, and noted that the glands were not prominent in any of the specimens. Duellman (1956:8) showed that *Scytotis hebes* (generotype of *Scytotis* by monotypy) is a *Phrynohyas*, and thus placed *Scytotis* Cope, 1862, in the synonymy of *Phrynohyas* Fitzinger, 1843.

Dunn and Emlen (1932:25) placed *Hyla lancasteri* Barbour in the synonymy of *Hyla boulengeri*; the former was known solely from one juvenile. They made no qualifying statements, but probably they were impressed by the strongly barred thighs, a coloration known among Central American hylids at that time only in *Hyla boulengeri* (Duellman, 1966a:271). Taylor (1952:856) followed Dunn and Emlen with reservation and noted some differences. Duellman (1966a:271) showed that the holotype of *lancasteri* was a juvenile of a species subsequently named as *Hyla moraviaensis* by Taylor (1952:865).

In Central America, *Hyla boulengeri* can be confused only with *Hyla foliamorta*; the latter is restricted to central and eastern Panamá and northern Colombia. The snout of *foliamorta* is more pointed and protruding, and the vocal sac is darker than in *boulengeri*; the groin of *foliamorta* usually is creamy white, whereas *boulengeri* usually has a dark spot. The skulls differ in that *boulengeri* has a frontoparietal fontanelle, the prevomer is larger and elongate, anteriorly connected to the premaxillary, and posteriorly separated from the sphenethmoid by cartilage; *foliamorta* lacks a fontanelle, the prevomer is smaller, anteriorly separated from the premaxillary by cartilage, but connected by a bony suture to the sphenethmoid. The mating call of *boulengeri* differs by having shorter notes, twice as many pulses per second, a higher fundamental frequency, and more closely approximated major frequencies than does that of *foliamorta*.

Hyla boulengeri need not be compared in detail with the other Central American members of the *Hyla rubra* group, because all of them are smaller and have shorter snouts, smoother skin, and dissimilar color patterns.

Distribution.—In Central America *Hyla boulengeri* inhabits the forested lowlands in locally humid areas in Guanacaste Province, Costa Rica, and in the humid Golfo Dulce region of Costa Rica; it occurs on the Caribbean lowlands from central Nicaragua to South America, where it ranges to Guyana and Ecuador. The highest elevations where *H. boulengeri* has been found are 620 meters at Turrialba, Cartago Province, and 700 meters at Tilarán, Guanacaste Province, Costa Rica (Fig. 4).

Specimens Examined.—Costa Rica: *Alajuela*: 9 km N Ciudad Quesada, near La Florencia, USC 8059 (4); 18 km N Florencia, USC 2624; Laguna Monte Alegre, KU 64334; Las Playuelas, 11 km S Los Chiles, USC 7216, 7217 (2), 7219; 3 km NE Muelle del Arenal, USC 2644 (5). *Cartago*: Turrialba, KU 24741. *Guanacaste*: 7 km N Liberia, USC 8096 (2), 8138 (6); 13.6 km N Liberia, USC 8151, 8171 (2); 20.5 km S Liberia, USC 8205; Taboga, 20 km SE Las Cañas, KU 102170, USC 7166; 4 km NE Tilarán, USC 8023; 6 km NE Tilarán, USC 523 (3), 6262, 7019. *Heredia*: Puerto Viejo, KU 64323-7 (skeletons), 104351-3 (skeletons), 64330-3, 103592-620; 1 km NE Puerto Viejo, UMMZ 126042; 1 km S Puerto Viejo, KU 84983-4 (skeletons), 86317-22, 87774 (skeleton); 4.2 km W Puerto Viejo, KU 64329, 64328 (skeleton). *Limón*: Mountain Cow Creek, near Banano, KU 37031, 41067 (skeleton); 3 km S Río

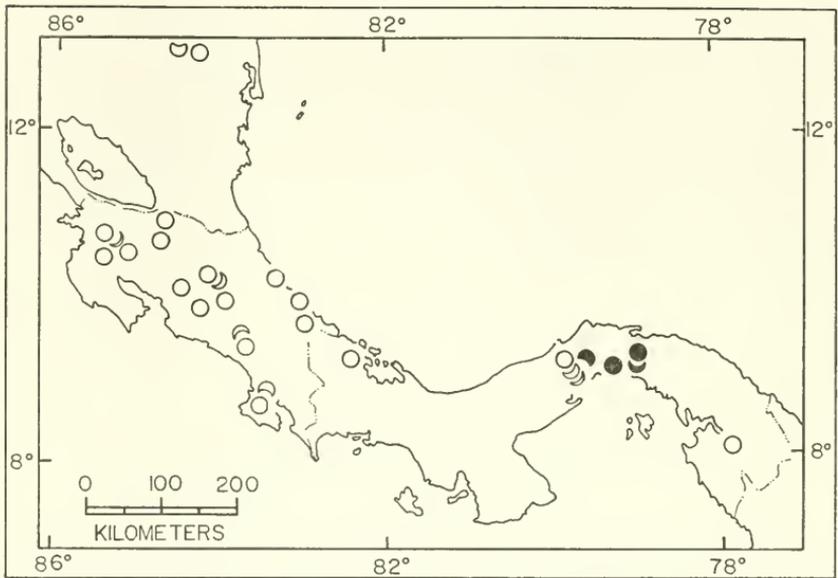


Fig. 4. Map showing locality records for *Hyla boulengeri* (circles) and *H. foliamorta* (dots).

Tortuguero, AMNH 69057; Suretka, KU 36482-8, 36699. *Puntarenas*: 4.8 km S Bahía Rincón on NW side Río Rincón, USC 705; Parrita, USC 6163; 4.5 km W Rincón de Osa, KU 102177-9, 104295-6 (tadpoles); 6 km SW Rincón de Osa, KU 102171-6; 4.4 km NW Villa Neilly, USC 8003; 10.5 km WNW Villa Neilly, KU 64321. *San José*: 21 km WSW San Isidro el General, KU 34104-6.

Panamá: *Bocas del Toro*: 3.2 km W Almirante, KU 95978. *Canal Zone*: Barro Colorado Island, FMNH 13379; near Clayton Reservation, UIMNH 42000; 2.6 km SW Fort Kobbe, KU 95977; Miroflores Locks, AMNH 69764-5; Summit, AMNH 73445, KU 97777, 101540-9, 104350 (skeleton). *Colón*: Río Gatuncillo, near Nuevo San Juan, KU 95976. *Darién*: El Real, KU 80451-3.

Hyla foliamorta Fouquette

Hyla foliamorta Fouquette, *Herpetologica*, 14:125, April 25, 1958 [Holotype. —TNHC 23109, 11 km. NW Miraflores Locks, Canal Zone, Panamá; M. J. Fouquette, Jr. collector].

Diagnosis.—Size medium (δ to 43 mm., ♀ to 41 mm.); skull longer than wide; frontoparietal fontanelle absent; snout acuminate, projecting; interorbital triangle bordered by white lines; scapular region having two or more elongate spots; dorsum smooth; vocal sac dark gray; groin creamy white; traces of web between fingers.

Description.—Head flattened, longer than wide; snout flat, pointed, protruding beyond lower lip; loreal region slightly concave; canthus moderately prominent; eyes smaller than interorbital space; tympanum distinct, 55 to 75 per cent of diameter of eye, smaller than internarial space; arms short; fingers having rudimentary webs; median palmar tubercle tripartite; inner palmar tubercle on base of first finger flat; subarticular tubercles distinct; discs of fingers smaller than diameter of tympanum; legs long; tarsal fold lacking;

inner metatarsal tubercle larger than outer; one phalanx free on second, third, and fifth toes, two and one half phalanges free on fourth toe; narrow fringe continuing from web to discs of toes; discs of toes about the size of those on fingers; skin smooth on dorsum and flanks, that on belly and posterior part of thighs granular; tongue oval, longer than wide; vocal slits oblique, about one half length of tongue.

In life, dorsum pale tan to pale reddish brown with irregular reddish brown markings; small dark spots on head; distinct dark brown triangular mark between eyes, bordered by thin white lines; apex of triangle always directed backward; supratympanic fold with black edge; scapular region having two to five small, elongate black spots; belly creamy tan with small brown spots; vocal sac uniformly dark brown with scattered creamy tan flecks; upper jaw dark brown; limbs creamy white below with scattered brown spots; groin marked with small brown spots in some specimens; anterior and posterior surfaces of thighs yellow-orange with three distinct black blotches; two dark bands on upper surface of shanks; webbing of feet yellowish tan with brown mottlings (Pl. 1B).

In preservative, dorsum brown or gray with darker markings; interorbital triangle distinct, bordered by white lines; supratympanic fold with black edge; two or more small elongate black spots in scapular region; belly white with numerous brown flecks; edge of upper lip dark brown; vocal sac dark gray; undersides of limbs creamy white; groin creamy white with or without brown spots; anterior and posterior surfaces of thighs having three black blotches separated by creamy white spaces; shanks having two brown bands; webbing of feet mottled with brown.

Variation.—Twenty-eight breeding males from the area between Chepo and Tocumen, Panamá, have snout-vent lengths of 39.0 mm. to 46.0 mm. (mean 42.5 mm.). In these specimens, the ratio of the tibia length to the snout-vent length is 0.54 to 0.61 (mean, 0.57); the ratio of the diameter of the tympanum to that of the eye is 0.55 to 0.75 (mean, 0.67). One female has a snout-vent length of 41.0 mm., tibia/snout-vent length ratio of 0.57, and tympanum/eye ratio of 0.76. Two to five (usually three) elongate black spots are present in the scapular region in different individuals. The flanks in some are spotted with brown; in others they are creamy white. A small black spot is present in the groin of some specimens. Usually two to four blotches are present on the anterior and posterior surfaces of the thighs; in some specimens the blotches are reduced to small spots. One or two brown spots are present proximally on the shanks in most specimens. In some individuals tuberculations are scattered on the head and in the tympanic and scapular regions, but the dorsum is smooth in most specimens; the belly is creamy white flecked with brown.

Cranial Osteology.—The skull of *Hyla foliamorta* is flat and longer than it is wide. The premaxillary is small and bears 13 to 16 teeth (mean for 2 specimens, 14.8). The alary process of the premaxillary is vertical and concave posteriorly. Ventrally, the premaxillary is completely separated from the prevomer by cartilage. The maxillary is slender; each bears 77 to 84 teeth (mean for 2 specimens, 81). The pars facialis of the maxillary is laterally convex and less than three times the height of the pars dentalis.

The nasal is large and pointed anteriorly and posteriorly in dorsal view.

The length of the nasal comprises about 40 per cent of the total length of the skull. The nasals are separated anteromedially by the cartilaginous septum nasi. One protuberance is present on the midlateral concavity of the nasal. Posteriorly, the nasal overlaps the sphenethmoid; posterolaterally the nasal articulates with the palatine. The sphenethmoid is completely ossified and pentagonal in dorsal view. The frontoparietal is elongate, without a pronounced anterior supraorbital process. The frontoparietals are sutured medially throughout their lengths; the frontoparietal fontanelle is absent.

The bony part of the proötic is narrowly separated dorsolaterally from the squamosal by the cartilaginous crista parotica. The squamosal is large; the anterior arm is pointed. The posterior arm of the squamosal is broad, rounded terminally, and articulates with the proötic medially.

The prevomer is short and separated anteriorly from the premaxillary and maxillary by cartilage. The posterior margin of the prevomer has a bony articulation with the sphenethmoid. Each prevomer bears five to seven teeth. The palatine is small and edentate. The anterior end of the parasphenoid is narrow (more pointed than in *Hyla Boulengeri*). The pterygoid is slender and well developed (Fig. 5A).

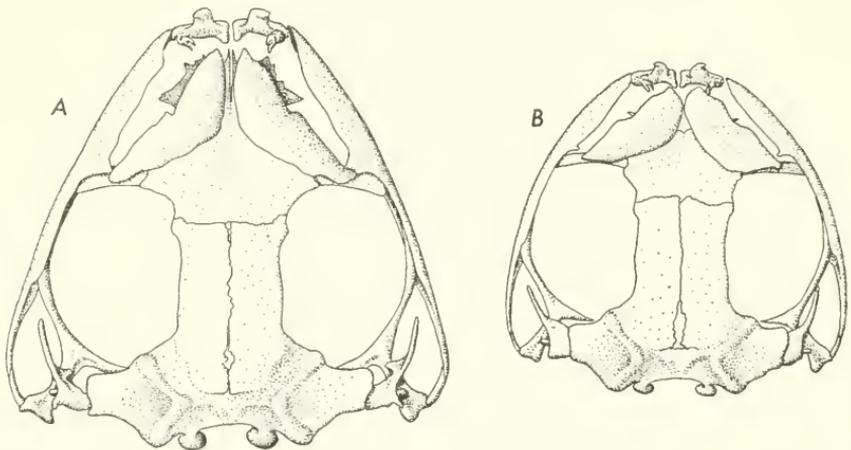


Fig. 5. Dorsal views of the skulls of (A) *Hyla foliamorta* (KU 77687) and (B) *H. elaeochroa* (KU 68289), $\times 3$.

Natural History.—*Hyla foliamorta* inhabits lowland forests in eastern Panamá and breeds in temporary ponds. Males have been observed calling from grasses, bushes, and emergent vegetation near temporary ponds and ditches along roads. William E. Duellman informed me that he found a breeding congregation of this species in June near Chepo, Panamá, where males were calling from spiny palms at the edge of a woodland pond. Fouquette (1958) found calling males in May, August, and September near Miraflores Locks, Canal Zone. Calling stations vary from one to two meters above ground. No clasping pairs have been found; only one female is known (KU 101589, from 8 km NE Tocumen, Panamá); this gravid individual was collected in early June.

The mating call of *Hyla foliamorta* consists of one pulsed, low-pitched, moderate trill of about 0.5 second duration. Each note is repeated at intervals of 5 seconds to a few minutes. The notes have about 50 pulses per second, a fundamental frequency of 56 cycles per second and a dominant frequency of about 3000 cycles per second (Table 2, Pl. 3B).

Egg deposition sites are unknown. No information is available concerning early development, and little is known about the breeding season of *Hyla foliamorta*. Probably its breeding activities are restricted to the rainy months.

Tadpoles.—Eight tadpoles were collected from a weedy temporary pond near Chepo, Panamá, in early June.

A typical tadpole in stage 35 of development (KU 104244) has a body length of 9.5 mm., tail length of 25.0 mm., and a total length of 34.5 mm. Other characters are as follows: depth of tail equal to length of body; body deeper than wide; distance between eye and nostril equal to distance between eye and spiracle; mouth anteroventral; median part of upper lip bare; rest of lip having one row of papillae; a few other rows of small papillae at corners of mouth; tooth rows 2/3; first upper row entire, second upper row interrupted medially, shorter than first; lower rows shorter than upper rows, third shortest; beak moderately robust; spiracle nearer eye than anus; anal tube short, aperture not extending to border of ventral fin; caudal musculature slender, extending to tip of pointed tail; dorsal fin extending onto body (Table 4).

TABLE 4.—Sizes of Tadpoles of *Hyla foliamorta* in Relation to Developmental Stages. (Means in parentheses below observed ranges; measurements in mm.)

Stage	N	Body length	Tail length	Total length
25.....	2	5.0-5.2 (5.1)	8.0-8.5 (8.3)	13.0-13.7 (13.4)
26.....	3	7.0-7.5 (7.2)	12.0-12.4 (12.1)	17.0-19.5 (18.6)
28.....	2	6.5-7.0 (6.8)	18.0	25.0
35.....	1	9.5	25.0	34.5

In life, yellow above, white below; caudal fin greenish yellow with black or gray reticulations; dark line from snout to eye; dark spot behind eye; tail unpigmented except for fine dark reticulations. In preservative body creamy white, transparent below with dark pigment above in some specimens.

Remarks.—*Hyla foliamorta* can be confused only with *Hyla Boulengeri*. The differences between adults of these species were discussed in *Remarks* on *H. Boulengeri*. The tadpoles of *foliamorta* have labial papillae on the lower lip and a stripe between the eye and the tip of the snout. By comparison the tadpoles of *Boulengeri* have a bare lower lip and no stripe between the eye and the tip of the snout.

Distribution.—*Hyla foliamorta* inhabits the subhumid Pacific lowlands

(elevations of less than 100 meters) of Central Panamá and Caribbean lowlands of northern Colombia (Fig. 4).

Specimens Examined.—Panamá: Panamá: 3 km WSW Chepo, KU 77164-9, 101573-5, 104243-4 (tadpoles); 6 km WSW Chepo, KU 77170, 101576-8; 1.5 km SW Naranjal, KU 77171, 77687 (skeleton); 2 km N Tocumen, KU 101579-83, 104349 (skeleton); 8 km NE Tocumen, KU 101584-92.

No specific locality: TNHC 24401.

Hyla rubra Laurenti

Hyla rubra Laurenti, Synopsis Reptilium Emendatum, p. 35, 1768. Daudin, Hist. Nat. Rainettes Grenouilles Crapauds, II:26, 1802. Daudin, Hist. Nat. Particuliere Reptiles, 8:53, 1803. Günther, Catalogue Batrachia Saliencia Brit. Mus., p. 110, 1859. Boulenger, Catalogue Batrachia Saliencia s. Ecaudata, p. 403, February 1, 1882. Dunn, Occas. Papers, Boston Soc. Nat. Hist., 5:413, October 10, 1931.

Hyla elaeochroa (part): Dunn and Emlen, Proc. Acad. Nat. Sci. Philadelphia, 84:25, March 22, 1932.

Diagnosis.—Size medium; skull longer than wide; frontoparietal fontanelle absent in adults; snout subovoid; choanae rounded; dorsal stripes present; black vermiculations on posterior surfaces of thighs.

Description.—Head flat, longer than wide; snout long, subovoid, slightly protruding beyond lower lip; loreal oblique, concave; canthus rounded, indistinct; diameter of eye about equal to interorbital space; tympanum large, about three fifths diameter of eye, smaller than internarial distance; supratympanic fold indistinct; arms short; fingers free of webs; subarticular tubercles distinct; median palmar tubercle large, bifid; inner palmar tubercle on base of first finger flat, elongate; disc of third finger about one half diameter of tympanum; legs moderately long; tarsal fold absent; inner metatarsal tubercle distinct, oval; toes about half webbed; web on fourth toe extending to disc; discs of toes about size of those on fingers; skin smooth above with small granules on head and in scapular region in some specimens; skin on flanks, throat, belly, and lower surfaces of thighs granular; tongue oval, longer than wide, not free behind; choanae small, oval; vocal slits long, lateral to tongue.

In preservative, dorsum pale brown with darker dorsolateral stripes; narrow dark brown line from nostril to eye; groin, anterior surface of thighs, and posteroventral surfaces of shanks creamy tan with dark brown vermiculations; white spots present on thighs in some specimens; throat flecked with brown; belly creamy white or gray.

Remarks.—The taxonomic history of *Hyla rubra* Laurenti is confused. Seba (1734:70) illustrated and diagnosed a frog for which he used the name *Ranula, Americana, Rubra*. Linnaeus (1758:213) considered Seba's frog to be a variety of *Hyla arborea*. Laurenti (1768:35) apparently examined the same individual that Seba called *Ranula, Americana, Rubra*. For this specimen, Laurenti used the binominal *Hyla rubra* and provided a brief diagnosis. The type locality was given as America.

Daudin (1802:26) redescribed the same specimen(s?) treated by Seba and Laurenti and provided a fairly good description and figures. Daudin restricted the type locality to Surinam and indicated that Marin de Baize was the probable collector. Daudin (1802:26 and 1803:53) neglected to consider Laurenti's work, but he applied the same name used by Laurenti. Most authors have

credited *Hyla rubra* to Daudin, but Rivero (1961:120) noted that *Hyla rubra* Laurenti, 1768, has priority over *Hyla rubra* Daudin, 1802. Since both Laurenti and Daudin worked on Seba's material, it is reasonable to assume that Daudin redescribed the same frog that was named by Laurenti; this was not an uncommon practice in the early nineteenth century. Thus I conclude that *Hyla rubra* Daudin, 1802, is a junior synonym of *Hyla rubra* Laurenti, 1768.

Dunn (1931a:413) first reported *Hyla rubra* from Central America; he recorded the species from the Canal Zone and San Pablo, Panamá. I have examined the material of *Hyla rubra* from Panamá deposited in various museums. Most of the specimens are faded, discolored, and do not have distinct brown vermiculations on the thighs. The specimens seem to be more like *Hyla rubra* than any of the other species in the *rubra* group. The presence of oval choanae and a tympanum larger than the largest finger disc separate these specimens from *Hyla elaeochroa*, a species with which *rubra* has been confused. *Hyla elaeochroa* does not occur in the Canal Zone or eastern Panamá. All museum specimens from Nicaragua, Costa Rica, and western Panamá that have been called *Hyla rubra*, plus those mentioned by Dunn and Emlen (1932:25) and Dunn (1933:61) are *Hyla elaeochroa*.

The taxonomic status of the many South American populations referred to *Hyla rubra* and of other populations now recognized as different species is not clear at the present time. Considerable variation in external characters and in cranial features has been observed in South American *rubra*. A review of the taxonomy of these populations is beyond the scope of this paper. Possibly the Central American specimens herein referred to *rubra* will ultimately be found to be specifically distinct from those in Surinam. Since I have no osteological material from Central America, I have been unable to describe the cranium in this account. Furthermore, I have no data on the ecology and life history of *rubra* in Central America.

Distribution.—*Hyla rubra* inhabits lowland tropical forests from central-eastern Panamá to northern South America and thence through lowlands east of the Andes to northern Argentina (Fig. 6).

Specimens Examined.—Panamá: Canal Zone: Gatun, UMMZ 52720 (2); Madden Dam, FMNH 67820; no specific locality, UMMZ 56517 (3), USNM 37863. Colón: Cerro Bruja, MCZ 13248. Darién: El Real, USNM 140569-70, 140573. Panamá: Juan Díaz, MCZ 17973; Las Sabanas, MCZ 17581; Río Trinidad, UMMZ 64003; San Pablo, MCZ 1398-9.

Hyla elaeochroa Cope

Hyla elaeochroa Cope, Jour. Acad. Nat. Sci. Philadelphia, 8:105, 1876 [Holotype.—USNM 30689, Sipurio, Limón Province, Costa Rica; William M. Gabb collector]. Günther, Biologia Centrali-Americana, Reptilia and Batrachia, p. 265, June 1901. Taylor, Univ. Kansas Sci. Bull., 35:859, July 1, 1952. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 17:270, June 17, 1966.

Hyla quinquevittata Cope, Proc. Amer. Philos. Soc., 23:273, April 1887 [Holotype.—USNM 14187, Nicaragua; J. F. Bransford collector]. Günther, Biologia Centrali-Americana, Reptilia and Batrachia, p. 268, June 1901. Noble, Bull. Amer. Mus. Nat. Hist., 38:340, June 1918.

Hyla rubra (part): Dunn and Emlen, Proc. Acad. Nat. Sci. Philadelphia, 84:25, March 22, 1932.

Hyla dulcensis Taylor, Univ. Kansas Sci. Bull., 39:37, November 18, 1958 [Holotype.—KU 32168, Golfito, Puntarenas Province, Costa Rica; Edward H. Taylor collector].

Diagnosis.—Size medium (δ to 38 mm., ♀ to 40 mm.); skull wider than long; nasals truncate anteriorly; frontoparietal fontanelle moderate in size; snout slightly protruding; tympanum about size of largest discs on fingers; dorsum marked by longitudinal stripes; dark stripe between eye and nostril; in life tan to olive-green with or without dark mark between eyes; bones greenish blue.

Description.—Head flat, longer than wide; snout long, rounded, protruding beyond mouth; canthus indistinct; length of eye equal to interorbital distance; loreal region not pronounced; tympanum distinct and about two-fifths diameter of eye; interorbital triangle present or absent; arms short; trace of web between fingers, extending as fringe along sides of fingers; first finger very short with small disc; other discs about size of those on toes; discs on third finger and fourth toe as large as tympanum; outer palmar tubercle moderate in size, partly bifid; inner palmar tubercle large, elongate, flat; subarticular tubercles distinct; legs moderately long; tarsal fold absent; inner metatarsal tubercle flat; outer metatarsal tubercle smaller, indistinct; subarticular tubercles moderate in size; fringe on toes to tip of disc of second toe; rest of toes about two-thirds webbed; foot length about two fifths snout-vent length; tibia length about one half snout-vent length; skin above smooth or with minute pustules; belly finely granular; ventral surfaces of thighs and areas below anus granular; skin on ventral surfaces of limbs smooth; tongue relatively large, longer than wide, barely notched behind; vocal slits elongate, lateral to tongue; choanae medium in size. In life, dorsum yellowish brown, olive green, or grayish brown with dark brown spots on snout, dark brown stripe from nostril to eye, dark yellow-brown interorbital triangle, and dark supratympanic region; generally five interrupted longitudinal dark brown stripes on dorsum (one on each flank, pair of paravertebral and one vertebral); flanks pale yellow; groin yellowish brown; thighs marked with one or two transverse yellow-brown blotches; shanks with two or three yellow-brown blotches above; spaces between blotches on thighs, shanks, tarsi, and feet yellow; brown spots on tarsi and in some specimens on feet; arm pale yellow with pale brown spots; belly creamy white having slight blue-green tint; vocal sac and chin yellow; axillary region yellow, blue-green in some specimens (Pl. 2A).

In preservative, head and dorsum yellowish brown; dark brown stripe from nostril to eye; dark brown spots on snout; a dark brown interorbital triangle with apex directed backward; dark brown supratympanic region; dorsal stripes same as in living individuals; flanks pale yellow with brown spots in some specimens; groin creamy white; thighs and shanks having or lacking transverse dark brown blotches; spaces between blotches creamy white or yellow-brown; arms pale yellowish brown; belly and vocal sac creamy white.

Variation.—Geographic variation in size and some proportions, such as the ratio of tibia length to snout-vent length and the ratio of the diameter of the tympanum to that of the eye, have been observed in this species. The largest individuals are from the Golfo Dulce region (samples from Piedras Blancas and Rincón de Osa), Puntarenas Province, Costa Rica. The smallest individuals are from El Recreo, Zelaya Province, Nicaragua, and from the Caribbean lowlands of Costa Rica.

The diameter of the tympanum is proportionately larger (relative to the size of the eye) in males from Tilarán, Guanacaste Province; the tympanum

is nearly as large in males from Piedras Blancas, Puntarenas Province, and Puerto Viejo, Heredia Province, Costa Rica. The lowest ratios occur in individuals from Almirante, Bocas del Toro, Panamá, in specimens from the Caribbean lowlands of Costa Rica (except Puerto Viejo), and in those from El Recreo, Zelaya Province, Nicaragua. In general, the tympanum is proportionately larger in females than in males; the tympanum is largest in females from the Pacific lowlands of Costa Rica (Table 5).

Color variation has been observed in individuals from the same population, as well as in individuals from different localities, between males and females, and from night to day. In life, most individuals from the Pacific lowlands of Costa Rica are dark tan to greenish gray above with dark brown longitudinal stripes that are entire or broken, but some specimens (mostly males) are dusky brown and lack longitudinal stripes or an interorbital triangle; females usually have the dark interorbital triangle and the stripes on the dorsum. Individuals from Turrialba, Cartago Province, Costa Rica, are pale olive-tan with olive-brown markings. Individuals from Puerto Viejo, Heredia Province, Costa Rica, are uniformly yellowish brown with or without dark longitudinal stripes. Specimens from El Recreo, Zelaya Province, Nicaragua, are like those from Puerto Viejo. Males from Almirante, Bocas del Toro, Panamá, are pale brown with dark brown longitudinal stripes and an indistinct interorbital triangle. Females have a distinct interorbital triangle and dark brown blotches on the thighs and shanks.

By night, the dorsum usually is pale yellow, and the belly is creamy white. By day, the dorsum is dark tan; the stripes and spots are darker, and the belly is yellowish white. Taylor (1952) noticed that considerable variation in color pattern occurred from night to day in individuals from Turrialba, Cartago Province, Costa Rica. At night some individuals lacked a dorsal pattern, but by day many of these individuals developed dorsal stripes.

Cranial Osteology.—The skull of *Hyla elaeochroa* is slightly wider than it is long, and flat. The premaxillary is small and bears 10 to 15 teeth (mean for 9 specimens, 12.3). The alary process of the premaxillary is small, vertical, and slightly concave posteriorly. Ventrally, the premaxillary is partially united to the prevomer by ossification. The maxillary is slender and bears 70 to 82 teeth (mean for 9 specimens, 74.3). The pars facialis of the maxillary is laterally convex and is about twice as high as the pars dentalis.

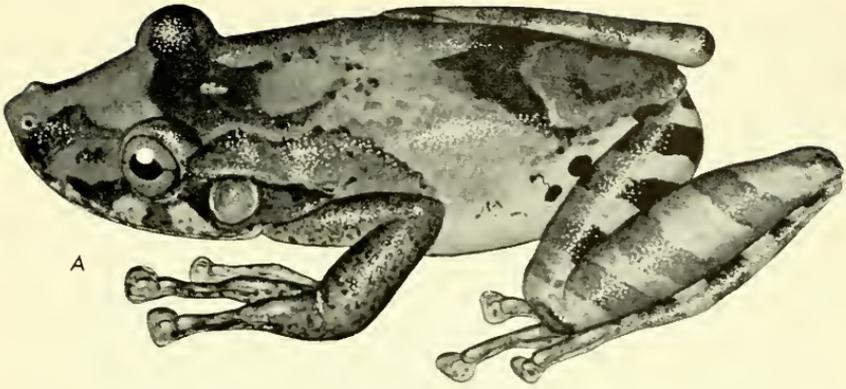
The nasal is large, robust, anteriorly truncate, but pointed posteriorly in dorsal view. The nasal comprises about 45 per cent of the total length of the skull. There is an anterior cartilaginous septum nasi separating the two nasals; the latter overlap the sphenethmoid posteriorly. Each nasal bears a shallow concavity in the midlateral side and lacks a maxillary process. Dorsally, the sphenethmoid is wider than long, roughly pentagonal in shape; the frontoparietal is elongate, smooth, and bears a small anterior supraorbital process. The sphenethmoid and frontoparietal form the anterior margin of the frontoparietal fontanelle; the fontanelle is narrow anteriorly and wider posteriorly (Fig. 5B).

The entire distal surface of the proötic is in contact with the posterior arm of the squamosal. A narrow cartilaginous crista parotica is visible dorsally in some specimens. The squamosal is broad posteriorly but its anterior arm is slender and not in contact with the maxillary.

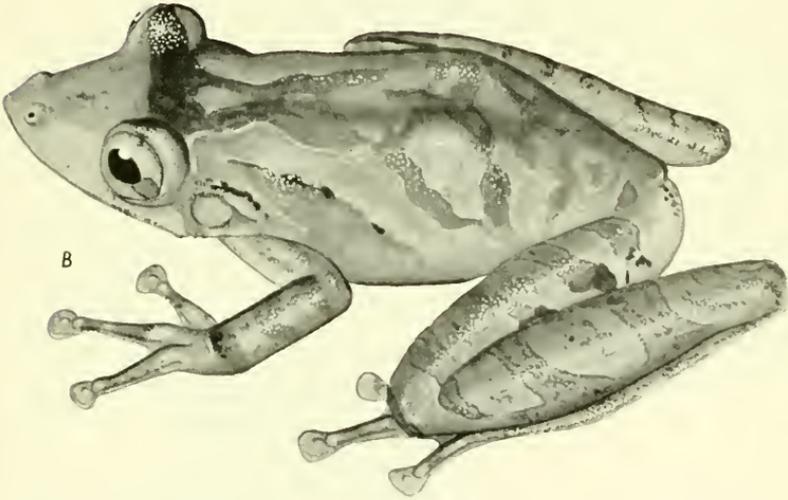
TABLE 5.—Geographic Variation in Size and Proportions in Males of *Hyla elacochroa*.
(Means in parentheses below observed ranges.)

Locality	N	Snout-vent length (mm.)	Tibia length/ snout-vent	Tympanum/ eye	Foot length/ snout-vent
Nicaragua: El Recreo.....	9	28.0-30.3 (29.3)	0.51-0.57 (0.55)	0.47-0.59 (0.51)	0.39-0.54 (0.41)
Costa Rica: Tilarín.....	21	28.8-33.6 (30.6)	0.47-0.57 (0.52)	0.48-0.65 (0.59)	0.40-0.46 (0.41)
Costa Rica: Puerto Viejo.....	22	26.3-32.4 (29.7)	0.49-0.54 (0.52)	0.48-0.65 (0.57)	0.38-0.45 (0.42)
Costa Rica: Turrialba.....	95	28.1-35.0 (30.6)	0.47-0.56 (0.51)	0.47-0.68 (0.56)	0.37-0.46 (0.41)
Costa Rica: Bataán, Limón, and Suretka.....	26	26.3-32.7 (30.0)	0.47-0.54 (0.51)	0.45-0.66 (0.50)	0.36-0.44 (0.41)
Costa Rica: Piedras Blancas.....	21	33.3-37.7 (35.2)	0.50-0.54 (0.51)	0.48-0.64 (0.57)	0.40-0.46 (0.43)
Costa Rica: Rincón de Osa.....	24	31.4-35.9 (34.1)	0.50-0.56 (0.53)	0.45-0.61 (0.54)	0.40-0.46 (0.43)
Panamá: Bocas del Toro.....	6	31.0-33.5 (32.1)	0.49-0.54 (0.51)	0.47-0.50 (0.48)	0.41-0.43 (0.42)

PLATE 1



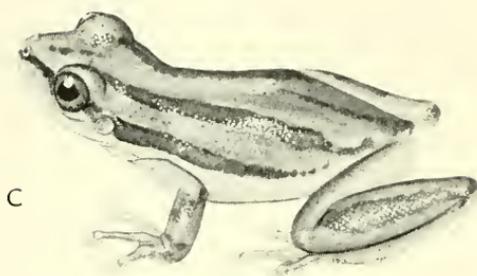
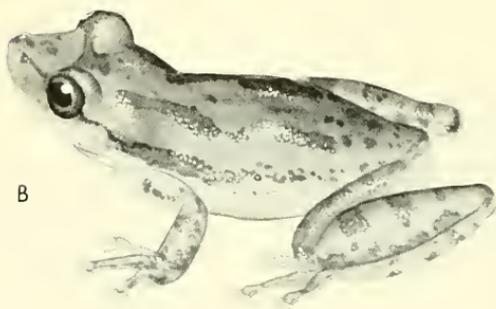
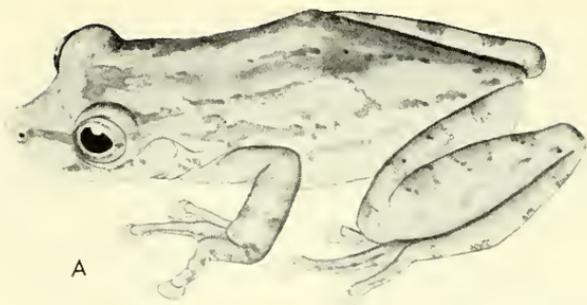
A



B

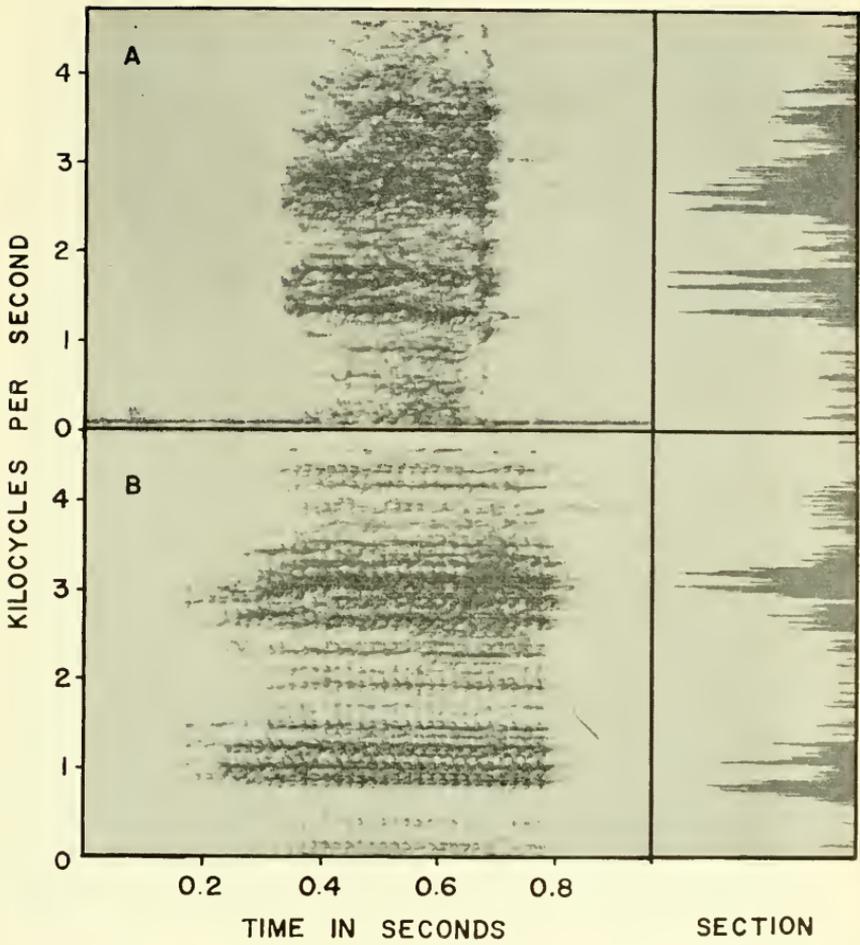
Living *Hyla*: (A) *H. boulengeri* (KU 86322) and (B) *H. foliamorta* (KU 101576), $\times 2$.

PLATE 2



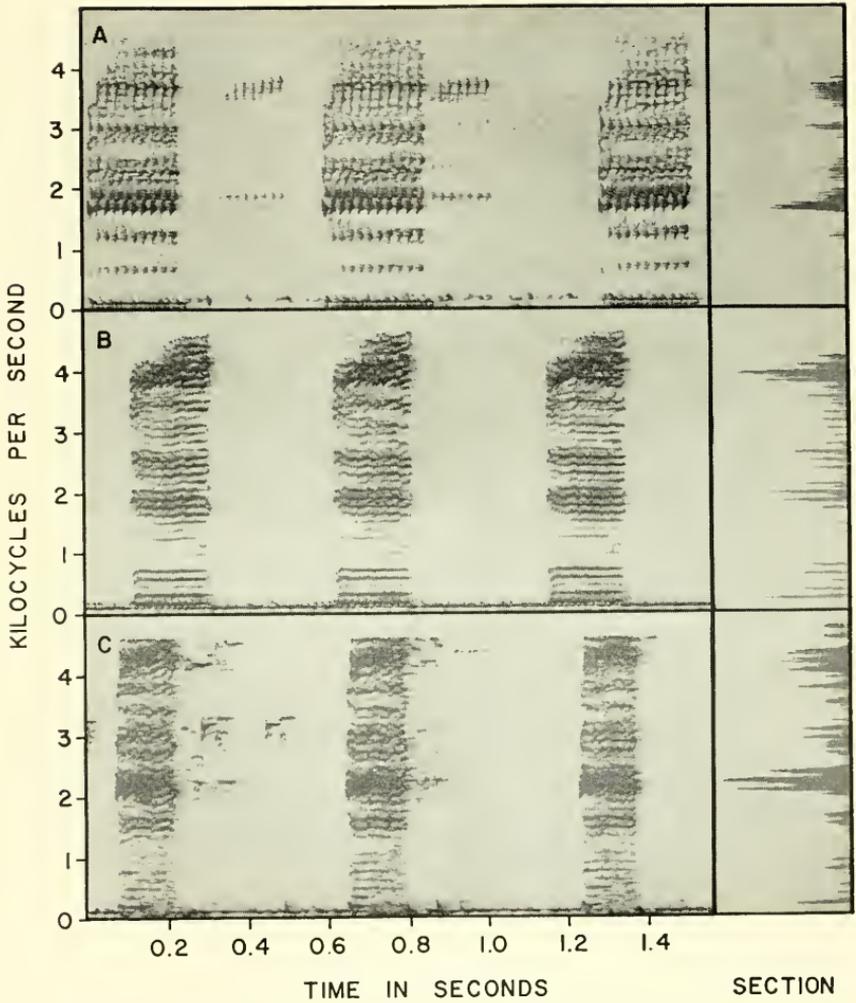
Living *Hyla*: (A) *H. elaeochroa* (KU 91688), (B) *H. staufferi staufferi* (KU 57791), and (C) *H. staufferi altae* (KU 101688), $\times 2$.

PLATE 3



Audiospectrograms and sections of mating calls of (A) *Hyla boulengeri* (KU Tape No. 511) and (B) *H. foliamorta* (KU Tape No. 288).

PLATE 4



Audiospectrograms and sections of mating calls of (A) *Hyla claeochroa* (KU Tape No. 97), (B) *H. s. staufferi* (KU Tape No. 93), and (C) *H. staufferi altae* (KU Tape No. 502).

The prevomer is short, and broadest anteriorly. The prevomer is joined to the premaxillary by ossification. The posterior margin of the prevomer bears a narrow cartilaginous articulation with the sphenethmoid. The anterolateral and posterolateral processes of the prevomer form an incomplete bony margin to the small choanae; each prevomer bears four to seven teeth. The palatine is small, curved anteriorly and edentate. The anterior part of the parasphenoid is robust and ends in a point. The pterygoid is slender and weakly developed.

Natural History.—*Hyla elaeochroa* inhabits humid lowland tropical forests in lower Central America and breeds in temporary ponds. Clasping pairs, gravid females, and calling males have been found mostly in June, July, and August. William E. Duellman informed me that he also found males calling in mid-February, late April, and May. Duellman (1967) reported detailed observations of the social organization in the mating call of *Hyla elaeochroa*. The choruses in this species are initially organized, but when many individuals call, the chorus loses organization. I observed this species breeding in a temporary pond at Puerto Viejo, Heredia Province, Costa Rica, in late June. Calling males and clasping pairs were extremely abundant within a few hours after a heavy rain. Males were mostly found calling from low emergent herbs in the pond and less commonly from bushes and trees to heights of six meters above the water. Calling males were also observed at Rincón de Osa, Puntarenas Province, Costa Rica, in late July. These breeding individuals were found in a shallow pond at the edge of a wet forest. Calling stations were less than two meters in height. John D. Lynch informed me that after a heavy rain in early August, he found several hundred individuals congregated in a small grassy pond less than a foot deep, at Rincón de Osa. Males were calling from sites on grass stems a few centimeters above the water.

The mating call of *Hyla elaeochroa* consists of short notes, repeated at intervals of about 0.40 second. Each note has a duration of 0.12 to 0.24 second. The fundamental frequency varies from 48 to 65 cycles per second, and the notes have 40-50 pulses per second; the dominant frequency is at about 2,900 cycles per second (Table 2, Pl. 4A).

The eggs are deposited in a mass in the water near floating vegetation. William E. Duellman informed me that he observed hatchlings oriented vertically with the tip of the mouth at the surface of the water. They gradually sank to bottom, but swam back to surface again. No additional information is available concerning early development. Tadpoles have been found in shallow grassy ponds in clearings and in temporary woodland ponds.

Tadpoles.—Three hundred and thirty-one tadpoles in various stages of development are available. Thirty-five tadpoles in stage 35 have a mean body length of 8.1 mm. (8.0-9.0 mm.), tail length of 17.7 mm. (15.0-19.5 mm.), and total length of 25.9 mm. (23.0-27.5 mm.). The largest tadpole examined is in stage 40 and has a total length of 34.5 mm. (Table 6).

A typical tadpole, stage 35 of development (KU 104134, from Puerto Viejo, Heredia Province, Costa Rica), has a body length of 9.1 mm., tail length of 17.7 mm., and a total length of 26.8 mm. Other characters are as follows: body depressed anteriorly; body length greater than depth of tail; internarial space as broad as interorbital distance; nostril equidistant between eye and tip of snout; eyes moderately large; mouth anteroventral and triangular; median

TABLE 6.—Sizes of Tadpoles of *Hyla elaeochroa* in Relation to Developmental Stages. (Means in parentheses below observed ranges; measurements in mm.)

Stage	N	Body length	Tail length	Total length
24.....	2	4.0-4.0 (4.0)	8.5-9.0 (8.8)	12.5-13.0 (12.8)
25.....	64	5.0-6.5 (5.7)	8.5-15.0 (11.8)	13.5-21.5 (17.6)
27.....	30	7.0-7.5 (7.1)	13.0-16.0 (14.2)	20.0-23.0 (21.3)
30.....	15	7.0-8.0 (7.3)	13.0-16.5 (15.0)	20.0-24.0 (22.4)
32.....	30	7.5-8.5 (7.8)	15.0-17.0 (16.1)	22.5-25.0 (23.8)
35.....	35	8.0-9.0 (8.1)	15.0-19.5 (17.7)	23.0-27.5 (25.9)
37.....	22	8.5-9.5 (9.0)	16.0-22.0 (18.8)	25.0-31.0 (27.8)
39.....	14	9.5-10.5 (9.9)	19.0-24.9 (21.1)	28.5-33.5 (31.0)
40.....	27	7.0-11.5 (9.1)	15.0-23.0 (22.0)	23.0-34.5 (31.2)
43.....	10	8.0-12.0 (10.2)	11.0-17.0 (13.5)	20.0-26.0 (23.7)
45.....	16	10.0-12.0 (11.2)	1.0-7.0 (3.4)	12.0-17.0 (14.6)
46.....	45	11.0-13.0 (11.8)

fourth of upper lip bare; rest of lip bordered by one row of papillae; clumps of small papillae at corners of mouth; tooth rows 2/3; upper rows equal in length; second row interrupted medially; lower rows shorter than upper rows, diminishing in length; beak rather weak with small serrations; spiracle short and nearer eyes than anus; anal opening not reaching edge of ventral fin; caudal musculature attenuated distally (Figs. 2B and 3B).

In life, dorsum yellowish tan with gray-brown mottling; belly and ventrolateral surfaces silvery-gold or white; black stripe from tip of snout to eye; two black blotches below eye, another blotch extending from eye to base of caudal musculature; caudal musculature and fins gray-brown. In preservative, yellowish tan and silvery-gold colors lost; black reticulations present on tail.

Remarks.—Cope (1876:105) described *Hyla elaeochroa* from Sipurio, Limón Province, Costa Rica. He based his description on a small specimen, 26.0 mm. in snout-vent length, having a dorsum uniformly colored and lacking an inter-

orbital triangle and blotches on the thighs. Cope (1887) described pigmented specimens from Nicaragua as *Hyla quinquevittata*, which he diagnosed as having dark brown bars on the hind limbs and five dark brown longitudinal stripes on the dorsum, the median one of which was expanded anteriorly so as to form a large triangular spot between the eyes. He thought this species was related to *Hyla eximia* Baird and noted that "the hinder legs are much larger; the muzzle is more acuminate and the color bands are much wider" than in *eximia*. Cope did not compare *quinquevittata* with *elaeochroa*, which he had described ten years before. Günther (1901:268), Noble (1918:340), and Nieden (1923:251) regarded both *elaeochroa* and *quinquevittata* as valid species. Dunn and Emlen (1932:25) regarded both as synonyms of *Hyla rubra*, but they made no qualifying statements. Taylor (1952:859) placed *quinquevittata* as a synonym of *elaeochroa* and indicated that *rubra* was another species.

Taylor (1958:37) described *Hyla dulcensis* from the humid tropical forests of Golfo Dulce, Puntarenas Province, Costa Rica. He thought this species was "related to *H. elaeochroa* but differs in its somewhat larger size, smaller finger and toe discs, the obsolete canthus rostralis; the loreal region concave and the choanae larger." Duellman (1966a:270) compared adults, tadpoles, and mating calls of *dulcensis* and *elaeochroa* and concluded that a single species was involved.

Hyla elaeochroa can be easily confused with the closely related *Hyla staufferi*. Although the durations of the calls are similar, the call of *elaeochroa* has only about one third the number of pulses per second, a much lower fundamental frequency, and a lower dominant frequency than that of *staufferi*. *Hyla elaeochroa* is larger and has a less pointed snout than does *staufferi*. Although the skulls of the two species are similar, that of *elaeochroa* differs in having broad palatines and comparatively larger nasals that are truncate anteriorly. In *staufferi* the nasal is rounded anteriorly and the palatine is absent.

Distribution.—*Hyla elaeochroa* occurs on the Caribbean lowlands from western Panamá through Costa Rica to eastern Nicaragua, and on the Pacific lowlands of southeastern Costa Rica and extreme western Panamá. Most localities where it has been collected are below 800 meters, but the species has been found at two localities above 1000 meters (El Silencio and Pacuare, Cartago Province) on the Caribbean slopes of the Cordillera de Talamanca, Costa Rica (Fig. 6).

Specimens Examined.—Nicaragua: *Zelaya*: El Recreo, UMMZ 79721 (9).

Costa Rica: *Alajuela*: Laguna Monte Alegre, KU 64499. *Cartago*: 2 km E Chitaría, KU 107058; El Silencio, 14.4 km NE Turrialba, KU 107059-60; 4.6 km ENE Pacuare, KU 64451-75, 64628-37; 4 km S Pavones, KU 64500; Turrialba (Instituto Interamericano de Ciencias Agrícolas), KU 30305-26, 24616-57, 30337-54, 31776-91, 31803, 31807-15, 64413-50, 68283-87 (skeletons), 68390-1 (young), 35042 (eggs), 25207-8 (skeletons), 25221 (skeleton), 41073-83 (skeletons). *Guanacaste*: 2 km E Tilarán, KU 86356-77, 87667-8 (young). *Heredia*: Puerto Viejo, KU 36696, 46466, 64501-17, 68288-91, 68387, 68388-9 (young), 91803 (young), 91688-9, 104134 (tadpoles), 104135 (young), 104354-6 (skeletons); 1.5 km N Puerto Viejo, KU 64518-23, 68386 (tadpoles); 1 km S Puerto Viejo, KU 84985-6 (skeletons), 87669 (young), 87772-3 (skeletons). *Limón*: Bataán, KU 30327-36; La Lola, KU 64478-98, 68281-2 (skeletons); Los Diamantes, KU 31800-02, 64476-7; Peralta, KU 31816-21; Puerto Limón, KU 31792-99; Suretka, KU 36467-79, 36697, 41084. *Puntarenas*: 5 km NW Buenos Aires, KU 107057; 10 km E Esparta, KU 87666 (tadpoles); Golfito, KU 32166-8; 8 km E Palmer Norte, KU 93939; 10.7 km SE Palmar Sur, KU 93938 (skeleton), 93940-51, 93952 (eggs), 93953-6 (tad-

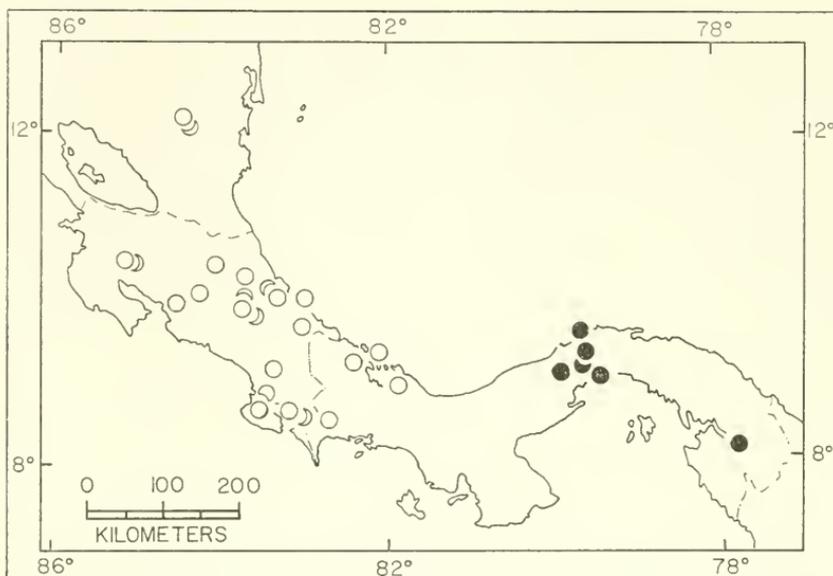


Fig. 6. Map showing locality records for *Hyla elaeochroa* (circles) and *H. rubra* (dots).

poles); Piedras Blancas, KU 103646-59; 4.5 km W Rincón de Osa, KU 102208-41, 104298 (tadpoles).

Panamá: *Bocas del Toro*: Almirante, KU 80079; Isla Bastimentos, KU 96008-11; Río Cricamola, 3.7 km from coast, KU 96012. *Chiriquí*: Río Gariché, 8.3 km ESE Paso de Canoas, KU 101571-2.

Hyla staufferi Cope

Hyla staufferi Cope, Proc. Acad. Nat. Sci. Philadelphia, 17:165, October 1, 1865 [Holotype.—USNM 15317, Orizaba, Veracruz, México; Francis Sumichrast collector].

Diagnosis.—Small frogs (δ to 29 mm., ♀ to 31.6 mm.); skull longer than wide; palatine absent; large cartilaginous crista parotica present; snout flat, elongate and protruding; dark interorbital bar and dorsal stripes usually present.

Description.—Head flat, especially in females, longer than wide; snout long, protruding beyond mouth; loreal region concave; canthus ill-defined; length of eye greater than internarial distance or width of eyelid; length of eye less than interorbital space; tympanum distinct; interorbital spot irregular; supratympanic fold faint; arms short; fingers free of webs; discs on third and fourth fingers equal to diameter of tympanum; inner matatarsal tubercle on base of first finger distinct; first finger shorter than second; palmar tubercle distinct (Fig. 1C); legs short (usually less than 50 per cent of snout-vent length); tarsal fold absent; metatarsal tubercles small, outer tubercle smaller than inner; subarticular tubercles small, simple, distinct; toes less than half webbed (Fig. 1D); skin smooth above with a few small pustules on head, scapular region, flanks, and supratympanic region; arms and legs smooth; skin of belly coarsely granular; posteroventral surfaces of thighs finely granular; tongue small, rounded,

longer than wide, slightly free and notched posteriorly; vocal slits small, lateral to tongue; choanae moderate in size.

Variation.—The largest males of *Hyla staufferi* are from Jalapa, Guatemala, and from San Salvador, El Salvador. In these samples the average snout-vent length is 27 mm. In Panamanian specimens the average snout-vent length is 23.6 mm. Slight variation in the ratio of tibia length to snout-vent length exists throughout the range; more variation exists in the ratio of the diameter of the tympanum to that of the eye; the tympanum is proportionately larger in northern populations (Table 7). The primary differences between Panamanian and more northern populations are in size, color pattern on the dorsum and shanks, amount of webbing between the toes, and duration of notes in the mating call (Table 2, Pl. 4).

The color in Panamanian *staufferi* is gray or gray-brown with a pair of distinct, complete, dark brown dorsolateral stripes, a pair of entire paravertebral stripes, and in some specimens a vertebral stripe. About five per cent of the individuals have interrupted stripes on the dorsum, whereas in the more northern populations complete paravertebral stripes are present in less than ten per cent of the specimens; when complete stripes are present, they are irregular. The dorsal ground color in non-Panamanian specimens is brown, olive-brown, or dark brown.

Transverse bars are present on the shanks in *Hyla staufferi* from Costa Rica northward to México, whereas in Panamá all the individuals have a longitudinal stripe on the shank (Table 7, Pl. 2). The interorbital spot or bar is more noticeable in northern populations than in specimens from Panamá. Frogs from Costa Rica and northward have the toes about three fourths webbed, whereas in Panamá the toes are about two fifths webbed. The mating calls of the northern and Panamanian populations are similar, but the notes have a longer duration in the northern populations and a higher dominant frequency in Panamanian populations.

Hyla staufferi is the most variable member of the *Hyla rubra* group in Central America. The Panamanian populations are geographically separated from the Costa Rican and more northern populations by an area of tropical rainforest in the Golfo Dulce region in southeastern Costa Rica and adjacent Panamá. *Hyla staufferi* does not occur on the Caribbean versant of Costa Rica and Panamá. The Golfo Dulce region and the Caribbean versant are humid and inhabited by *Hyla elaeochroa*. *Hyla staufferi* is an inhabitant of subhumid and xeric areas.

On the basis of the discontinuous variation in several characters which correlate with the disjunct distribution of the two populations, two subspecies of *Hyla staufferi* are recognized. The accounts that follow apply equally to each.

Cranial Osteology.—The skull of *Hyla staufferi* is flat and longer than wide. The premaxillary is small and bears 9 to 13 teeth (mean for 5 specimens, 11.3). The alary process of the premaxillary is small, concave posteriorly and vertical. Ventrally, the premaxillary is united to the prevomers by partially ossified cartilage. The maxillary is slender and usually bears 49 to 70 teeth (mean for 5 specimens, 60.7). The pars facialis of the maxillary is convex and less than twice the height of the pars dentalis.

The nasal is large, rounded anteriorly, and pointed posteriorly in dorsal view. The nasal comprises about 40 per cent of the total length of the skull. Antero-

TABLE 7.—Geographic Variation in Size and Color in Males of *Hyla staufferi*.
(Means in parentheses below observed ranges.)

Locality	N	Snout-vent length (mm.)	Complete dorsal stripes (per cent)	Barred shanks (per cent)
Veracruz.....	47	23.0-27.3 (25.4)	0.0	100
Campeche.....	20	24.6-27.5 (25.5)	0.0	100
Oaxaca.....	75	24.0-28.7 (26.4)	9.3	100
Chiapas.....	20	23.2-27.8 (25.5)	10.0	100
Guatemala.....	22	25.0-29.0 (26.9)	10.9	100
El Salvador....	21	24.7-28.6 (27.0)	0.0	100
Honduras.....	34	20.6-27.0 (24.9)	3.3	100
Nicaragua.....	67	21.5-26.8 (24.9)	3.0	92.7
Costa Rica.....	54	20.7-26.6 (24.2)	5.5	98.1
Total Non-Panamanian	360	20.7-29.0 (25.9)	5.4	98.3
Panamá.....	72	21.7-26.0 (23.6)	94.5	0.0

medially the two nasals converge; posteriorly they overlap the sphenethmoid. The nasals lack a concavity in the midlateral surface. Dorsally, the sphenethmoid is wider than long, roughly pentagonal in shape; the frontoparietal is elongate, narrow, and smooth, with a small supraorbital process anteriorly. The frontoparietal fontanelle is narrow anteriorly and wide posteriorly.

Only a narrow connection exists between the posterior, pointed arm of the squamosal and the lateral edge of the proötic. The crista parotica is visible dorsally along the lateral edge of the bony proötic. The squamosal is narrow anteriorly and posteriorly.

The prevomers are short and separated anteriorly by partly ossified cartilage of the overlying solum nasi. The prevomer is joined to the premaxillary by cartilage. The posterior margin of the prevomer articulates directly with the sphenethmoid. The anterolateral and posterolateral processes of the prevomers form the incomplete bony internal margin of the choanae. Each prevomer

bears three to six teeth. The palatine is absent. The anterior part of the parasphenoid is narrow and ends in a point. The pterygoid is slender and weakly developed.

Natural History.—Throughout its range *Hyla staufferi* occurs in subhumid forests and savannas; consequently, the breeding activities are limited by the seasonal occurrence of rainfall, which accumulates in temporary ponds where this species breeds. Clasping pairs and gravid females have been found mostly from June to August throughout its range. This species was observed calling at Finca Taboga, Guanacaste Province, Costa Rica, in mid-July. The males were calling from temporary grassy and weedy ponds in which *Hyla microcephala* also was calling, but the two species had different calling sites. *Hyla staufferi* called at stations at heights of five to 80 cm. near the edge of the pond, whereas *Hyla microcephala* called from emergent vegetation in the middle of the pond. Charles W. Myers informed me that at Penonomé, Coclé, Panamá, he found *staufferi* calling from grass in puddles where *microcephala* was absent, and at El Caño, Coclé, Panamá, *staufferi* was calling from higher sites ("several inches to a few feet above water") than *microcephala*.

Stuart (1948:34) reported breeding individuals from La Libertad, Guatemala, after rainfall in late May, and Schmidt and Stuart (1941:239) reported *staufferi* breeding in July in the Salamá basin, Alta Verapaz, Guatemala. Stuart (1935:38) and Duellman (1960:63 and 1963:226) agreed that this species breeds early in the rainy season. However, Rand (1957:519) stated that in El Salvador "these frogs did not begin to call until almost a month and a half after the beginning of the rains." Blair (1960:133) reported that males call in June and July in Chiapas, Oaxaca, Veracruz, and Tamaulipas, México.

The mating call of this species is a series of closely spaced notes having a fundamental frequency of about 100 cycles per second. Each note has a duration of 0.13 to 0.23 second, repeated at intervals that are longer than the duration of the call. The notes are moderately low-pitched and have a dominant frequency of more than 3,000 cycles per second and about 120 pulses per second (Table 2).

Tadpoles.—Measurements of the 33 tadpoles that are available are given in Table 8. The largest tadpole examined is in stage 38 and has a total length of 29.5 mm.

A typical tadpole in stage 38 of development (KU 104162, 5 km ESE Córdoba, Veracruz, México) has a body length of 10 mm., tail length of 19.5 mm., and a total length of 29.5 mm. Other characters are as follows: body as deep as wide, depressed anteriorly; body as long as depth of tail; interorbital space greater than distance between eye and snout but equal to internarial space; nostril equidistant between eye and tip of snout; distance between spiracle and eye less than distance between eye and snout; eyes large, situated dorsolaterally; mouth anteroventral, approximately triangular in outline; one row of papillae covering lower lip and all except median fourth of upper lip; scattered papillae at corners of mouth; tooth rows $\frac{2}{2}$; first upper row entire, second row interrupted medially, shorter than first; lower rows shorter than upper rows; beak weak; spiracle short and nearer eyes than anus; anal opening not reaching edge of ventral fin; dorsal fin barely extending onto body; caudal musculature pointed distally.

TABLE 8.—Sizes of Tadpoles of *Hyla s. staufferi* in Relation to Developmental Stages. (Means in parentheses below observed ranges; measurements in mm.)

Stage	N	Body length	Tail length	Total length
25.....	3	6.0-7.0 (6.7)	12.0-13.0 (12.5)	18.0-20.0 (19.2)
26.....	2	7.0-7.5 (7.3)	14.0-15.0 (14.5)	21.5-22.0 (21.8)
27.....	9	7.0-8.0 (7.6)	13.0-17.0 (14.5)	21.0-25.0 (22.0)
32.....	1	8.5	15.5	24.0
36.....	2	8.0-10.0 (9.0)	16.5-17.0 (16.8)	25.0-26.5 (25.8)
38.....	6	9.0-10.0 (9.6)	19.0-20.5 (19.5)	28.0-29.5 (29.1)
41.....	1	10.0	14.0	24.0
42.....	6	11.0-14.0 (11.8)	10.0-13.0 (11.9)	20.0-29.0 (24.8)
45.....	1	12.5	0.5	13.0
46.....	1	13.0

In life, body pale olive-tan, belly silvery white with pinkish-orange reticulations in some specimens; tail creamy white with silvery flecks and black or brown reticulations. In preservative, tan and pinkish-orange coloration lost; body transparent, reticulations on tail present.

Remarks.—*Hyla staufferi* was described by Cope (1865:195) on the basis of specimens from Orizaba, Veracruz, México. He described the color pattern as "color above dark olive, with a short black bar over each scapula, and one from eye to eye, with a trace along the coccyx." Cope (1887:14) placed *staufferi* as a subspecies of *Hyla eximia*, but he did not justify his action. Günther (1901:262) also considered *staufferi* to be conspecific with *eximia* without making any qualifying statement. Dunn and Emlen (1932:24) named *Hyla culex* from Tela, Honduras, on the basis of a male (MCZ 16098) having a snout-vent length of 25.1 mm., and a female (USNM 20267) from Patuca, Honduras. They diagnosed the species as having "discs larger than tympanum . . . black interorbital triangle, traces of black dorsal marking; three black bars on anterior and posterior face of thighs, two black bars on tibia, on tarsus and on forearm." The holotype now is faded but has some of the pattern described. Dunn and Emlen did not compare *culex* with *staufferi* but did compare it with *boulengeri* and *rubra*.

Dunn (1933:61) named *Hyla altae* from Summit, Canal Zone. His description was based on a male (MCZ 17972) having a snout-vent length of 25.1 mm., the color pattern was described as "gray with four darker dorsal stripes

. . . a faint trace of mid-dorsal striping. . . ." Dunn defined the the *Hyla rubra* group and recognized *boulengeri*, *altae*, *culex*, and *rubra* as members. *Hyla elaeochroa* and *staufferi* were omitted from his key to the group in Central America.

Kellogg (1932:174) compared *staufferi* with *eximia* and concluded that the two were probably distinct species. Stuart (1935:38) considered *altae* to be a synonym of *culex*. Gaige (1936:293) considered *altae* and *culex* to be conspecific but regarded *staufferi* as a different species. She also suggested that *staufferi* was not related to *eximia* but belonged to the *rubra* group. Taylor (1952:865) and Duellman (1966a:274) considered *altae* and *culex* to be synonyms of *staufferi*.

The only other worker besides Cope and Günther to consider *Hyla staufferi* as a member of the *eximia* group was Blair (1960:129), who suggested the relationship on the basis of similarities in the structure of the calls of *eximia* and *staufferi*. Taylor (1938:421) and Smith and Taylor (1948:78) excluded *staufferi* from the *eximia* group on the basis of morphological characteristics. I consider *culex* to be inseparable from *staufferi*, whereas *altae* is recognizable as a Panamanian subspecies of *staufferi*.

Hyla staufferi staufferi Cope, New Combination

Hyla staufferi Cope, Proc. Acad. Nat. Sci. Philadelphia, 17:195, October 1865 [Holotype.—USNM 15317, Orizaba, Veracruz, México; Francis Sumichrast collector]. Brocchi, Mission Scientifique au Mexique et dans L'Amérique Centrale, 1881, p. 36. Boulenger, Catalogue, of the Batrachia Salientia s. Ecaudata, p. 400, February 1, 1882. Kellogg, Bull. U. S. Natl. Mus., 160:173, March 31, 1932. Smith and Taylor, Bull. U. S. Natl. Mus., 194:88, 1948. Taylor, Univ. Kansas Sci. Bull., 35:862, July 1, 1952. Rand, Fieldiana Zool. Chicago Nat. Hist. Mus., 34:518, April 18, 1957. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 17:274, June 17, 1966.

Hyla eximia staufferi Cope, Bull. U. S. Natl. Mus., 32:14, January 16, 1887.

Hyla eximia (part): Günther, Biologia Centrali-Americana, Reptilia and Batrachia, p. 261, June 1901. Nieden, Das Tierreich, Anura I, p. 245, June 1923.

Hyla culex Dunn and Emlen, Proc. Acad. Nat. Sci. Philadelphia, 84:24, March 22, 1932 [Holotype.—MCZ 16098, Tela Honduras; Raymond A. Stadelman collector]. Stuart, Misc. Publ., Univ. Michigan Mus. Zool., 29:38, October 1935. Gaige, Carnegie Inst. Washington Publ., 457:293, 1936.

Diagnosis.—Small frogs (♂ to 29 mm., ♀ to 31.6 mm.); dorsolateral stripes irregular; paravertebral stripes usually broken; two or three transverse bars on shanks; thighs spotted or not; arms usually barred; interorbital bar usually present; toes about three fourths webbed; color brown, tan, or olive-green.

Variation.—Three hundred and sixty males chosen at random from throughout the range have snout-vent lengths of 20.7 to 29 mm. (25.9 mm.). The smallest individuals are from Costa Rica and Nicaragua (means 24.2 and 24.4 mm., respectively). The largest individuals are from Guatemala and El Salvador (mean of each 27.0 mm.). The ratio of the diameter of the tympanum to that of the eye is more than 60 per cent in most samples, but in those from Costa Rica and British Honduras it is smaller. The color pattern is highly variable. Some specimens are dark brown or pale brown in color. Incomplete dorsal stripes are present in 94.6 per cent of the specimens, and transverse bars are present on the shanks in 98.3 per cent of the specimens. The inter-

orbital spot varies from transverse to longitudinal in position, and an irregular white line extends from the upper jaw to the arm in some specimens (Table 7).

Distribution.—*Hyla staufferi staufferi* inhabits savanna and subhumid and xeric forests in the lowlands and moderate elevations from southern Tamaulipas southward to Nicaragua on the Caribbean versant and from Guerrero, México to northwestern Costa Rica on the Pacific lowlands (Fig. 7). Duellman (1963: 226) commented that a specimen from Chinajá, Guatemala, possibly was transported there in the cargo from Toocog, because with this one exception the species is unknown in tropical rainforest in Guatemala.

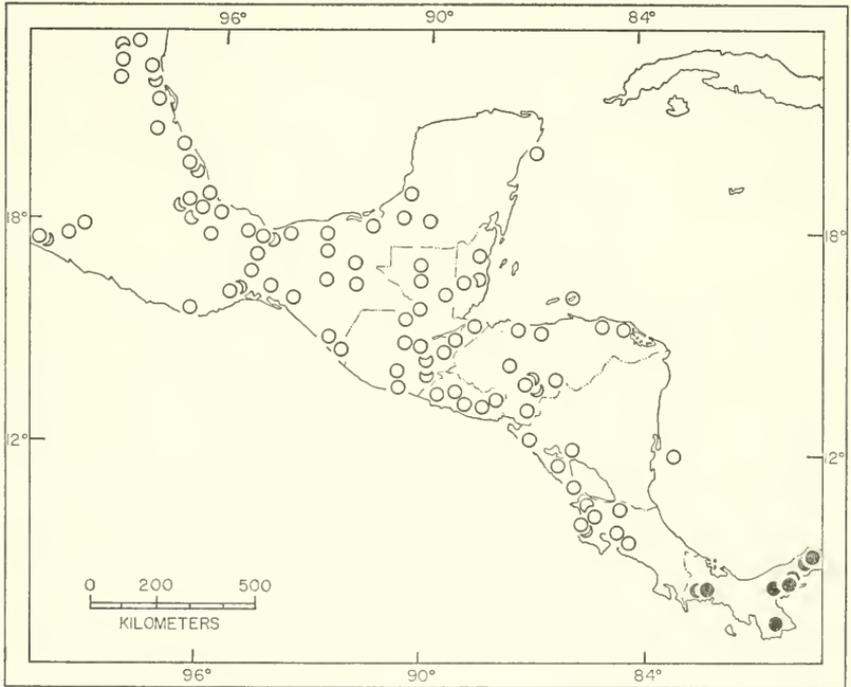


Fig. 7. Map showing locality records for *Hyla staufferi staufferi* (circles) and *H. staufferi altae* (dots).

Specimens Examined.—México: *Campeche*: 5 km S Champotón KU 71296-7; 7 km W Escárcega, KU 71298-308; 13 km W, 1 km N Escárcega, KU 71309-10, 75090-4. *Chiapas*: 32 km S Arriaga, KU 57789-92; 4 km N Ixtapa, KU 5776-81; 3.6 km SW Las Cruces, KU 37740; 17 km S Las Cruces, KU 57793-4; 24 km S Las Cruces, KU 104160 (tadpoles); 11 km S Tapachula, KU 57782-8, 60000 (young). *Guerrero*: El Limoncito, near La Venta, KU 31392-401; Mexcala, near Balsas River, KU 31391; Organos, S El Trienta, KU 31390. *Oaxaca*: 26 km N Matías Romero, KU 33878-82; 2.5 km S Pochutla, KU 59924-7 (skeletons); 5 km S Pochutla, KU 57795-801; 3.2 km E Tapanatepec, KU 37877-902; 17.6 km WNW Tapanatepec, KU 65033-4; Temascal, USC 8243 (8); 3.2 km S Tolocita, KU 39657-8; 0.5 km Tuxtepec, KU 87073-81, 87610 (tadpoles); 17 km S Tuxtepec, KU 65035-7; 1 km W Zanatepec, KU 104161 (tadpoles). *Quintana Roo*: Isla Cozumel, 3.5 km N San Miguel, KU 71710-11 (young). *San Luis Potosí*: Valles, KU 31490. *Tabasco*: Teapa,

UMMZ 118887 (3), 119203 (13); 9.6 km N Teapa, UMMZ 119202; 24 km N Teapa, UMMZ 119961 (5); 29 km N Teapa, UMMZ 119960; 3.5 km S Villahermosa, UMMZ 119201 (2); 17.6 km S Villahermosa, UMMZ 119200 (8). *Tamaulipas*: 1 km E Chamal, UMMZ 110706; Gómez Farías, UMMZ 110701 (3); 5 km SE Gómez Farías, UMMZ 110705; 8 km NE Gómez Farías, UMMZ 11282 (2), 11283 (3); Kilometer 615 between Río Limón and Llera, UMMZ 80455 (2); 5 km W San Geraldo, UMMZ 110702 (4), 110703 (3); 8 km W San Geraldo, near Río Frío, UMMZ 110704 (5). *Veracruz*: 3 km SW Boca del Río, KU 10494-8; 5 km SW Boca del Río, KU 23701; 5 km ESE Córdoba, KU 104162 (tadpoles); Cuautlapán, KU 57098-102, 26787; Hacienda Tamiahua, Cabo Rojo, KU 62871; 2 km ENE Mata Oscura, KU 105627; 5 km SE Paso del Toro, KU 40144; Portrero Viejo, KU 23911-2, 26786, 27413, 57094-7.

Guatemala: *Alta Verapaz*: Chinajá, KU 57769; Finca La Cubilquitz, UMMZ 90871, 90872 (5), 91379 (2). *Baja Verapaz*: 1 km S San Jerónimo, UMMZ 84077 (7), 84078 (14). *Chiquimula*: 1.6 km SE Chiquimula, UMMZ 98114 (2); Esquipulas, UMMZ 106784 (4), 106785 (14). *El Petén*: No specific locality, USNM 25143, 24825-6; La Libertad, FMNH 27096-7, KU 57770, UMMZ 75339 (15), 75340 (15), UMMZ 94341-2. *Esquintla*: 20 km N San José, AMNH 74369-76. *Guatemala*: 16 km NE Guatemala, KU 43539. Izábal: Puerto Barrios, TCWC 16671-73, 16646-56; 2.5 km NE Río Blanco, KU 57774-5. *Jalapa*: Jalapa, UMMZ 106788 (44). *Jutiapa*: Finca La Trinidad, UMMZ 107730 (12), 107731 (16); Jutiapa, UMMZ 106786 (2). *Zacapa*: 14 km ENE Mayuelas, KU 57773; 7 km ENE Río Hondo, KU 57771-2, 59999 (young).

British Honduras: *Belize*: Belize, FMNH 4406. *El Cayo*: San Agustín, UMMZ 80741 (8). *Stann Creek*: 10 km S Stann Creek on Hummingbird Highway, UMMZ 12570-1.

El Salvador: *Cuscatlán*: 7 km WNW Cojutepeque, TNHC 32004-10. *La Libertad*: 16 km NW Santa Tecla, KU 43540-1. *La Unión*: 2.5 km Santa Rosa, TCWC 16669-70. *Morazán*: Dividendero, USNM 73288-92. *San Salvador*: San Salvador, FMNH 65101-06, KU 61932-44, 61989-92, 62152 (eggs), USNM 117588, 118391 (3), 118394; 1.6 km NW San Salvador, KU 43162-3.

Honduras: *Atlantida*: Ceiba, USNM 117592. *Choluteca*: Choluteca, KU 85361-6; 2 km E Choluteca, UMMZ 118395 (7); 3.2 km NE Choluteca, KU 100500-01; 6.2 km E Choluteca, KU 65046-56; 10 km E Choluteca, KU 65045; 5 km S Choluteca, USC 2700 (4). *Colón*: Isla Guanaja (Islas de la Bahía), TCWC 21551, TNHC 32011. *Cortés*: Agua Azul, TCWC 19178-9; East side Lago Yojoa, KU 65038-44. *El Paraíso*: Valle de Jamastrán, AMNH 54800-04. *Francisco Morazán*: Escuela Agrícola Panamericana, AMNH 54963-73; 14.5 km NW Comayagua, KU 100499; El Zamorano, KU 103224; 29 km N Tegucigalpa, TNHC 32003, 32012.

Nicaragua: *Chinandega*: Finca San Isidro, 10 km S Chinandega, KU 85311-33. *Managua*: 13 km E Managua, KU 85339; 2 km S Tipitapa, KU 85334-8. *Rivas*: 9.5 km SE Rivas, KU 85355-6; 18 km SE Rivas, KU 85354; 7.7 km NE San Juan del Sur, KU 85346-53; 16.5 km NE San Juan del Sur, KU 85340-5; 5 km SE San Pablo, KU 43151-61. *Zelaya*: Isla Grande del Maiz, KU 85357-60.

Costa Rica: *Alajuela*: *Los Chiles*, USC 7215 (2), 7217. *Guanacaste*: 4 km W Bagaces, USC 7019 (5); Finca Taboga, KU 102265-5; 12 km S La Cruz, USC 8091; Las Cañas, KU 41113 (skeleton); 27 km N Las Cañas, USC 8171 (5); Guardia, Río Tempisque, USC 8214; 10 km N Guardia, KU 102266-7; 1.6 km N Guayabo de Bagaces, USC 7023 (3); Liberia, KU 36510-22; 4 km W Liberia, KU 36449-64, USC 102 (10), 103 (9), 104 (7), 105; 6 km N Liberia, USC 8096; 8 km NNW Liberia, KU 65032; 14.5 km N Liberia, USC 8079, 8138 (2); 14.5 km S Liberia, USC 8238 (5); 6 km N Nicoya, USC 8229 (11); 4 km S Nicoya, USC 8230, 8231; Peñas Blancas, KU 102263; 8.6 km ESE Playa del Coco, USC 8137 (14); 21 km E Playa del Coco, USC 8138 (2); Santa Cruz,

USC 8232 (2); 3 km E Santa Rosa, TCWC 16663-68; Tenorio, KU 32159; Tilarán, KU 36509. *Puntarenas*: 10 km WNW Esparta, KU 65022-9, 68614 (skeleton); 4.5 km WNW Esparta, KU 65030; 12 km WNW Esparta, KU 65031; 6 km E Esparta, KU 86477; Hotel Maribella, KU 32157-8; 3 km W Puntarenas, TCWC 16657-62.

Hyla staufferi altae Dunn, New Combination

Hyla altae Dunn, Occas. Papers Boston Soc. Nat. Hist., 8:61, June 7, 1933 [Holotype.—MCZ 17972, Summit, Canal Zone, Panamá; Emmett R. Dunn collector].

Hyla culex: Stuart, Misc. Publ. Univ. Michigan Mus. Zool., 29:38, October 1, 1935. Gaige, Carnegie Inst. Washington Publ., 457:293, 1936.

Hyla staufferi: Taylor, Univ. Kansas Sci. Bull., 35:862, July 1, 1952. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 17:274, June 17, 1966.

Diagnosis.—Small frogs (δ to 26 mm., ♀ to 27 mm.); dorsolateral and paravertebral stripes complete; longitudinal dark gray stripe on shank; thighs unmarked; interorbital bar usually absent; toes about three fifths webbed; gray to brownish gray above.

Variation.—*Hyla staufferi altae* is less variable in size, proportions, and color pattern than is *H. s. staufferi*. The size varies from 21.7 to 26 mm. (23.6) in 72 males. The ratio of tibia to snout-vent length is 0.42 to 0.50 (0.45), slightly less than in the northern subspecies. In color pattern 94.5 per cent of the individuals have complete dorsal stripes, and all have a longitudinal stripe on the shank (Table 7).

Distribution.—This subspecies is restricted to subhumid forests and savannas on the Pacific lowlands of Panamá. *Hyla s. altae* is presently known to occur from Chepo in east-central Panamá through the Azuero Peninsula to Concepción, Chiriquí, in western Panamá (Fig. 7).

Specimens Examined.—Panamá: Canal Zone: No specific locality, TNHC 24406; 2.8 km SW Fort Kobbe, KU 101679. Chiriquí: 14.4 km E Concepción, AMNH 69799-801; 6.6 km N David, TNHC 32013-4; 2 km S David, AMNH 68802. Coclé: 1 km NE El Caño, KU 101662-75; El Valle de Antón, AMNH 59601-5, KU 77333-47; 7 km SSW Penonomé, KU 101654-61. Los Santos: Tonosí, KU 101246 (tadpoles), 101697-701. Panamá: 2 km WSW Chepo, KU 101680-8; 6 km WSW Chepo, KU 77324-27; El Cangrejo (Panamá), KU 101676-8; Nueva Gorgona, AMNH 69991, 69798; 1.5 km W Pacora, KU 77328-32; 2 km N Tocumen, KU 101689-95; 8 km NE Tocumen, KU 101696.

EVOLUTIONARY HISTORY

My assumptions regarding the evolutionary history of the *Hyla rubra* group in Central America were derived partly from interpretations of the evolutionary history of other animal groups (Simpson, 1943, 1965; Dunn, 1931b; Stuart, 1950; Duellman, 1958, 1960, 1963, 1965; and Duellman and Trueb, 1966). The origin and early evolution of the group probably occurred prior to the Mid-Pliocene in the lowlands of South America, because the greatest diversity of the group is in Brazil. Differentiation into two or more subgroups took place in South America prior to the late Pliocene. At the end of

the Pliocene, shortly after the closure of the Colombian Portal, many South American animals migrated into Central America (Simpson, 1943, Maldonado-Koerdell, 1964, and Savage, 1966). It is likely that the *Hyla rubra* group entered Central America at that time; apparently two stocks (*rubra-elaechroa-staufferi* stock and *boulengeri-foliamorta* stock) migrated into Central America.

Hyla elaeochroa is closely related to *rubra* and probably differentiated from *rubra* through spatial isolation. Thus, we have *elaechroa* in Central America and *rubra* in South America; most likely only in relatively recent times has *rubra* migrated into eastern Panamá from northern South America. The differentiation and dispersal of *elaechroa* and *staufferi* took place in Central America after the Pliocene. Probably the events of the Pleistocene resulted in the isolation of populations. One of these (*Hyla staufferi* stock) was restricted in the subhumid Pacific lowlands, whereas the *Hyla elaeochroa* stock occupied the tropical wet forests of the Caribbean lowlands. *Hyla elaeochroa* apparently more closely resembled the parental stock by being restricted to the tropical rain forests, whereas *staufferi* adapted to subhumid environments and thereby was able to disperse throughout most of the subhumid regions of Central America.

After geographical separation took place the initial genetic divergence between the two populations was maintained by means of ecological and ethological isolating mechanisms. Under these circumstances it can be supposed that the different ecological preferences of *elaechroa* and *staufferi* depend on the climatic changes that took place during the Pleistocene. On this basis it may be proposed that when the original prototype broke up into the two incipient species, the *staufferi* stock became physiologically and behaviorally adapted to subhumid conditions and dispersed into dry areas of the lowlands of Middle America. The tropical evergreen forests on the Caribbean side of lower Central America and the uplift of the Talamanca range in the Pliocene were barriers to the dispersal of *staufferi*. Consequently, this frog dispersed along the Pacific lowlands.

At the present time *staufferi* occupies the length of the Pacific lowlands in Central America, except in the rainforest of the Golfo Duce region, which apparently is a relict stand and now separates the ranges of two subspecies of *Hyla staufferi*. This species crossed the central Nicaraguan lowlands and reached the Caribbean lowlands of Nicaragua and nuclear Central America. The species

migrated through the subhumid corridor in northern Honduras and eastern Guatemala (Comayagua Valley in Honduras and the Motagua Valley of Guatemala) to the Isthmus of Tehuantepec. Duellman (1960) hypothesized "that during the times of glacial advances (Pleistocene) the lowlands of the Isthmus probably were more extensive and had more semiarid tropical environments than at the present" and that when semiarid environments were continuous from the Pacific slope across the isthmus to the Gulf lowlands *staufferi* and other amphibians migrated northward to southeastern Tamaulipas, México.

Hyla elaeochroa dispersed along Caribbean lowland routes. This species not only occurs in the wet forests of the Golfo Dulce region but also in Guanacaste. It is possible that *elaeochroa* entered Guanacaste and moved to the Golfo Dulce region when the intervening area was less xeric than now (Duellman, 1966b). *Hyla elaeochroa* extended its range to eastern Nicaragua, but even though northeastern Nicaragua has over 2,000 mm. of precipitation annually (Vivo Escoto, 1964), this species has not spread into Honduras and Guatemala.

Hyla boulengeri is widespread in Amazonian and northern South America, whereas *foliamorta* occurs only in eastern Panamá and in north-central Colombia. The ancestral *boulengeri-foliamorta* stock probably invaded Central America in the late Pliocene and dispersed through humid forested environments to Nicaragua. Apparently a peripheral population established itself in the dry Pacific lowlands of Panamá. This population differentiated from *boulengeri* of the humid Caribbean lowlands and evolved into *foliamorta*, which subsequently expanded its range into Colombia.

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INTRODUCTION

In comparison with the more plastic external features, the skeletal elements of vertebrates are generally considered to be evolutionarily conservative. Because of the relative stability of skeletal features, these characters have been relied upon heavily in the classification of higher categories and in the determination of general evolutionary trends. External morphological variation in color, general form, and particular structure is well known in hylids. Internal morphology, on the other hand, has been largely ignored in favor of the more readily apparent external characters. Our knowledge of the osteology of hylids is particularly deficient.

There seems to be remarkably little variation in the postcranial skeleton in hylids. Cranially, hylids are generally marked by a trend towards reduced ossification compared with frogs of most other families. However, within the hylids there are several genera which seem to represent a contradiction to the evolutionary trend of the rest of the group. These are the so-called "helmeted" hylids having heavily ossified skulls molded into solidly roofed and extraordinarily bizarre cranial formations of crests, ridges, and flanges. The unusual condition of the skulls in these genera has led to their widespread designation as the "casque-headed hylids."

These peculiar frogs were first brought to my attention by the acquisition of a large series of adults and a developmental series of young *Triprion petasatus*, one of the strangest of the casque-headed hylids. Originally, it was my intention to trace the development of the cranium in this species in an attempt to understand how the adult acquired such an unusual skull. The next logical step in the investigation was a comparison of the developmental and adult cranial morphology of *Triprion* with a presumably generalized hylid. The study was carried to its logical conclusion by an investigation of the other genera of casque-headed hylids. Several authors (Carvalho, 1941; Myers, 1942; Peters, 1955; Smith, 1957; and Rivero, 1961) have commented on the phylogenetic relationships of the casque-headed hylids. On the whole their work was based on superficial examination; the authors were hindered by insufficient knowledge of the basic structures of the skulls and the derivations of the cranial modifications.

My investigations of the cranial osteology of these frogs and a wide array of other hylids have led to the formulation of a phylogenetic arrangement which seems to show that the casque-headed

hylids have been derived from several phyletic lines. In each case the individual lines have undergone similar types of modifications in response to similar environmental situations. These frogs, which seemingly represent a reversal in the evolutionary trend in hylids, show several unique morphological characteristics by which they are functionally adapted to specialized modes of existence, first alluded to by Cope (1865:194) in reference to *Triprion petasatus*: "It is interesting that an animal living in rocky situations should present such a cranial bony development; this, in connection with its colors, no doubt, aids especially in concealment, and is another instance of the Creator's bountiful care for his humblest creatures."

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Materials and Methods

The descriptive accounts and discussions which follow are based on the study of 374 osteological preparations (254 dried skeletons, 99 cleared and stained specimens, and 21 sets of serial cross-sections; see list of specimens examined). Radiographs were made of four other specimens; three of these were stereo radiographs prepared by the method described by Smith and Smith (1967).

Dried skeletons were prepared from preserved specimens or by means of dermestid beetles from carcasses dried in the field. Cleared and stained preparations were obtained from specimens stored either in 70 per cent alcohol or 10 per cent formalin. Specimens were cleared in two per cent potassium hy-

dioxide, and the ossified parts of the skeletons were stained with alizarin sulfonate of sodium; final preparations were stored in glycerin.

Most specimens used for sectioning were fixed and preserved in 10 per cent formalin. One dried skull was used, somewhat unsuccessfully, in the preparation of serial cross-sections. The entire heads were sectioned exclusive of the lower jaw anterior to the articular region. Sections were cut between thicknesses of 10 and 35μ , depending upon the size of the specimen and the area of the cranium being sectioned. It was found that large skulls could be sectioned at thicknesses ranging between 25 and 35μ without suffering distortion or loss of visible detail of internal structure, whereas small skulls were more satisfactorily sectioned between thickness of 10 and 20μ . Sections made through the olfactory regions of the crania were cut 5 to 10μ thinner than sections made through posterior parts of the skull.

Baldauf's (1958b) suggested procedures for the preparation, staining and sectioning of adult anuran heads were followed. A few modifications of his technique are worth noting. For most anurans three days are minimally necessary for decalcification in Perényi's Fluid; five to six and one-half days are required for large anurans or frogs with heavily ossified or co-ossified skulls. No tissue damage has been observed in smaller specimens which have been in Perényi's Fluid as long as six and one-half days. I suggest that Baldauf's staining schedule be modified for larger material, cut at thicknesses between 20 and 25μ , to include two initial changes of xylol at a maximum time of five minutes each. Azocarmine G must be substituted for Azocarmine B, a biological stain which apparently is no longer available. Only 11 to 15 minutes are required to stain sections cut at 20μ in Azocarmine G, compared to the 30 minutes indicated for Azocarmine B in Baldauf's Heidenhain's Azan technique.

The following descriptive accounts are organized in the same manner. The skull has been divided arbitrarily into the following sections: olfactory region (including the upper jaw); sphenethmoid and orbital regions; otic and occipital regions; and the articular region. At the beginning of each account a diagnostic list of morphological characters is provided for the species. Within each succeeding section, external dermal bones are discussed first and followed by internal bones and cartilage. The first descriptive account, that of *Tripriion petasatus*, is the most detailed. The successive accounts are more general and do not deal with characters that do not show significant variation. Unless specifically stated otherwise, all descriptions are given in an anterior to posterior sequence.

Repeated use has been made of such terms as "appears," "extends," and "level." The reader should view the meaning of these terms in the context of the study at hand. Thus "level" is any transverse plane, perpendicular to a line lying between the anterior and posterior ends of the skull. With respect to sets of serial cross-sections used, each cross-section represents a different level of the skull. Words such as "appears" and "extends" should be interpreted in the dynamic sense, so that as we progress through the skull, level by level, by means of serial cross-sections, various structures "extend" from one level to another, or "appear" at a certain level. Particular care should be exercised not to give words such as "appearance" the chronological connotation common in developmental studies. An effort has been made to provide reasonable and consistent anatomical designations. These are based on studies of Baldauf (1955; 1957; and 1958a) and Baldauf and Tanzer (1965); changes in termi-

nology involve the anglicization of Latin terms which are commonly used in English and awkward to use in Latin. A glossary of terms used, their derivation, and definitions follows the list of specimens examined.

All illustrations of cross-sections were made by use of a microprojector. Only bone, cartilage, and the external outline of the head are shown. Each account (except *Trachycephalus jordani*) is illustrated by two or three cross-sections of the anterior end of the skull and followed by illustrations at the levels of all of the cranial nerve foramina except the trochlear foramen, and the jugular foramen of *Corythomantis greeningi*. Dorsal and ventral views of the skulls of a member of each genus or species group are provided.

Cranial Anatomy of a Generalized Hylid Frog

The data and conclusions which follow are based on the premise that a thorough understanding of the structure of the anuran skull is obtained by examination of both external and internal features. Unfortunately, external similarities between the skulls of two species often mask internal differences, or, in some instances, the converse may be true. Internal anatomy principally involves the structure of the chondocranium and/or endochondral bones derived from the chondocranium. I think the endochondral cranial structure among hylids has been subject to much less evolutionary and adaptive alteration than have bones of dermal origin; therefore, variation involving internal structures should be carefully evaluated. Examination of internal anatomy is possible through use of serial cross-sections. Interpretation of serial sections is often difficult for the casual reader. I have prepared below a description of the anatomy of a generalized hylid skull. The account is functionally oriented, relating internal to external anatomy, in order to make the descriptions which follow more easily understood.

Functionally, the structure of the hylid skull fulfills at least three important needs. The braincase is a receptacle for sense organs (the eyes, ears, and nose), and it houses the central nervous system; the jaws provide a mechanical system for the ingestion of food. Several dermal bones suspend, or brace the jaws against the central braincase, and dermal covering bones form a protective casing around the braincase and sense organs.

The nasal capsules are the most anterior sense organs of the cranium. The capsules lie between the maxillaries and posterior to the premaxillaries; they form an anterior extension of the sphenethmoid. Dorsally the olfactory region is covered by the nasals and anteroventrally it is protected by the prevomers (Fig. 1). A nasal capsule consists of three cavities lying above one another. The nasal cavities are encased in cartilage and supported internally by carti-

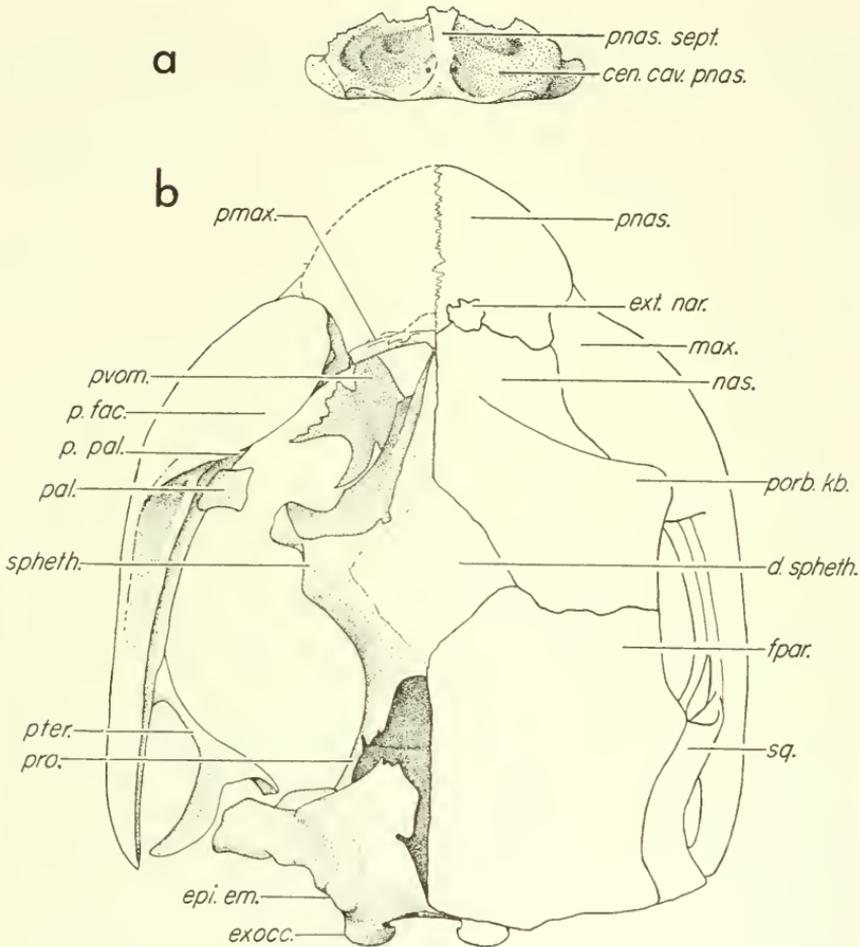


FIG. 1. Partially disarticulated skull of *Triprion petasatus* (KU 71759), ♂. $\times 4$: (a) posterior view of prenasal; (b) dorsal view of skull with left frontoparietal, squamosal, quadratojugal and nasal, left half of prenasal removed. Abbreviations: *cen. cav. pnas.*, central cavity of prenasal; *d. spheth.*, dermal sphenethmoid; *epi. em.*, epiotic eminence; *exocc.*, exoccipital; *ext. nar.*, external naris; *fpar.*, frontoparietal; *max.*, maxillary; *nas.*, nasal; *p. fac.*, pars facialis of maxillary; *p. pal.*, pars palatina; *pal.*, palatine; *pmax.*, premaxillary; *pnas.*, prenasal; *pnas. sept.*, prenasal septum; *porb. kb.*, preorbital knob; *pro.*, prootic; *pter.*, pterygoid; *pvom.*, prevomer; *spheth.*, sphenethmoid; *sq.*, squamosal.

lage and bone (the prevomer and septomaxillary). The cavum principale is the largest and dorsalmost of the nasal cavities; the external naris opens into the anterior end of this cavity. The cavum medium is a small cavity which lies beneath the anterior end of the cavum principale. Structurally the cavum medium is important because its posterior bifurcation produces the nasolacrimal duct laterally; medial to the nasolacrimal duct, the cavum principale

opens from above and the *cavum inferius* from below into the *cavum medium*. The *cavum inferius* is a large, depressed cavity which lies ventral to the *cava principale* and *medium*. At the posterior terminus of the *cavum medium*, the *cava principale* and *inferius* unite via the *cavum medium*, and extend posteriorly as a single, large cavity into which the olfactory eminence protrudes ventrally and the internal naris opens posteriorly.

Anteriorly two rods of cartilage, the superior and inferior prenasal cartilages, extend from the premaxillary to the nasal capsule posteriorly. The superior prenasal cartilage fuses with the alary cartilage which surrounds the anterolateral part of the *cavum principale* posterior to the opening of the external nares. The inferior prenasal cartilage fuses with the cartilaginous floor of the nasal capsule, the *solum nasi*, anteromedial to the prevomer. The anterior part of the olfactory capsule is formed of four parts, the alary cartilage laterally, the *solum nasi* ventrally, the *septum nasi* medially, and the *tectum nasi dorsally*. The *cava medium* and *inferius* lie ventral to the *cavum principale* and protrude anteriorly into the *solum nasi*, dividing the latter into three layers. The ventral layer of cartilage, lying between the prevomer and the *cavum inferius* is the *solum nasi*. The cartilage separating the *cavum inferius* and *cavum medium* is the *lamina inferior* and that separating the *cavum medium* and *cavum principale*, the *lamina superior*. The septomaxillary bone lies in the *lamina superior* and supports the confluence of the *cavum principale* and *cavum medium* and the divergence of the nasolacrimal duct from the *cavum medium*.

Between the levels of the external and internal nares, lateral support of the nasal capsule is furnished by the *planum terminale*, which forms by the fusion of the *cartilago obliquo* (which diverges dorsolaterally from the *tectum nasi*) and the posterolateral end of the *lamina inferior* lateral to the *cavum principale*. The *solum nasi* and *septum nasi* provide ventral and medial support, respectively, of the nasal capsule at the level of the internal nares. At the posterior margin of the internal naris, the *solum nasi* fuses with the *planum antorbitale* laterally to encase the nasal capsule completely. Ventrally, the *solum* is underlain by the palatine; dorsally and laterally, the nasal capsule is covered by the nasal bone. The cartilage surrounding the posterior ends of the nasal cavities is replaced by the bones of the sphenethmoid.

The orbits are formed by several bones and cartilages. The *planum antorbitale* and the overlying nasal bone form the anterior

margin of the orbit, the maxillary the ventral margin, and the anterior arm of the squamosal the posterior margin. The medial aspect of the orbit is formed by the cartilaginous sclera surrounding the internal and proximal surface of the eye, which lies adjacent to the braincase.

The otic region is encased by the prootic. The otic capsule lies posterior to the orbit and lateral to the braincase; the capsule is formed by the ventrolateral part of the prootic. The dorsolateral part of the prootic, the crista parotica (Fig. 1), forms the roof of the otic capsule and extends laterally to articulate with the anterior and posterior arms of the squamosal. The columella, or stapes, lies ventral to the crista parotica and consists of three parts. The distal end of the columella, the pars externa plectri, is cartilaginous and lies adjacent to the tympanic membrane. The pars externa plectri is suspended from the distal end of the crista parotica by a small rod of cartilage, the pars ascendens plectri. Proximally, the pars externa plectri attaches to the bony medial part of the columella, the pars media plectri. The proximal end of the columella is formed by the cartilaginous pars interna plectri which lies between the pars medial plectri and the otic capsule and articulates with the cartilaginous operculum posteriorly. The operculum lies over the foramen ovale in the posterolateral part of the otic capsule.

The braincase is formed by three endochondral bones and two dermal investing bones. The sphenethmoid (Fig. 1) surrounds the anterior end of the brain. The bone lies between the olfactory capsule anteriorly and the prootic posteriorly, and is in synchondrotic continuity with both structures. The posterior part of the brain is housed by the prootic and exoccipital which are synosteotically united in adult frogs. Ventrally, the cartilaginous union of the sphenethmoid and prootic and the venter of the otic capsule are supported by a dermal investing bone, the parasphenoid. Dorsally, the frontoparietal overlies the posterior part of the sphenethmoid and the tectum synoticum of the prootic, forming a partial or complete bony roof to the braincase.

The upper jaw of a hyloid is composed of paired premaxillaries anteriorly, maxillaries laterally, and quadratojugals posterolaterally. The premaxillaries bear slender dorsal processes, the alary processes, against which the superior and inferior prenasal cartilages of the olfactory capsule abut. Posteriorly the maxillaries overlap the quadratojugal laterally. Near the posterior end of the quadratojugal, the ossification of the latter invades the cartilage of the

quadrate process which lies medial to the quadratojugal. The quadrate process articulates with the ventral arm of the squamosal dorsally, the posterior ramus of the pterygoid medially and Meckel's cartilage ventrally. Together, all these elements compose the articular region of the jaw. The lower jaw is composed of the paired endochondral mentomeckelian bones anteriorly, dermal dentary bones which laterally invest Meckel's cartilage, and posterolaterally, the dermal angulosplenials lying ventrolateral to Meckel's cartilages.

The principal function of the palatine and pterygoid is to brace the upper jaw against the braincase. The palatine articulates with the maxillary and sphenethmoid and forms the posterior margin of the internal nares. The pterygoid consists of three rami. The anterior ramus lies medially adjacent to the maxillary and cartilaginous posterior maxillary process in the region of the orbit. The medial ramus extends toward and sometimes articulates with the anteroventral corner of the otic capsule. The third, posterior ramus of the pterygoid articulates with the medial surface of the quadrate process posteriorly.

CRANIAL OSTEOLOGY OF *Tripriion petasatus*

The skull of *Tripriion petasatus* is longer than wide (Pl. 2a and b; Fig. 1). All dorsal surfaces of the skull are involved in integumentary-cranial co-ossification. Dorsally, all dermal bones are finely sculptured in a pattern of parallel or reticulate ridges. The distal margins of all dermal bones terminate in small spinose protuberances; the latter are best developed on the outer edges of the maxillary and the prenasal, the canthal ridge near the orbit, and the occipital crest. The skull of *Tripriion petasatus* is characterized by the presence of a dermal sphenethmoid, a prenasal, and extensive labial flanges on the maxillary and prenasal anterior to the orbit. The vocal sac is bilobed and subgular.

EXTERNAL DERMAL BONES OF THE OLFACTORY REGION

The dermal bones of the olfactory region include the prenasal (*pnas.*), premaxillary (*pmax.*), septomaxillary (*spmax.*), prevomer (*pvom.*), palatine (*pal.*), and the anterior parts of the maxillary (*max.*) and nasal (*nas.*).

Prenasal.—The prenasal, named here for its external association with the nasals and external nares, lies anterior to the premaxillaries and nasals (Pls. 2a, b and 3a; Fig. 1a, b). The bone is approximately triangular in dorsal, ventral, and cross-sectional views (Figs. 1-4); the dorsal surface is involved with integumentary-cranial co-ossification. The posterior margin of the prenasal is connected by bony sutures to the maxillaries distally, and to the nasals dorsomedially, except where the prenasal forms the anterior margin of the external nares. Ventromedially, the posterior margin of the prenasal lies adjacent to the premaxillaries; it is separated from the latter by dense connective tissue.

Premaxillary.—Because of the presence of the prenasal anteriorly, the premaxillary is largely internal; only the pars dentalis of the premaxillary, lying

along the posteroventral margin of the prenasal, is visible in ventral view (Pl. 2b). The premaxillaries are narrowly separated medially by connective tissue; laterally the bone is separated from the pars palatina (*p. pal.*) and the pars dentalis of the maxillary by an area of dense connective tissue. A small, but well-developed palatine process is present posteromedially on the premaxillary. The palatine processes are separated from each other by a thin area of dense connective tissue. The premaxillary bears a large alary process about 4.5 times as long as the pars dentalis of the premaxillary is deep. The alary process is strongly convex and anterodorsally lies within cavities in the prenasal bone.

Prevomer.—In ventral view (Pl. 2b; Fig. 1b), the prevomer lies lateral to the midline of the skull and ventral to the solum nasi and the sphenethmoid. The anterior end of the prevomer lies dorsal to the lateral part of the pars palatina of the premaxillary; the posterior, dentigerous part of the bone lies at a slight angle and just lateral to the midline. Laterally the prevomer bears a delicate, wing-like extension which forms the anterior and anteromedial margins of the internal nares. The prevomerine dentigerous processes are small and transverse. Internally, the anterior end of the prevomer lies dorsal to the premaxillary and is associated with the ventral surface of the solum nasi at the level of the infundibulum (Fig. 9). Posteriorly, the prevomer expands dorsally to provide a bony support of the olfactory eminence (*olf. em.*, Figs. 12-13).

Palatine.—The palatine (Pl. 2b; Fig. 1b) is a flat, rectangular-shaped bone which lies lateral to the internal nares. The distal end is lodged in connective tissue between the pars facialis and pars palatina of the maxillary (Figs. 14 and 15). The palatine extends dorsomedially from the maxillary; the proximal end lies ventral to the lateral wall of the nasal. The bone is edentate.

Nasal.—The nasal is extremely large (Pls. 2a and 3a; Fig. 1b). Anteriorly the nasal articulates with the prenasal except where the nasal forms the posterior margin of the external nares. Laterally the nasal is attached to the pars facialis (Pl. 3a) of the maxillary, and posterolaterally, it forms the bony anterior margin of the orbit. Medially and anterior to the dermal sphenethmoid (*d. spheth.*, Pl. 2a; Fig. 1b) the nasals converge. The posterior margin of the nasal is attached by a bony suture medially to the anterior margin of the dermal sphenethmoid and laterally to the anterior margin of the frontoparietal (*fpar.*). The dorsal surface is completely involved in integumentary-cranial co-ossification. The nasal bears a well developed canthal ridge extending from the anterior medial margin to terminate in a large, spiny preorbital knob at the anterodorsal corner of the orbit (Pls. 2a and 3a; Fig. 1b). Lateral to the canthal ridge the surface of the nasal is striated; the striations parallel the canthal ridge. Medial to the canthal ridge, the striations form a radiate pattern centered about three-fourths of the distance from the anterior to the posterior end of the nasal and midway between the supraorbital margin of the nasal and the edge of the dermal sphenethmoid.

Maxillary.—The maxillary is large, massive, and deeply concave dorsally; throughout most of its length the maxillary bears a broad flange extending dorsolaterally from the pars dentalis of the bone (Pls. 2b and 3a). The flange is most extensive anterior to the orbit, reduced in width lateral to the orbit, and moderately developed posterior to the orbit. The dorsal surface of the maxillary is involved in integumentary-cranial co-ossification. Medially, the maxillary bears a well developed pars palatina (Pl. 2b; Fig. 1b) extending the length of

the bone dorsal to the pars dentalis. The process is most pronounced in the dentigerous region. Dorsal to the pars palatina and anterior to the orbit, the maxillary bears a large pars facialis (Fig. 1b). It is this part of the maxillary that lies adjacent to the nasal and posteriorly forms the bony ventral margin to the anterior edge of the orbit. Posteriorly, the quadratojugal (*qj.*) lies within a slight medial depression of the maxillary formed by the extension of the pars palatina from the dentigerous region (Pl. 2b).

INTERNAL BONES AND CARTILAGES OF THE OLFACTORY REGION

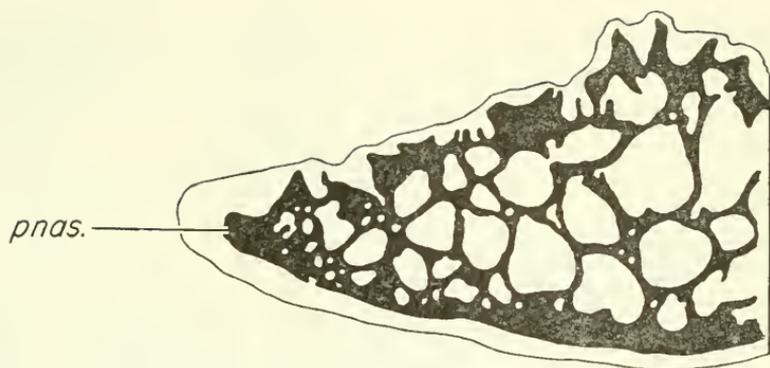
Prenasal and Alary Process of Premaxillary.—Internally, the anterior part of the prenasal (Fig. 2) is characterized by a thick ventral base overlain by a series of small cavities. Farther posteriorly, the central cavities coalesce to form a large cavity (Fig. 3). The cavity is filled with fat and blood vessels and is flanked on either side by two to four smaller cavities. At about one-half the length of the prenasal, the central cavity is separated by a bony vertical septum called the prenasal septum (*pnas. sept.*). The alary process (*al. proc.*) of the premaxillary lies within the two larger cavities separated by the prenasal septum (Fig. 4). The prenasal persists dorsomedially to a level just posterior to the external nares where it is replaced by the nasals (Figs. 5 and 6).

Alary cartilage.—The alary cartilage (*al. c.*, Figs. 4-5 and 7a, b) appears slightly posterior to the superior prenasal cartilage. The anterior end of the alary cartilage lies within the prenasal cavity just posterior to the tip of the alary process of the premaxillary. In subsequent sections the cartilage becomes arcuate in shape and lies along the lateral edge of the prenasal cavity. Immediately anterior to the external nares the alary cartilage joins the tectum nasi (*tect. nas.*) dorsally to form a roof over the anterior end of the cavum principale (*cav. prin.*). The cartilage diminishes in size and disappears shortly posterior to the appearance of the cavum medium (*cav. med.*).

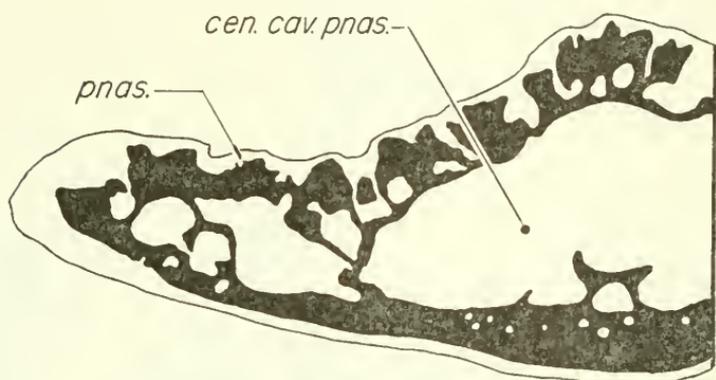
Tectum nasi.—The tectum nasi (Fig. 4) is present only in anterior sections between the anterior end of the alary cartilage and the posterior end of the prenasal septum. The unusually short tectum nasi lies just medial to the central part of the prenasal. The tectum meets the alary cartilage dorsal to the cavum principale, and expands ventromedially to join the anterior end of the septum nasi (*sept. nas.*). In sections posterior to the opening of the external nares (Fig. 5) the tectum is reduced to a small dorsal flange-like projection of the septum nasi which supports the edge of the nostril lateral to the medial part of the prenasal. Just anterior to the posterior edge of the nostril the tectum nasi terminates. At this point the cartilago obliquo (*c. obl.*, Fig. 6) diverges dorsolaterally from the septum nasi.

Prenasal cartilages.—The anterior end of the superior prenasal cartilage lies against the posterodorsal surface of the alary process of the premaxillary. The cartilage joins the alary cartilage posteriorly. The inferior prenasal cartilage (*inf. pnas. c.*) appears on the posteromedial surface of the base of the alary process of the premaxillary (Fig. 6) at a level of the anterior end of the recessus medialis (*rec. med.*) of the cavum inferius. The cartilage extends dorsally (Fig. 8) and fuses with the solum nasi (*sol. nas.*) at the posterior levels of the septomaxillary where the cavum principale is confluent with the cavum inferius (*cav. inf.*).

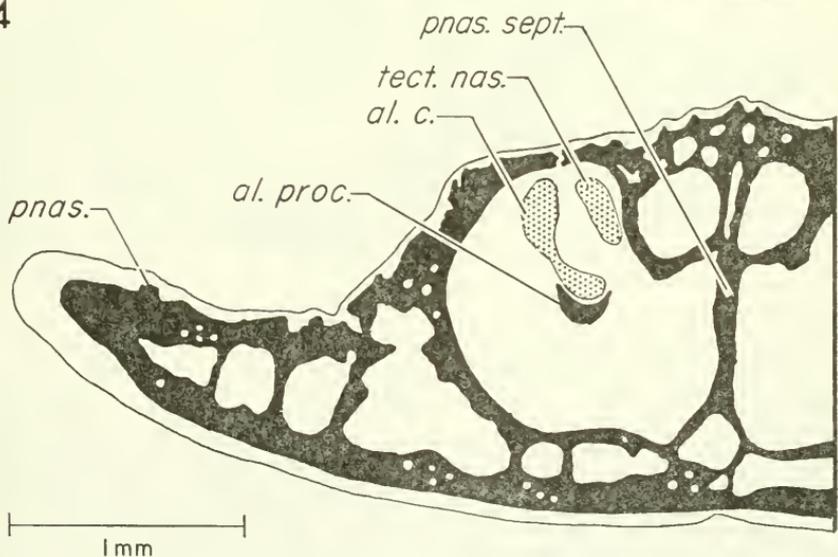
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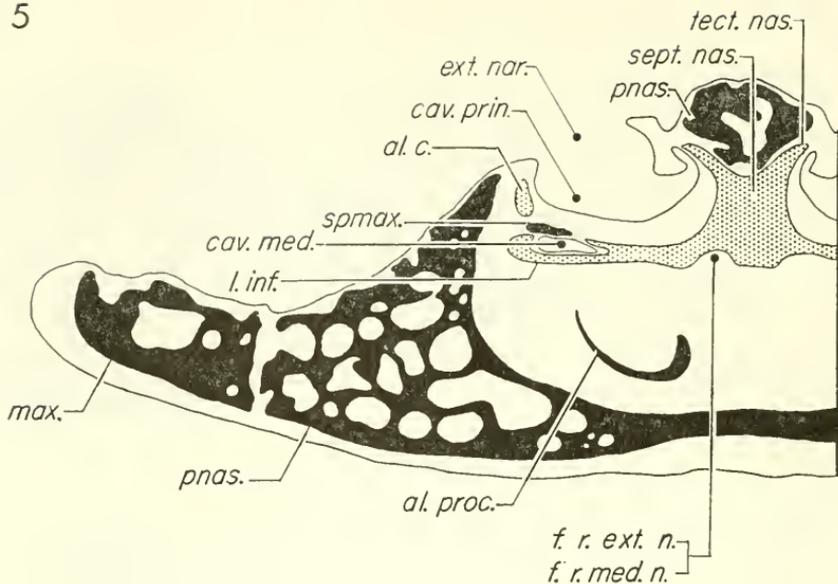


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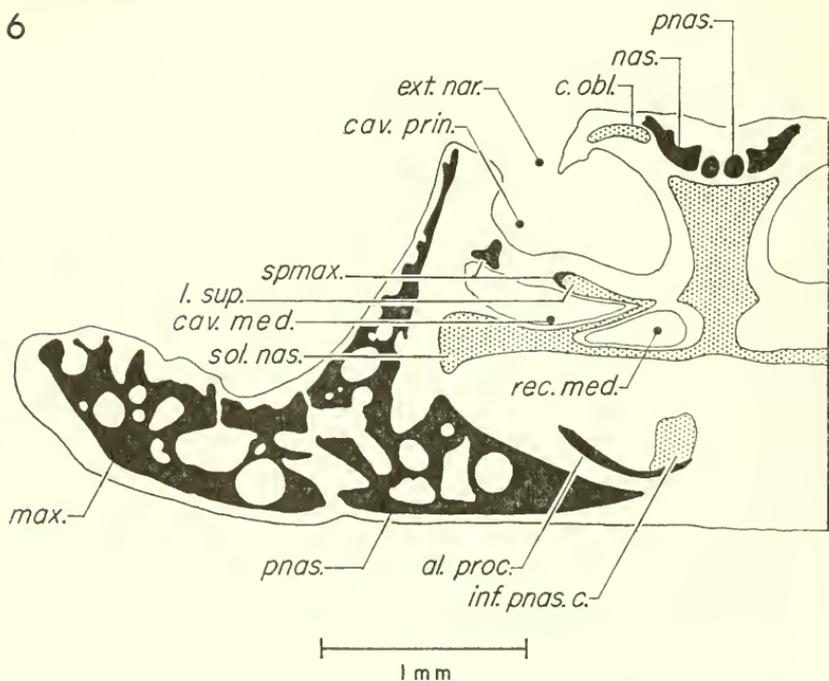


FIGS. 2-4. Transverse sections through prenasal at anterior end of skull of *Tripirion petasatus* (KU 71745): (2) anterior end of prenasal; (3) central cavity of prenasal; (4) prenasal septum. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *cen. cav. pnas.*, central cavity of prenasal; *pnas.*, prenasal; *pnas. sept.*, prenasal septum; *tect. nas.*, tectum nasi.

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FIGS. 5-6. Transverse sections through anterior end of olfactory capsule of *Tripirion petasatus* (KU 71745): (5) anterior level of cavum medium; (6) level of recessus medialis of cavum inferius. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *c. obl.*, cartilago obliquus; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *ext. nar.*, external naris; *f. r. ext. n.*, foramen ramus externus narium; *f. r. med. n.*, foramen ramus medialis narium; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *nas.*, nasal; *pnas.*, prenasal; *rec. med.*, recessus medialis of cavum inferius; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spmax.*, septomaxillary; *tect. nas.*, tectum nasi.

Septum nasi.—The septum nasi (*sept. nas.*) replaces the prenasal septum posteriorly. The anterior end is connective tissue which unites the tecta nasi medially at a level anterior to the cavum principale. Cartilage (other than the tecta nasi) is first associated with the septum in the lateral part of the solum

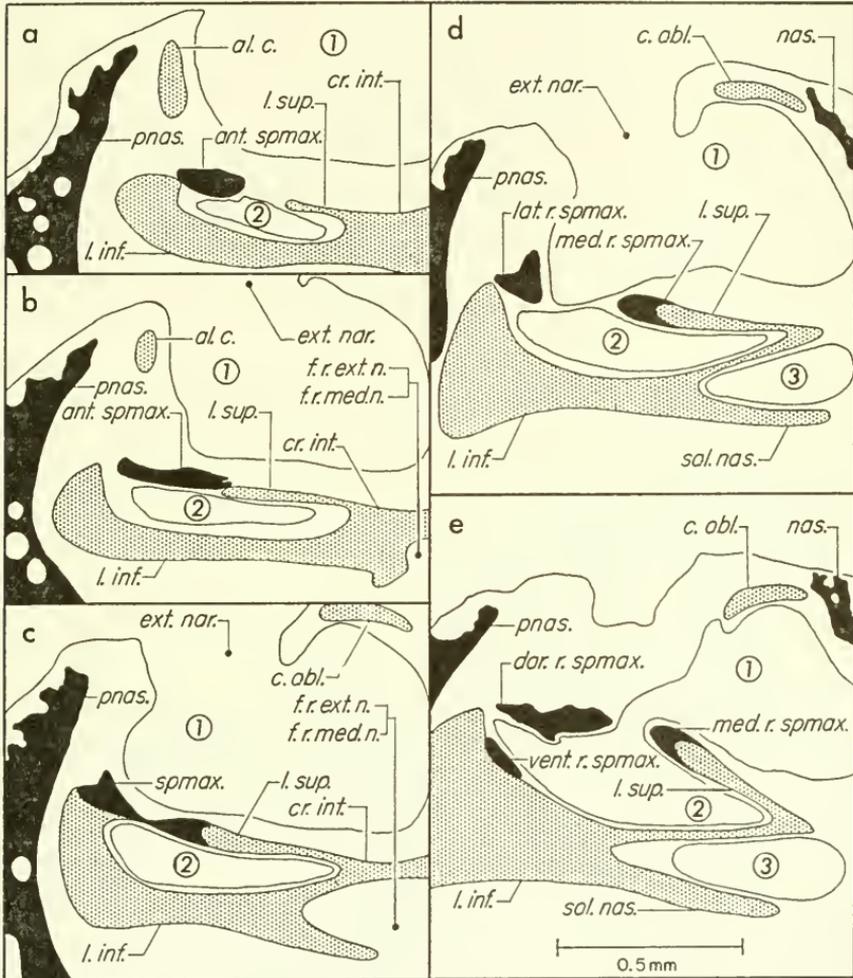


FIG. 7. Transverse sections through olfactory capsule of *Triprion petasatus* (KU 71745) in region of septomaxillary: (a-b) anterior end of septomaxillary; (c-d) medial divergence of septomaxillary; (e) dorsal, ventral, and medial rami of septomaxillary. Encircled numbers represent the nasal cavities as follows: 1) cavum principale; 2) cavum medium; and 3) recessus medialis of cavum inferius. Abbreviations: *al. c.*, alary cartilage; *ant. spmax.*, anterior end of septomaxillary; *c. obl.*, cartilago obliquus; *cr. int.*, crista intermedia; *dor. r. spmax.*, dorsal ramus of septomaxillary; *ext. nar.*, external naris; *f. r. ext. n.*, foramen ramus externus narium; *f. r. med. n.*, foramen ramus medialis narium; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *lat. r. spmax.*, lateral ramus of septomaxillary; *med. r. spmax.*, medial ramus of septomaxillary; *nas.*, nasal; *pnas.*, prenasal; *sol. nas.*, solum nasi; *spmax.*, septomaxillary; *vent. r. spmax.*, ventral ramus of septomaxillary.

nasi at the level of the anterior ends of the septomaxillary and cavum medium. In subsequent sections, the connective tissue is replaced in distal areas first, until the septum nasi is completely cartilaginous at the level of the foramen ramus externus narius (*r. ext. n.*) and ramus medius narius (*r. med. n.*, Fig. 5). Peripheral ossification appears first at the level just anterior to the posterior end of the recessus medialis followed posteriorly by internal ossification (Fig. 11). The dorsal part of the septum nasi is the last to ossify. At the level of the olfactory eminence (Fig. 12) the septum nasi is completely ossified. Posteriorly, the septum nasi is continuous with the sphenethmoid.

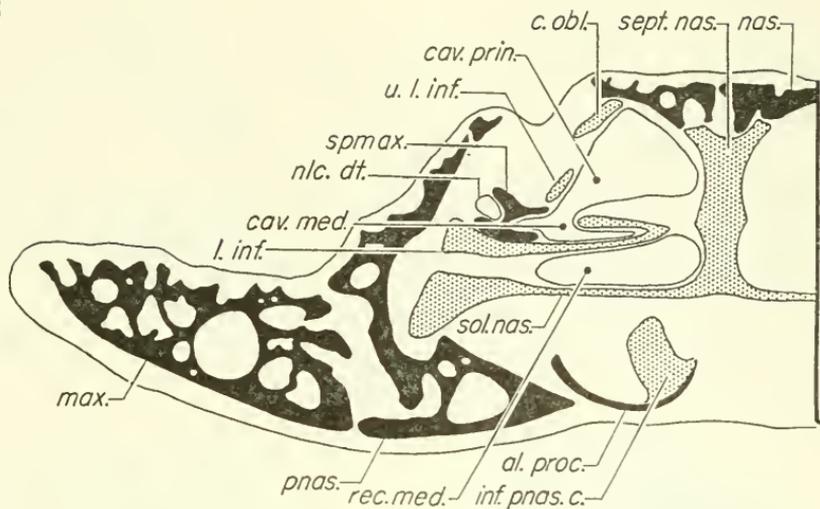
Nasal cavities and associated structures.—The cavum principale (*cav. prin.*) is the anteriormost to appear. The anterior end is bordered by the alary cartilage laterally, the tectum nasi dorsomedially, and the septum nasi medially. A short distance posterior to the anterior end of the cavum the external naris opens dorsally (Fig. 5). The cavum is supported ventrally by the solum nasi. The cavum principale extends posteriorly within the anterior recesses of the sphenethmoid to a level slightly anterior to the disappearance of the medial septum (Fig. 17).

The cavum medium (*cav. med.*) appears ventral to the cavum principale within the solum nasi. The anterior end of the cavum lies at a level just posterior to the appearance of the septomaxillary and the opening of the external naris, and anterior to the level of the foramen ramus externus narius and ramus medius narius (Fig. 5). The presence of the cavum differentiates the lamina superior (*l. sup.*) lying between the cavum principale and cavum medium, and the lamina inferior (*l. inf.*), lying ventral to the cavum medium (Figs. 6 and 7). As the cavum medium increases in width posteriorly, the laminae lose their lateral connection. The lateral part of the cavum medium diverges as the nasolacrimal duct (*n.l.c. dt.*, Fig. 8) at a level posterior to the external naris where the cavum medium joins the cavum principale. The cavum medium terminates near the posterior end of the septomaxillary.

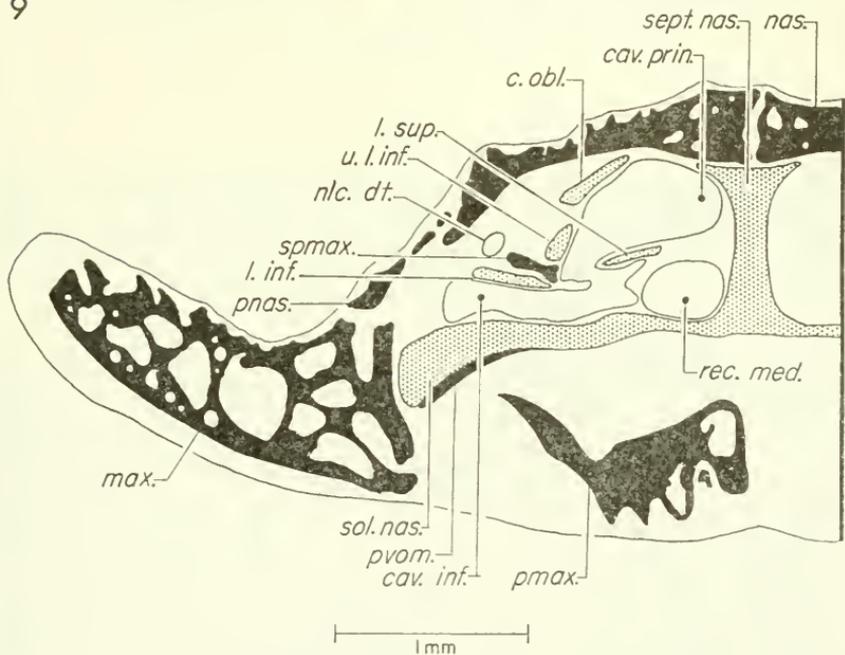
The anterior end of the recessus medialis (*rec. med.*) of the cavum inferius lies slightly posterior to the foramen of the ramus externus narius and ramus medius narius (Figs. 5-7). The presence of the recessus medialis differentiates the crista intermedia (*cr. int.*, Fig. 7) dorsally as a cartilaginous stalk joining the laminae superior and inferior to the septum nasi. Immediately anterior to the nasolacrimal duct the crista intermedia loses its medial connection to the septum nasi (Figs. 6 and 7 d-e); shortly thereafter the recessus medialis expands laterally to form the anterior part of the cavum inferius (*cav. inf.*, Fig. 8). In subsequent sections the crista intermedia gradually recedes laterally from the septum nasi, the cavum inferius grows larger, the solum nasi extends laterally to meet the maxillary, the prenasal disappears, and the pars dentalis of the premaxillary appears (Figs. 8 and 9). At the latter level the cavum principale is confluent with the recessus lateralis (*rec. lat.*) of the cavum inferius, whereas the recessus medialis has lost its connection with the recessus lateralis. Slightly posterior to the appearance of the prevomer, the recessus medialis disappears.

The crista subnasalis (*cr. sub.*, Fig. 11) differentiates from the lateral edge of the solum nasi. The crista lies adjacent to the maxillary in sections posterior to the recessus medialis. The crista subnasalis persists as a rod of cartilage, which gradually diminishes in diameter and finally terminates at the anterior limits of the olfactory eminence (Fig. 12).

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FIGS. 8-9. Transverse sections through olfactory capsule of *Triprion petasatus* (KU 71745): (8) level of infundibulum; (9) level of recessus lateralis of cavum inferius. Abbreviations: *al. proc.*, alary process of premaxillary; *c. obl.*, cartilago obliqua; *cav. inf.*, cavum inferius; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *nas.*, nasal; *nlc. dt.*, nasolacrimal duct; *pmax.*, premaxillary; *pnas.*, prenasal; *pvom.*, prevomer; *rec. med.*, recessus medialis of cavum inferius; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spmax.*, septomaxillary; *u. l. sup.*, upper part of lamina superior.

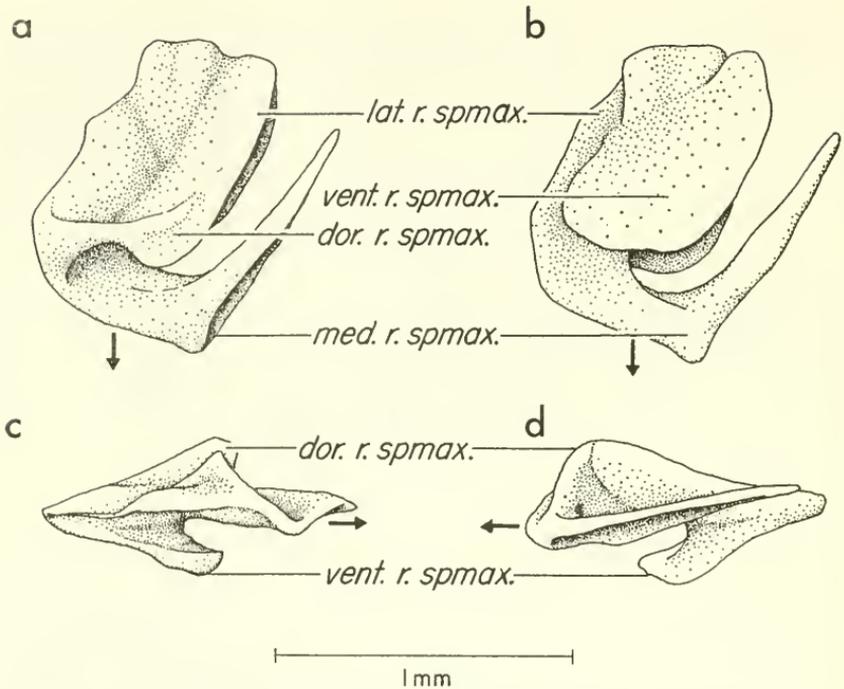
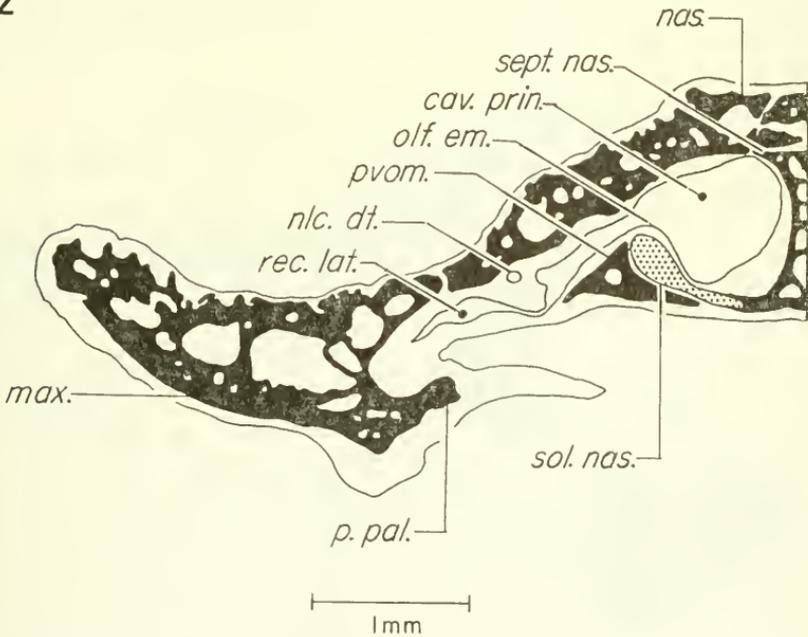
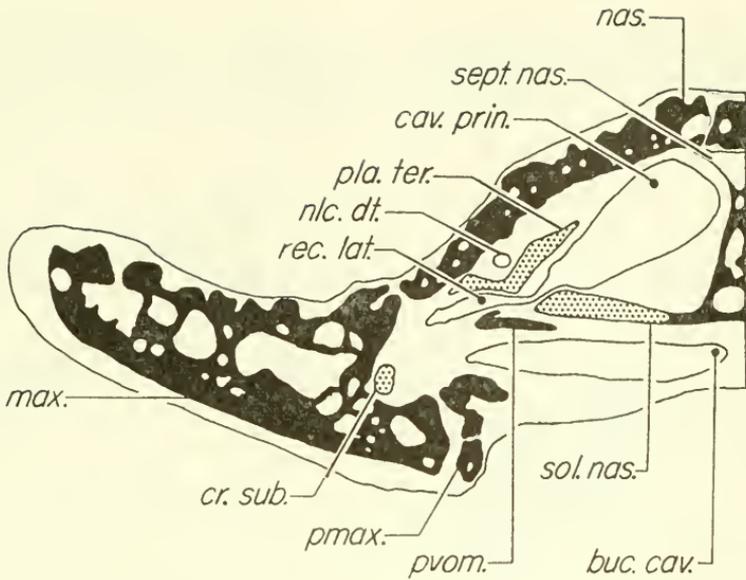


FIG. 10. Septomaxillary bone drawn from dried skeletal preparation of *Triprion petasatus* (KU 71759) ♂: (a) dorsal view; (b) ventral view; (c) lateral view; (d) medial view. Arrows indicate anterior ends. Abbreviations; *dor. r. spmax.*, dorsal ramus of septomaxillary; *lat. r. spmax.*, lateral ramus of septomaxillary; *med. r. spmax.*, medial ramus of septomaxillary; *vent. r. spmax.*, ventral ramus of septomaxillary.

Septomaxillary.—The septomaxillary (*spmax.*, Fig. 10) first appears ventral to the alary cartilage as a small, horizontally-oriented bone overlying the lateral half of the anterior end of the cavum medium (Figs. 5 and 7 a-b). It gradually widens and just anterior to the recessus medialis becomes depressed medially and bifurcates (Fig. 7 c-d) into medial and lateral rami to accommodate the connection of the cavum principale with the cavum medium. A ventral ramus of the septomaxillary projects ventral to the cavum medium (Fig. 7e). Slightly posterior, the ventral ramus joins the dorsal ramus of the septomaxillary (Fig. 8), thereby separating the main part of the cavum medium from its lateral part. The latter is the anterior end of the nasolacrimal duct. Posteriorly, the septomaxillary gradually reduces in size. The medial branch terminates just as the recessus medialis joins the recessus lateralis; the lateral branch terminates slightly posterior to the medial branch.

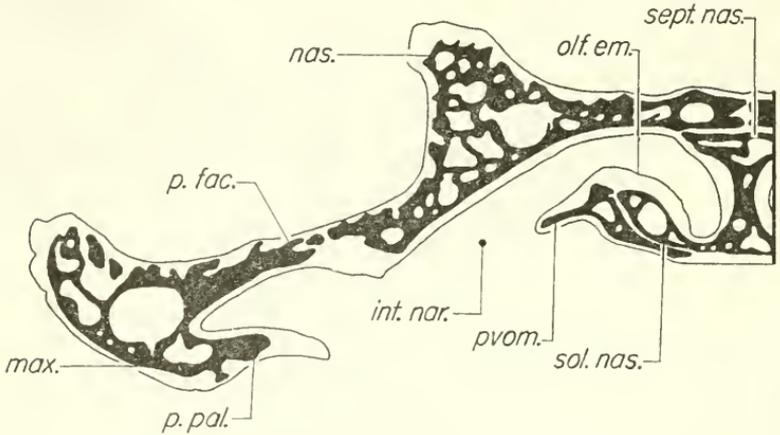
Planum Terminale.—The cartilago obliqua (*c. obl.*) maintains its dorsolateral position posterior to the appearance of the recessus medialis (Fig. 6). Posterior to the infundibulum and septomaxillary, at the level of the confluence of the cavum principale and medium, the dorsolateral remnant of the lamina inferior joins the cartilago obliqua to form the anterior end of the planum terminale (*pla. term.*, Fig. 11). The planum is arcuate in cross-section, narrow dorsally, and broad



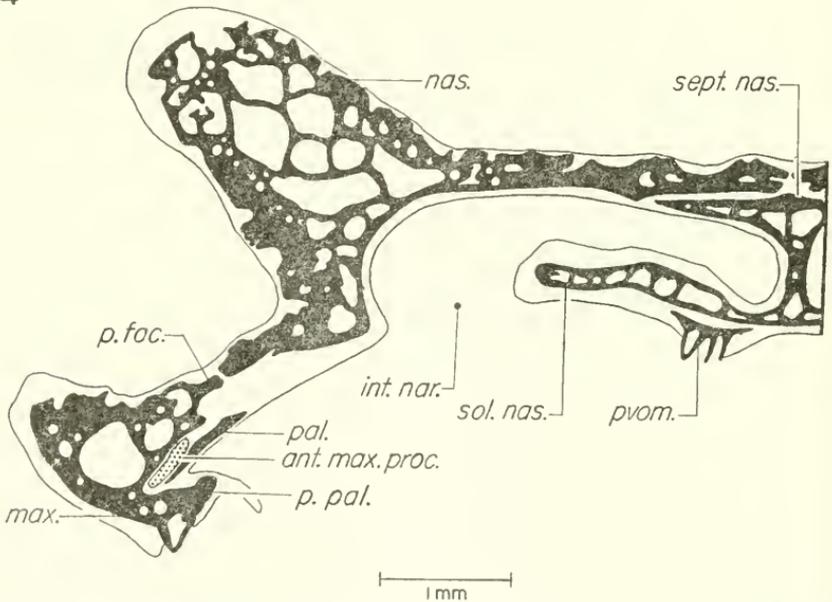
FIGS. 11-12. Transverse sections through posterior part of olfactory capsule of *Triprion petasatus* (KU 71745): (11) level of planum terminale; (12) anterior level of olfactory eminence. Abbreviations: *buc. cav.*, buccal cavity; *cav. prin.*, cavum principale; *cr. sub.*, crista subnasalis; *max.*, maxillary; *nas.*, nasal; *nlc. dt.*, nasolacrimal duct; *olf. em.*, olfactory eminence; *p. pal.*, pars palatina of maxillary; *pla. term.*, planum terminale; *pmax.*, premaxillary; *pvom.*, prevomer; *rec. lat.*, recessus lateralis of cavum inferius; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi.

ventrally and lies lateral to the cavum principale. In subsequent sections the planum is reduced in width and then expanded ventrolaterally to form a lateral ledge of cartilage separating the nasolacrimal duct from the recessus lateralis.

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FIGS. 13-14. Transverse sections through skull of *Triprion petasatus* (KU 71745) at level of olfactory eminence: (13) anterior level of internal nares; (14) level of palatine bone. Abbreviations: *ant. max. proc.*, anterior maxillary process; *int. nar.*, internal naris; *max.*, maxillary; *nas.*, nasal; *olf. em.*, olfactory eminence; *p. fac.*, pars facialis; *p. pal.*, pars palatina; *pal.*, palatine; *pvom.*, prevomer; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi.

At the anterior edge of the olfactory eminence the planum terminale is restricted to a dorsal strip of cartilage lying medial to the nasolacrimal duct, between the nasal bone and the cavum principale. It gradually diminishes in size posteriorly and disappears anterior to the opening of the internal naris.

Anterior and Posterior Maxillary Processes.—The anterior terminus of the anterior maxillary process (*ant. max. proc.*) lies in the medial part of the maxillary at a level just posterior to the opening of the internal naris. In subsequent sections the process extends medially, out of the maxillary, and then dorsally along the medial face of the pars facialis and the nasal bone in the region of the palatine (Fig. 14). In sections immediately posterior to the internal naris, the anterior process meets the beginning of the transition zone between the solum nasi and the planum antorbitale (*pla. ant.*, Fig. 15). Posterior to the zone of transition and the disappearance of the planum antorbitale, the anterior maxillary process is replaced by the posterior maxillary process (*post. max. proc.*). The latter is a small rod of cartilage between the pars palatina and pars facialis of the maxillary (Fig. 17-19). Posteriorly, the cartilage is associated with the pterygoid as the pterygoid process (*pter. proc.*, Fig. 20).

Planum Antorbitale.—The planum antorbitale (*pla. ant.*) appears adjacent to medial face of the nasal, posterior to the closing of the internal naris. It is a small structure which united the tectum dorsally and the solum nasi and anterior maxillary process ventrally (Figs. 15 and 16). Posterior to this fusion, the cartilage is replaced by the bony sphenethmoid, leaving only a small dorsolateral remnant of the planum antorbitale which quickly diminishes and disappears.

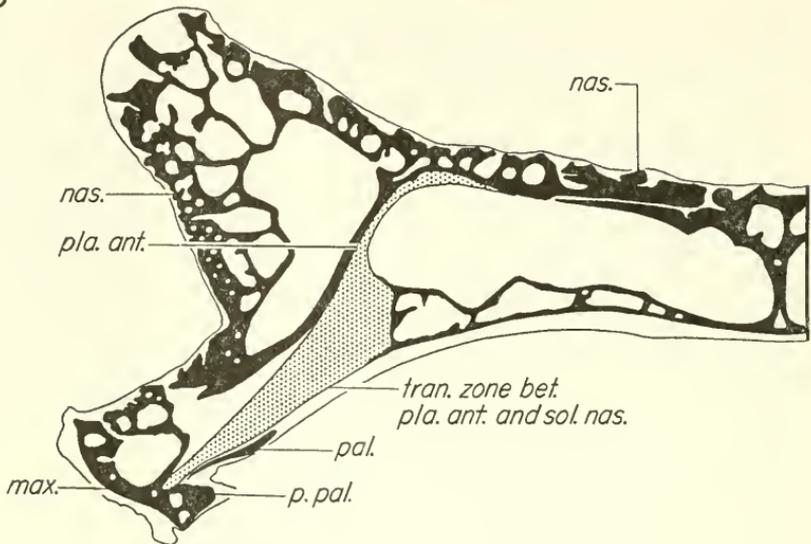
The Sphenethmoid and External Dermal Bones Associated with the Sphenethmoid Region

The frontoparietal (*fpar.*), the sphenethmoid (*spheth.*), and the anterior part of the parasphenoid (*prsph.*) are included in the sphenethmoid region.

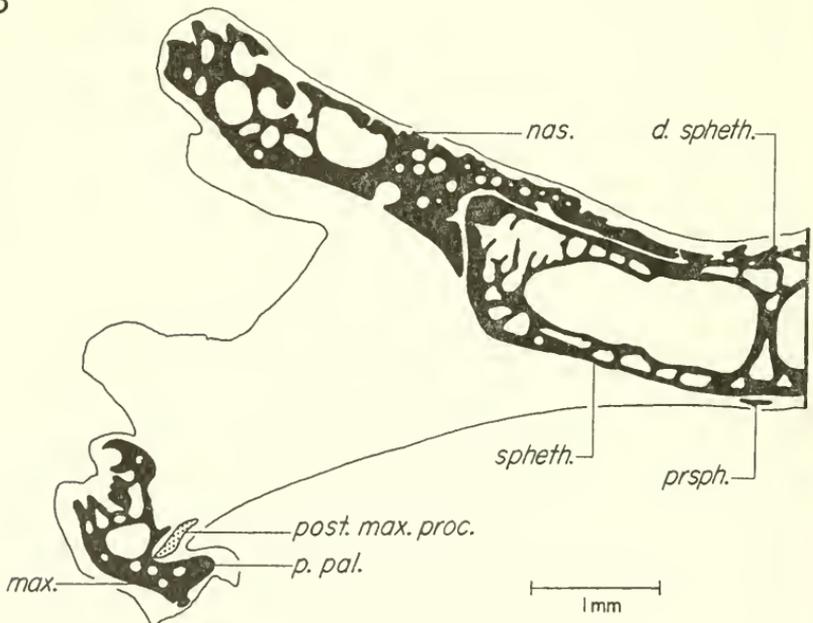
Frontoparietal.—The frontoparietal (*fpar.*, Pl. 2a; Fig. 1b) is an approximately rectangular-shaped element which articulates anterolaterally with the posterior margin of the nasal and anteromedially with the posterior margin of the dermal sphenethmoid. Laterally, the frontoparietal extends over the orbit as a bony shelf; posterolaterally it is attached to the squamosal. The posterior margin of the frontoparietal terminates in an upturned flange (Pls. 2a and 3a) referred to as the occipital crest. Ventral to the occipital crest, the frontoparietal is attached, but not fused, to the exoccipital (Pl. 3b). Posterior to the dermal sphenethmoid the frontoparietals converge. The dorsal surface of the frontoparietal is involved in integumentary-cranial co-ossification. Like the nasal, the frontoparietal is characterized by bony striations which form a radiate pattern centered at the mid-length of the bone slightly lateral to the mid-width. The striations are most prominent anteriorly and medially over the orbit, and posteriorly on the margin of the occipital crest where they terminate in spinose processes.

Sphenethmoid.—The dermal sphenethmoid (*d. spheth.*, Pl. 2a; Fig. 1b) is a diamond-shaped bone occupying the depressed central region of the skull. The anterolateral margins of the dermal sphenethmoid articulate with the posteromedial edges of the nasals, and the posterolateral margins of the bone with the anteromedial edges of the frontoparietals. The dermal sphenethmoid is com-

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FIGS. 15-16. Transverse sections through skull of *Triprion petasatus* (KU 71745) at anterior level of sphenethmoid: (15) level of planum antorbitale; (16) anterior end of parasphenoid. Abbreviations: *d. spheth.*, dermal sphenethmoid; *max.*, maxillary; *nas.*, nasal; *p. pal.*, pars palatina of maxillary; *pal.*, palatine; *pla. ant.*, planum antorbitale; *post. max. proc.*, posterior maxillary process; *prsph.*, parasphenoid; *spheth.*, sphenethmoid; *tran. zone bet. pla. ant. and sol. nas.*, transition zone between planum antorbitale and solum nasi.

pletely involved in integumentary-cranial co-ossification and is marked by a centrally located, radiate pattern of striations. The dorsally-exposed dermal sphenethmoid is confluent with the underlying endochondral sphenethmoid as described in *Hyla septentrionalis* (Trueb, 1966).

The endochondral sphenethmoid (*spheth.*, Fig. 1b) is an extensive element which is completely covered dorsally by the dermal roofing bones. The sphenethmoid is in synchondrotic continuity with the septum nasi; thus, in ventral view (Pl. 2b) it appears to originate anteriorly in a pointed process dorsal to the palatine processes of the premaxillaries. The floor of the sphenethmoid widens posteriorly, forming the posteromedial and posterior margins of the internal nares. Posterior to the palatines, the venter of the sphenethmoid reaches its widest extent and attaches to the medial surface of the nasals anterior to the orbit. The sphenethmoid narrows abruptly in the anterior region of the orbit and posteriorly narrows more gradually to its terminus at the foramen of the optic nerve.

Parasphenoid.—The parasphenoid (*prsp.*, Pl. 2b) is a long, delicate bone which lies on the ventromedial surfaces of the sphenethmoid and prootics. The narrow, anterior end of the parasphenoid lies just posterior to the prevomer. The bone widens posteriorly, but is medially constricted in the region of the sphenethmoid-prootic junction; it abruptly widens ventral to the prootic and then narrows to a terminal point, which lies just anterior to the foramen magnum. The parasphenoid bears an odontoid-like structure in the form of an irregular, thin, ventral projection (Pl. 3a), which extends from a point just posterior to the level of the orbitonasal foramen to the posterior edge of the orbit.

Internal Bones and Cartilages of the Sphenethmoid Region

The synchondrotic union of the septum nasi and the sphenethmoid precludes a clear distinction between the olfactory and sphenethmoid regions. Generally the posterior border of the internal naris is a convenient point to terminate description of the olfactory region. However, in *Tripurion* the dermal sphenethmoid and palatine are present anterior to this point, and the septum nasi and cavum principale posterior to it. The anterior end of the sphenethmoid region is arbitrarily established at the level of the union of the solum nasi with the planum antorbitale posterior to the internal naris (Fig. 15).

Sphenethmoid.—At the anterior end of the sphenethmoid (Figs. 15 and 16), the bone is divided medially by a bony partition which is continuous with the septum nasi anteriorly. The only cartilage associated with the sphenethmoid at this level is a small dorsolateral remnant of the planum antorbitale; the latter disappears in sections just anterior to the orbitonasal foramen. Immediately posterior to the orbitonasal foramen the medial septum of the sphenethmoid terminates (Fig. 18). At this level a small amount of cartilage is located at the distal tip of the anterolateral wing of the sphenethmoid underlying the nasal; the rest of the sphenethmoid is bony. In subsequent sections, the cartilage disappears as the lateral wings of the sphenethmoid diminish in size (Fig. 19). Just posterior to the end of the dermal sphenethmoid, the roof of the sphenethmoid splits beneath the frontoparietals to form the frontoparietal fontanelle (*fpar. fon.*, Fig. 20). Anterior to the optic foramen the taenia tecta marginalis (*t. t. mar.*, Fig. 20) appears dorsally, and the sphenethmoid is re-

stricted to form the bony, V-shaped floor of the neurocranium. Immediately anterior to the optic foramen, the ventral part of the sphenethmoid is replaced by cartilage joining the sphenethmoid and prootic.

Because of the unusual dual nature of the sphenethmoid and the size of the nasals and frontoparietals, a brief description of the internal relations of these bones is included. The anterior end of the dermal sphenethmoid appears dorso-medially between the nasals at the level of the transition zone between the solum nasi and planum antorbitale (Fig. 15). The dermal and endochondral sphenethmoid are continuous and, as a unit, both are separated from all adjacent elements by connective tissue. The dermal sphenethmoid attains its maximum width in the mid-orbital region (Fig. 18) at the articulation between the nasal and frontoparietal. This articulation is not a simple juxtaposition. The frontoparietal bears an anterior flange which underlies the posterior margin of the nasal (Fig. 18). At the posterior terminus of the dermal sphenethmoid, the frontoparietals converge medially over the endochondral sphenethmoid (Fig. 20). In subsequent sections the endochondral sphenethmoid diverges medially to form the frontoparietal fontanelle. The frontoparietal overlying the fontanelle is noticeably thicker than the same bone in previous sections; perhaps this is a structural compensation for the loss of the underlying sphenethmoid. The fontanelle is covered by connective tissue continuous with that separating the sphenethmoid and frontoparietal anteriorly and laterally.

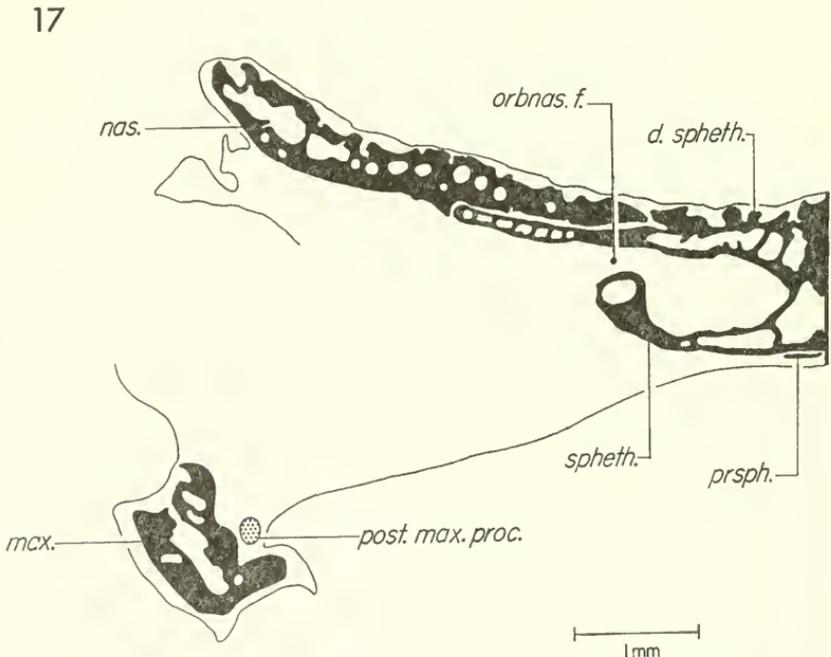
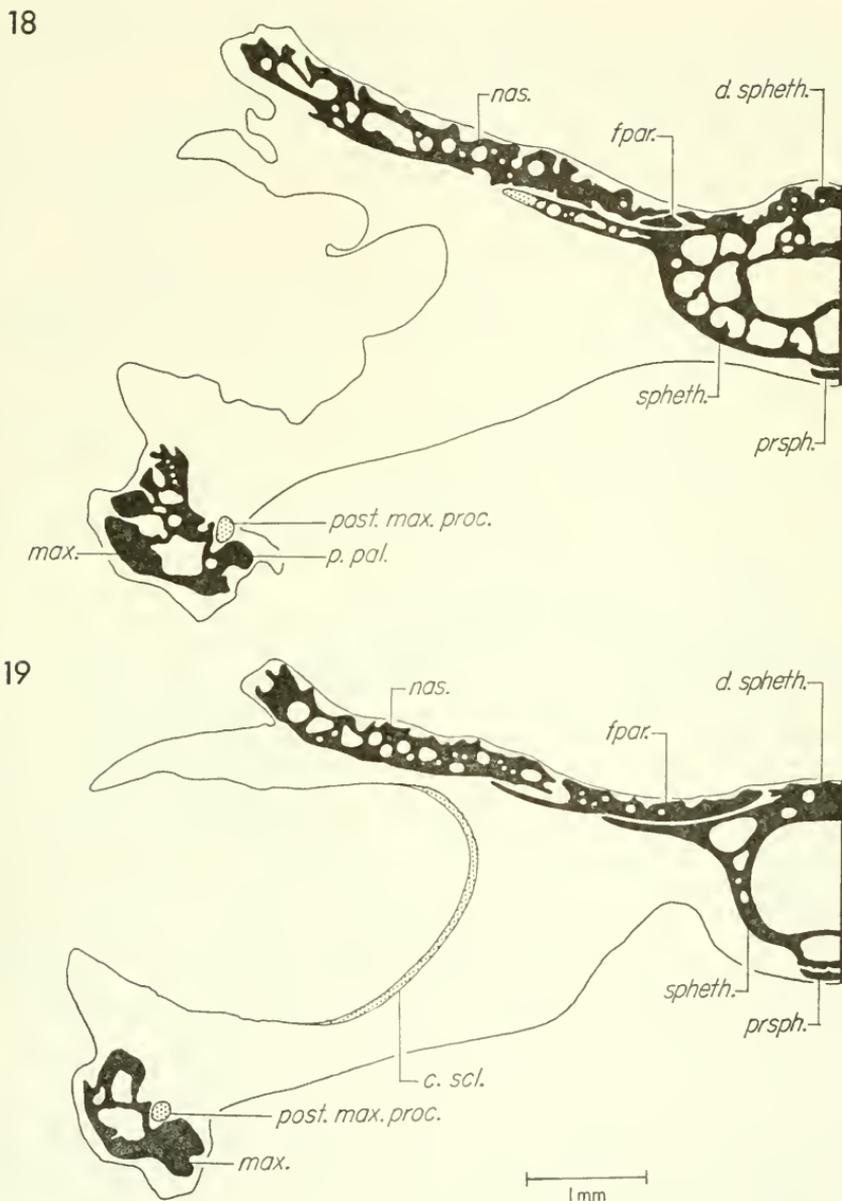


FIG. 17. The transverse section through skull of *Tripriion patasatus* (KU 71745) at level of orbitonasal foramen. Abbreviations: *d. spheth.*, dermal sphenethmoid; *max.*, maxillary; *nas.*, nasal; *orbnas. f.*, orbitonasal foramen; *post. max. proc.*, posterior maxillary process; *prsph.*, parasphenoid; *spheth.*, sphenethmoid.



FIGS. 18-19. Transverse sections through skull in orbital region of *Triprion petasatus* (KU 71745) showing relationships of sphenethmoid, nasal, and frontoparietal: (18) anterior level of frontoparietal; (19) posterior level of nasal. Abbreviations: *c. scl.*, cartilaginous sclera; *d. spheth.*, dermal sphenethmoid; *fpar.*, frontoparietal; *max.*, maxillary; *nas.*, nasal; *p. pal.*, pars palatina of maxillary; *post. max. proc.*, posterior maxillary process; *prsph.*, parasphenoid; *spheth.*, sphenethmoid.

Parasphenoid.—The parasphenoid (*prsph.*, Figs. 16-27) is a delicate bone which lies ventral to the endochondral sphenethmoid. The parasphenoid is separated from adjacent bones by connective tissue and generally conforms in shape to the floor of the neurocranium.

Orbitonasal Foramen.—The orbitonasal foramen (*orbnas. f.*, Fig. 17) is present in sections just anterior to the posterior end of the medial sphenethmoid septum. The foramen is completely bordered by bone and lies in the dorso-lateral corner of the neurocranium.

External Bones of the Orbital, Otic, and Occipital Regions

The squamosal, pterygoid, quadratojugal, and posterior part of the the frontoparietal and parasphenoid are included as external bones of the orbital, otic, and occipital regions. The external relations of the frontoparietal and parasphenoid have been described in the previous section.

Frontoparietal.—The frontoparietal (Pl. 2a; Fig. 1b) completely covers the orbital and otic regions; it is separated from the underlying exoccipital by a layer of connective tissue. The frontoparietal spans the prootic (Pl. 3b; Figs. 24 and 25), thereby providing space for the attachment of the adductor mandibulare anterior and posterior muscles to the dorsum of the prootic and to the lateral regions of the exoccipital; the posterolateral corner of the frontoparietal attaches to the head of the squamosal.

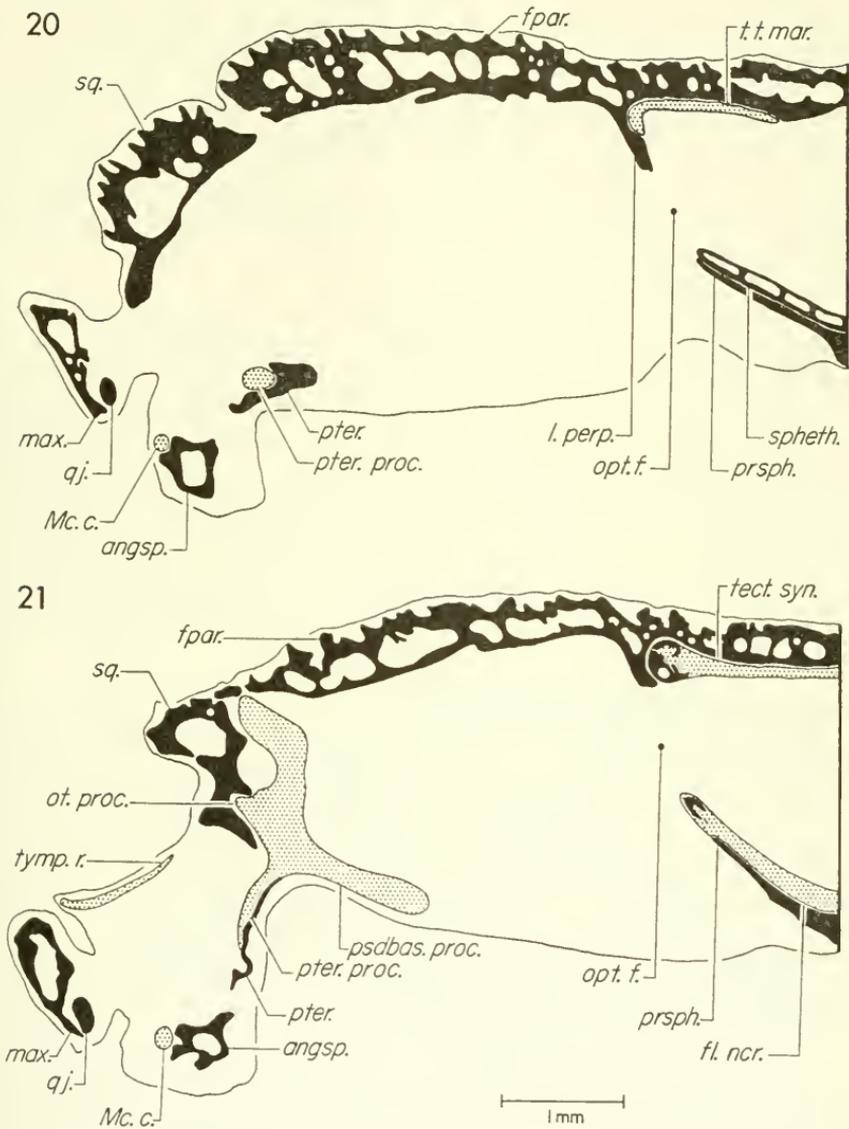
Squamosal.—In dorsal view the squamosal (*sq.*, Pl. 2a) is an arcuate bone which extends posteriorly from the posterior edge of the orbit to the level of the occipital crest. The dorsal and dorsolateral surfaces of the head of the squamosal are completely involved in integumentary-cranial co-ossification. The anterior arm of the squamosal is robust (Pl. 3a) and forms the posterior margin of the orbit and terminates ventrally on the medial edge of the maxillary. The posterior arm is as robust as the anterior arm and bears a heavy tendinous connection to the quadratojugal ventrally. The ventral arm of the squamosal extends posteroventrally from the mid-point of the arc formed by the anterior and posterior arms of the squamosal.

Pterygoid.—The pterygoid (Pl. 2b; Fig. 1b) is moderately robust but small. The anterior ramus attaches to the pars dentalis of the maxillary just anterior to the maxillary-quadratojugal articulation. The posterior ramus articulates with the quadrate process in the articular region of the skull. The medial ramus is reduced and does not articulate with the prootic.

Quadratojugal.—The well developed quadratojugal (Pls. 2b and 3a) articulates with the quadrate process and ventral arm of the squamosal medially and with the maxillary laterally and anteriorly. The quadratojugal lies adjacent to the maxillary in the recess formed by the pars facialis and pars palatina of the maxillary. The anterior end of the quadratojugal articulates with the posterior end of the pars dentalis of the maxillary.

Internal Bones and Cartilages of the Orbital, Otic, and Occipital Regions

Nerve Foramina of the Orbital, Otic, and Occipital Regions.—The optic foramen (*opt. f.*, Figs. 20 and 21) has a complete, bony margin; the anterior and ventral edges are formed by peripheral ossification of the sphenethmoid, the dorsal margin by the prootic. The trochlear foramen (*trac. f.*) lies just



FIGS. 20-21. Transverse sections through skull of *Triprion petasatus* (KU 71745) at level of optic foramen; (20) anterior level of optic foramen; (21) posterior level of optic foramen. Abbreviations: *angsp.*, angulosplenic; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *l. perp.*, lamina perpendicularis of frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *opt. f.*, optic foramen; *ot. proc.*, otic process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *qj.*, quadratojugal; *spheth.*, sphenethmoid; *sq.*, squamosal; *t. t. mar.*, taenia tecti marginalis; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

posterior and dorsal to the optic foramen. Slightly posterior and ventral to the optic foramen, the oculomotor foramen (*ocul. f.*, Fig. 22) appears in the prootic bone. The foramen bears a complete bony margin and is only narrowly separated posteriorly from the large prootic foramen (*pro. f.*, Fig. 23) housing the ganglion prootic commune and abducens nerve. Considerably posterior, at the level of the operculum (*op.*, Fig. 26), the anterior acoustic foramen (*ant. acus. f.*) appears. It is separated by a narrow region of cartilage from the posterior acoustic foramen (*post. acus. f.*, Fig. 27). A narrow bridge of bone separates the posterior acoustic foramen from the more ventral jugular foramen (*jug. f.*, Fig. 28). Slightly posterior and lateral to the latter, the foramen perilymphaticum appears.

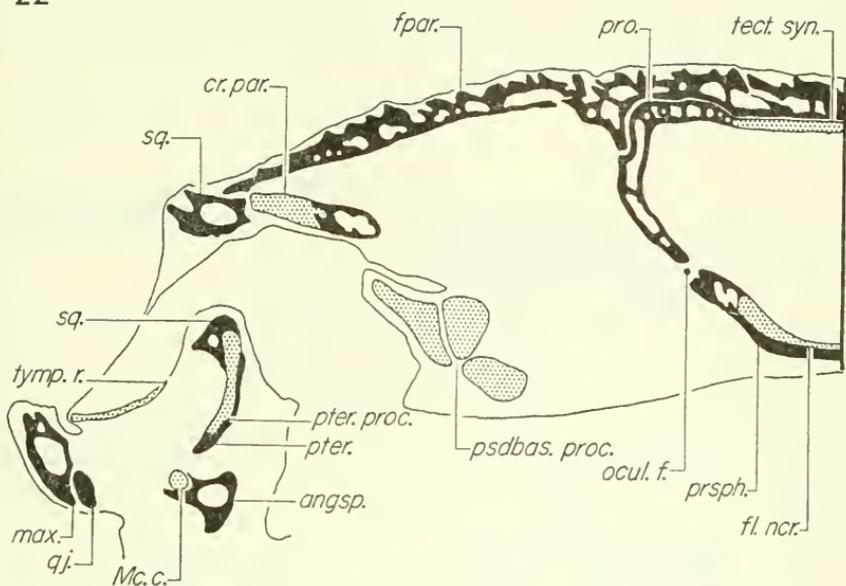
Otic Region.—The otic process (*ot. proc.*) first appears at the level of the optic foramen, posterior to the entry of the optic nerve into the neurocranium. Initially the oval cartilage is encased in the head of the squamosal. The process lengthens and comes to lie medial to the squamosal head. Somewhat posteriorly (Fig. 21), the otic process fuses ventrally with the pterygoid and pseudobasal processes. Just anterior to the oculomotor foramen, the otic process loses its connection with the ventral cartilages and assumes a horizontal position as the crista parotica (*cr. par.*, Figs. 22-25). The crista parotica joins the ossified prootic medially. The pterygoid process loses its connection with the pseudobasal process and the cornu principalis of the hyale (*corn. prin.*, Figs. 23 and 24) diverges laterally from the pseudobasal process. The pseudobasal process is short; it coalesces after a short distance with the ventrolateral ledge of the otic capsule medially (*vl. l. ot. c.*, Figs. 23 and 24).

At the level of the prootic foramen (Fig. 23) the cornu principalis is restricted ventrally; the pars externa plectri (*p. ext. pl.*) has appeared laterally and the pars media plectri (*p. med. pl.*) at the ventrolateral tip of the otic capsule. The pars externa plectri is joined to the crista parotica for a short distance by the pars ascendens plectri (*p. asc. pl.*). The cornu principalis extends posteroventrally from the pseudobasal process and terminates just anterior to the fenestra ovalis. The pars interna plectri (*p. int. pl.*, Fig. 25) lies in the fenestra ovalis at the level of the anterior acoustic foramen. The operculum (*op.*, Fig. 26) appears immediately lateral to the pars interna plectri as a small crescent-shaped cartilage. The pars interna plectri disappears and the operculum effects the lateral closure of the fenestra ovalis, uniting the dorsal and ventral components of the otic capsule at the level of the posterior acoustic foramen. Anterior to the closure of the foramen the operculum disappears.

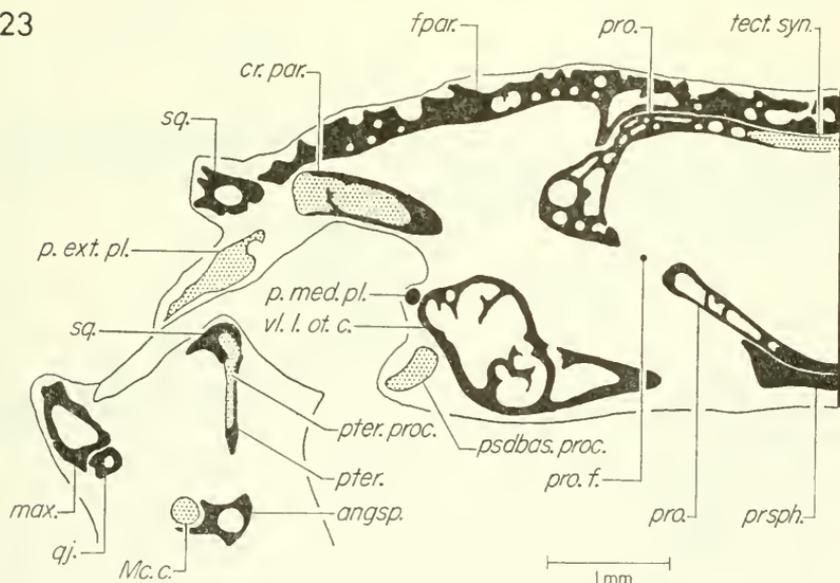
Pterygoid.—The pterygoid appears at the mid-level of the orbit and invests the pterygoid process dorsomedially. At subsequent levels the pterygoid extends posteromedially toward the ventrolateral ledge of the otic capsule (Figs. 20-23). The bony medial ramus of the pterygoid does not meet the otic capsule, although the pterygoid process fuses with the ventral block of cartilage which gives rise to the cornu principalis and pseudobasal process. In more posterior sections, the pterygoid is present as a thin, bony element which invests the medial side of the pterygoid and quadrate processes and lies medial to the ventral arm of the squamosal. The pterygoid extends posterior to the posterior termini of the quadratojugal and angulosplenic bones.

Ossification in the Otic and Occipital Regions.—At the posterior level of the optic foramen (Fig. 21) the floor of the neurocranium (*fl. ncr.*) is only peripherally ossified; likewise the roof, the tectum synoticum, is peripherally ossified.

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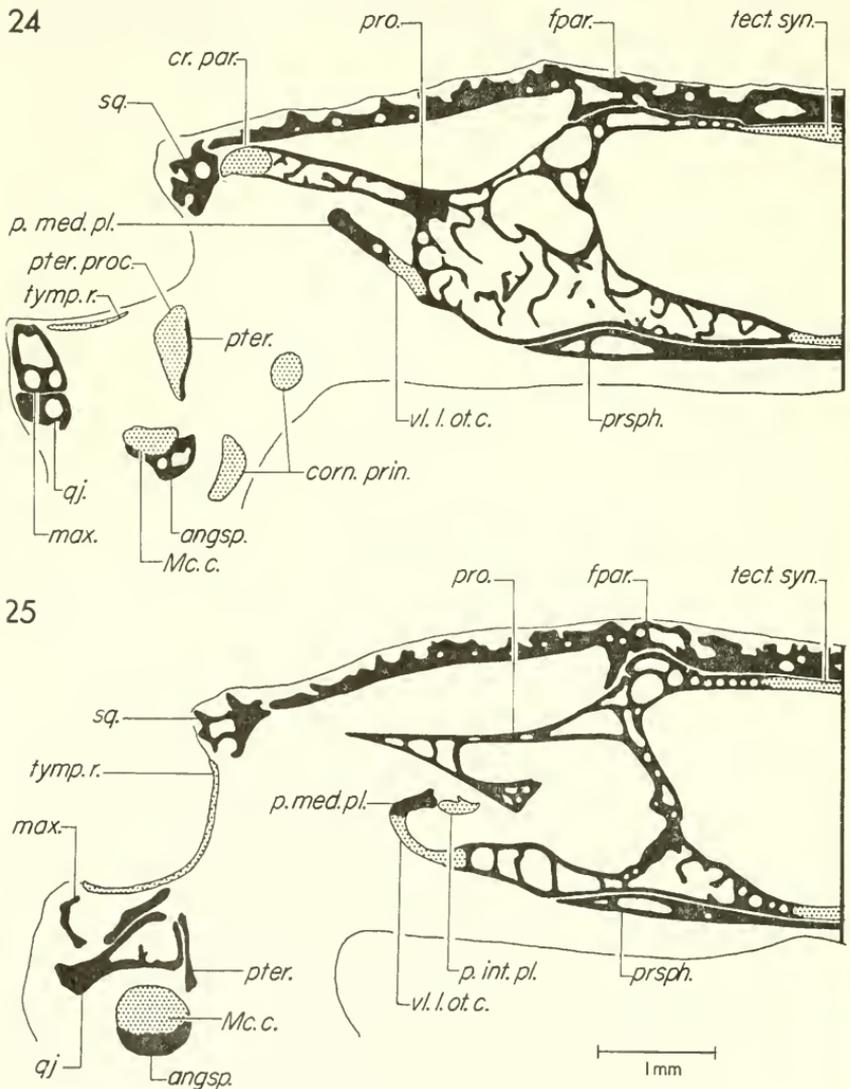


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FIGS. 22-23. Transverse sections through skull of *Triprion petasatus* (KU 71745) at anterior level of otic region: (22) level of oculomotor foramen; (23) level of prootic foramen. Abbreviations: *angsp.*, angulosplenic; *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *ocul. f.*, oculomotor foramen; *p. ext. pl.*, pars externa plectri; *p. med. pl.*, pars media plectri; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring; *vl. l. ot. c.*, ventrolateral ledge of otic capsule.

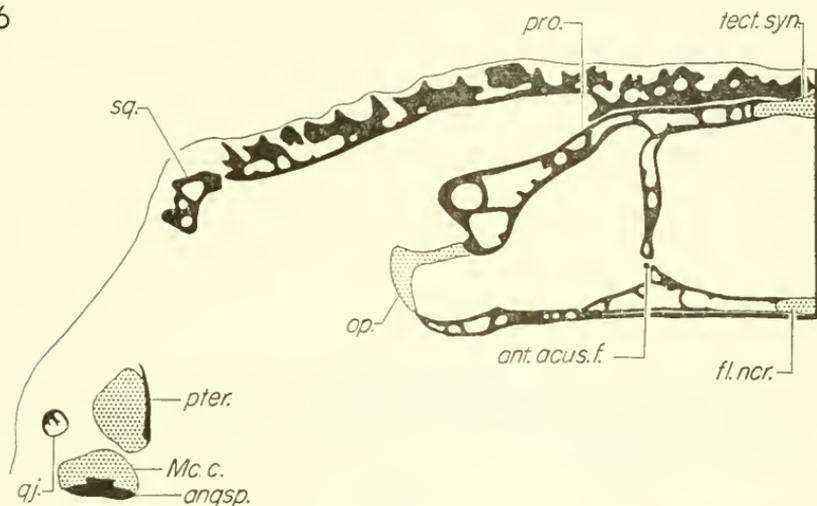
The ventral cartilage presumably represents the junction between the sphenethmoid and prootic bones. Ossification increases posteriorly in the walls of the neurocranium; at the posterior limits of the skull only a small mid-ventral



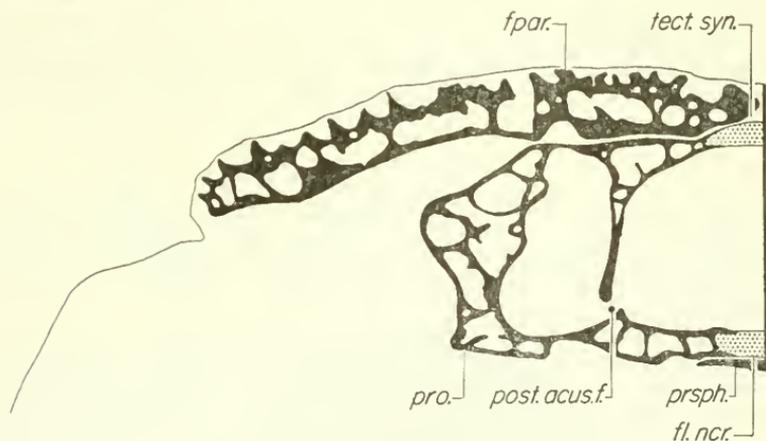
FIGS. 24-25. Transverse sections through otic region of skull of *Triprion petasatus* (KU 71745): (24) level of pars media plectri; (25) level of pars interna plectri. Abbreviations: *angsp.*, angulosplenial; *corn. prin.*, cornu principalis; *cr. par.*, crista parotica; *fpar.*, frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *pro.*, prootic; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tym. r.*, tympanic ring; *vl. l. ot. c.*, ventrolateral ledge of otic capsule.

section of the exoccipital remains cartilaginous (Fig. 28). The otic capsule is almost entirely ossified with the exception of its ventrolateral ledge (Figs. 24 and 25), which is cartilaginous. The pars media plectri is totally ossified, but the crista parotica, pars externa plectri, pars ascendens plectri, pars interna plectri, and operculum are cartilaginous.

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FIGS. 26-27. Transverse sections of skull of *Tripirion petasatus* (KU 71745) through posterior part of otic region: (26) level of anterior acoustic foramen; (27) level of posterior acoustic foramen. Abbreviations: *angsp.*, angulosplenial; *ant. acus. f.*, anterior acoustic foramen; *fl. ncr.*, floor of neurocranium; *Mc. c.*, Meckel's cartilage; *op.*, operculum; *post. acus. f.*, posterior acoustic foramen; *pro.*, prootic; *prsph.*, parasphenoid; *pter.*, pterygoid; *sq.*, squamosal; *tect. syn.*, tectum synoticum.

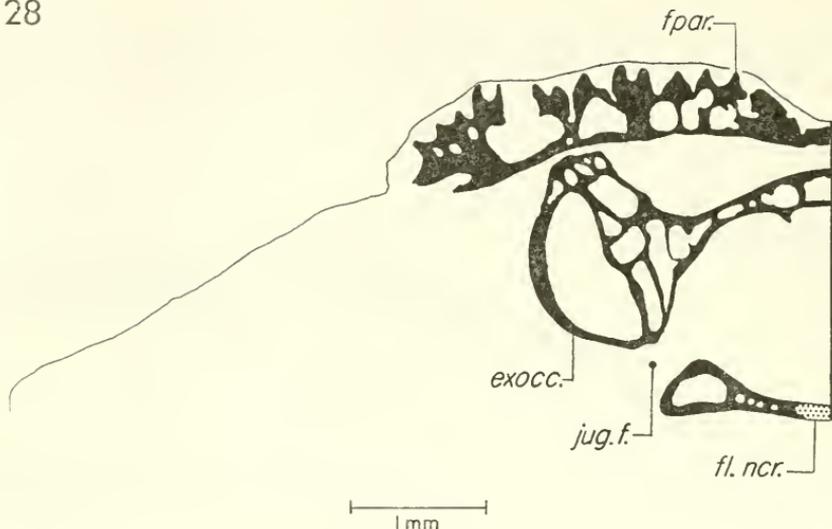


FIG. 28. Transverse section of skull of *Triprion petasatus* (KU 71745) at level of jugular foramen. Abbreviations: *exocc.*, exoccipital; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *jug. f.*, jugular foramen.

The Bursa Angularis Oris

The bursa angularis oris (*b. ang. o.*, Fig. 29) is present as a mass of lymphoid tissue between the maxillary and pterygoid bones in the posterior part of the orbit. The bursa lacks organized glandular structure and distinct boundaries; it has no lumen and is separated from the oral cavity by cuboidal ciliated epithelium.

The Articular Region

Anterior to the articular region, Meckel's cartilage is small and lies dorso-lateral to the angulosplenic bone. Posteriorly, it enlarges and takes a dorsal position with respect to the angulosplenic while the latter assumes a shallow crescentic shape.

The quadratojugal first appears in sections just posterior to the orbit. From an initial position medial to the maxillary the quadratojugal enlarges posteriorly and moves to a position ventral to the maxillary, while the latter decreases in size. The quadratojugal later joins the quadrate process medially. Perichondral and endochondral ossification of this element persists posterior until the loss of the angulosplenic; thereafter the posterior quadrate process articulates with Meckel's cartilage. Both elements disappear at the posterior level of the posterior acoustic foramen.

Summary of the Description of the Skull of *Triprion*

1. All dorsal and lateral parts of the skull are involved in integumentary-cranial co-ossification. Dermal roofing bones are extensive and form a complete casque, or cranial roof. The skull is

distinguished by spinose maxillary and prenasal flanges, a spinose preorbital knob, transverse rows of spines across the occipital region, and ornate sculpturing of all dorsal and lateral surfaces of dermal bones.

2. A dermal sphenethmoid and prenasal are present.

3. Most of the septum nasi and part of the solum nasi are ossified. The olfactory eminence is supported by a cartilaginous part of the solum nasi and by the bony prevomer.

4. Both the inferior and superior prenasal cartilages are present.

5. The lingual process is absent and there is no palatal cartilage isolated between the maxillaries.

6. The anterior end of the cavum medium lies anterior to the cavum inferius.

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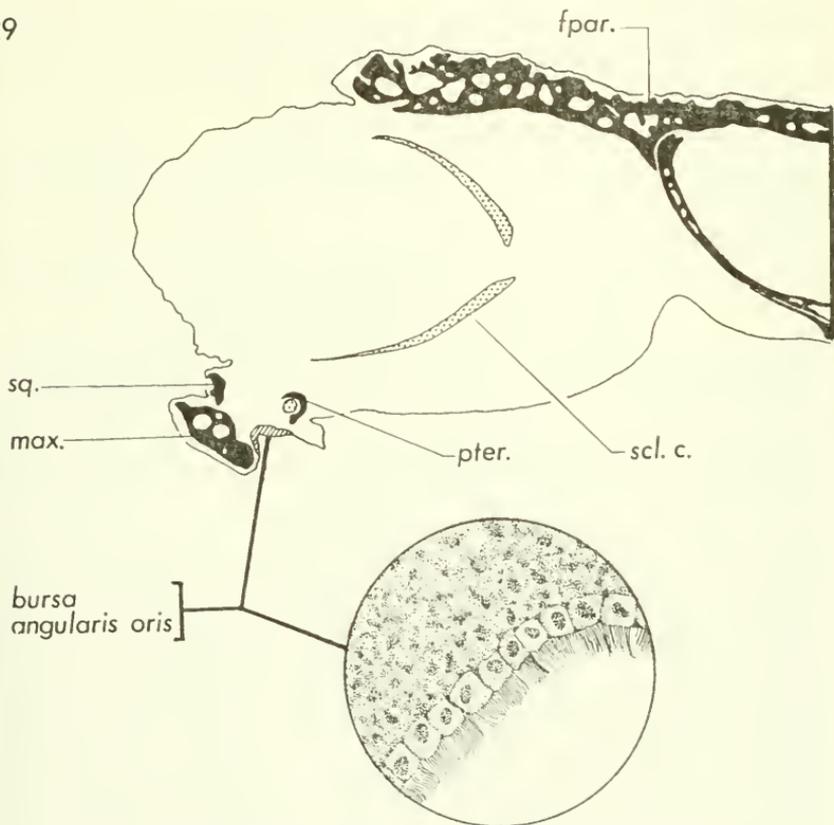


FIG. 29. Transverse section of skull of *Triprion petasatus* (KU 71745) in orbital region at level of bursa angularis oris. Inset shows enlargement ($\times 570$) of bursa angularis oris. Abbreviations: *fpar.*, frontoparietal; *max.*, maxillary; *pter.*, pterygoid; *scl. c.*, cartilaginous sclera; *sq.*, squamosal.

7. The septomaxillary is basically a U-shaped structure which has a shallow dorsal ramus and ventral ramus on the lateral branch.
8. A distinct pars nasalis is absent on the maxillary.
9. The palatine is reduced to a small, flat, rectangular bone which lies adjacent to the maxillary.
10. A cartilaginous sclera is present.
11. Remnants of the taenia tecti marginalis and tectum synoticum are evident in the adult.
12. The external part of the plectral apparatus (the columella) is directed anterolaterally. The pars ascendens is fused with the crista parotica.
13. The pseudobasal process is fused to the otic capsule.
14. The cornu principalis of the hyale is fused with the pseudo-basal process.
15. Two acoustic foramina are present.
16. The sphenethmoid and prootic are synchondrotically united.
17. The frontoparietal is separate from the prootic and exoccipital.
18. The prootic and exoccipital are fused.
19. The medial ramus of the pterygoid does not articulate with the prootic.
20. A bursa angularis oris is present.

COMPARISON OF THE CRANIAL MORPHOLOGY OF
Tripriion petasatus AND *Smilisca baudini*

The principal reason for selecting *Smilisca baudini* for comparison with *Tripriion* is that the cranial morphology of *S. baudini* seems to be unspecialized, even generalized, when compared with that of other hylids. *Smilisca* shows neither the loss of bones and reduction of ossification, nor the specialization of added bones and dermal ornamentation characteristic of some hylids.

With some exceptions, the cranial characters of hylids seem to be correlated with either habitat or size, or both. Loss of elements and reduction in ossification are generally characteristic of smaller frogs and/or frogs that breed in lotic situations, as opposed to the moderate-sized lentic breeders such as *Smilisca baudini*. *Hyla microcephala*, *H. eximia*, *H. phlebodes*, and *H. elaeochroa* are a few examples of small lentic breeders. These frogs show a reduction of ossification and a tendency toward loss of cranial elements as compared with *S. baudini*. The skull is poorly roofed; the frontoparietal fontanelle is characteristically large; the anterior arm of the squamosal is not in contact with the maxillary; the quadratojugal-max-

illary articulation is weak or absent; the pars facialis of the maxillary is reduced, and the nasal often lacks a maxillary process. The same kinds of reduction are characteristic of smaller lotic-breeding hylids, such as *Smilisca sordida*, *Hyla uranochroa*, *H. legleri*, *H. rufoculis*, *H. lancasteri*, and members of the genus *Ptychohyla*. The reduction or complete loss of the quadratojugal is especially marked among the smaller stream-breeders.

Larger lotic-breeding hylid frogs such as *Hyla chaneque*, *H. taeniopus*, *Plectrohyla*, and members of the *Hyla bistincta* group have more massive skulls than their smaller counterparts, but probably this cranial massiveness is attained secondarily. All of these frogs have frontoparietal fontanelles, and some lack a quadratojugal. The squamosal varies in size, but in none is it in contact with the maxillary. The nasal usually lacks a strong maxillary process, but in almost all of these frogs the pars facialis of the maxillary has a strong posterior process, which probably complements the function of the maxillary process of the nasal. The foregoing characters suggest that the crania of the lotic-breeding hylid frogs have evolved from a more generalized lentic ancestor, conceivably a frog having a cranium resembling that of *Smilisca baudini*. Smaller lentic and lotic hylids have reduced amounts of bone in their skulls. Perhaps this evolutionary pattern corresponds to a reduced need for protection and support; more likely, the meagerly ossified skulls are the result of arrested development.

Large lentic-breeding frogs, such as *Hyla boans*, *H. rosenbergi*, and *Phrynohyas*, tend to have more solidly roofed skulls than *Smilisca baudini*. A strong articulation exists between the quadratojugal and maxillary, and the frontoparietal fontanelle is absent in some, but in none does the squamosal articulate with the maxillary.

Apart from these general patterns, there are some bizarre cranial modifications among the hylids, exemplified by such frogs as *Anothea coronata* and frogs of the genus *Hemiphractus*. The skull of *Anothea* is characterized by spines along the canthal ridge, the edge of the frontoparietal over the orbit, across the occipital ridge, and on the anterior and posterior arms of the squamosal. Except for the extensive development of the frontoparietals, nasals, and pars facialis of the maxillary, the basic structure of the skull is similar to that of *Smilisca baudini*. However, *Hemiphractus* is markedly different from the majority of hylids. The skull is triangular in shape and characterized by large nasals and frontoparietals which completely roof the top of the skull. The massive squamosals are in

contact with the maxillaries anteriorly, and posteriorly in association with the frontoparietals, form posterolateral wings to the skulls. The skull is further distinguished by large prevomers, palatines and pterygoids, and a small prootic region.

Some of the most remarkable cranial modifications have taken place among frogs such as *Tripriion*, in which the cranial integument is co-ossified with the underlying bone. Included in this group are the genera *Trachycephalus*, *Osteocephalus*, *Pternohyla*, *Tripriion*, *Aparasphenodon*, *Corythomantis*, *Anothea*, *Amphignathodon*, *Nyctimantis*, some members of the genus *Gastrotheca*, *Hyla septentrionalis*, *H. brunnea*, *H. dominicensis*, and *H. lichenata*. The basic architecture of the skulls of all these species is not unlike that of *Smilisca baudini*. However, their external appearances have been greatly altered by the extensive development of the dermal roofing bones (forming flanges and crests in some species), the presence of ornate sculptured patterns on the surfaces of dermal bones and in some species the appearance of a dermal sphenethmoid and additional dermal elements in the nasal region.

On the basis of the variation noted among hylids in the preceding discussion, it is evident that *Tripriion* and the other casque-headed hylids are highly specialized. The degree and nature of the morphological specialization can be assayed most efficiently by the comparison of *Tripriion* with the generalized and well-known *Smilisca baudini*. The genus *Smilisca* was treated systematically by Duellman and Trueb (1966), and the cranial morphology of *S. baudini* was described by Trueb (1968). In the following comparison of *S. baudini* with *Tripriion petasatus* emphasis has been placed on internal rather than the obvious external differences. The two species are referred to by their generic names throughout.

The Olfactory Region

Anteriorly, the most obvious external difference between the two genera are the anterior position of the external nares and the presence of the prenasal in *Tripriion*. The premaxillary has rotated anteriorly, apparently in association with the prenasal. Thus the alary processes of the premaxillaries lie within the cavities of the prenasal, and the entire olfactory apparatus occupies a more anterior position than in *Smilisca*, in which the alary processes of the premaxillaries incline slightly posteriorly. The alary cartilage is shorter in *Tripriion* than in *Smilisca*. The alary cartilage is similarly located in both species, but in *Tripriion* the cartilage lies anterior to the solum nasi and thus does not fuse with the solum. The tectum nasi is much less extensive in *Tripriion* and does not form a roof to the cavum principale as it does in *Smilisca*.

The nasal cavities are similarly disposed with respect to one another in both species. However, the *cavum principale* is proportionately much larger in *Tripriion* than in *Smilisca*; in the former, the anterior end lies anterior to the premaxillary. The anterior end of the *cavum medium* occurs slightly anterior to the foramen for the *ramus externus* and *medius narium* in *Tripriion* and at the level of the foramen in *Smilisca*. The external nares are located in a more anterior position in *Tripriion*; the nares open into the *cava principalae* immediately posterior to the anterior end of the *cava*.

The superior prenasal cartilage is much longer in *Tripriion* than in *Smilisca*. The anterior end of the inferior prenasal cartilage lies at the base of the alary process of the premaxillary in both species, but in *Smilisca* the anterior end of the inferior prenasal cartilage lies at the level of the *recessus medialis*, whereas in *Tripriion* the anterior end of the cartilage lies posterior to this point. The inferior prenasal cartilage extends directly posterior to fuse with the *solum nasi* in *Tripriion*; in *Smilisca* it curves dorsally along the posterior surface of the alary process of the premaxillary before extending posteriorly to meet the *solum*. The inferior prenasal cartilage joins the *solum nasi* at the same level in both species.

The septomaxillaries of *Tripriion* and *Smilisca* are only slightly different. The medial and dorsal rami are more extensive in *Smilisca* than in *Tripriion*. In both species the ventral ramus is an anteroventral spur on the posterior end of the septomaxillary.

The *crista subnasalis* is situated farther posteriorly with respect to the nasal cavities in *Tripriion* than in *Smilisca*. Similarly, the anterior end of the anterior maxillary process lies more posterior in *Tripriion*. The *plana terminalae* of both species are similar. The *planum antorbitale* is much less extensive in *Tripriion* than in *Smilisca* and is not closely associated with the posterior end of the *planum terminale* as it is in *Smilisca*. Both species lack a *processus lingularis*.

The Sphenethmoid and Orbital Regions

The sphenethmoid and orbital regions of *Tripriion* and *Smilisca* differ primarily in the degree of ossification, and in the presence of a dermally ossified sphenethmoid and greatly reduced palatine in *Tripriion*. Few differences obtain in the internal bones and cartilages of these regions. The bony medial septum of the sphenethmoid terminates posterior to the orbitonasal foramen in *Tripriion* and anterior to the orbitonasal foramen in *Smilisca*. The margin of the orbitonasal foramen is cartilaginous in *Smilisca* and bony in *Tripriion*. The entire sphenethmoid, except for a small part of the dorsolateral tip in the orbital region and the partly ossified *taenia tecta marginalis*, is bony in *Tripriion*, whereas the anterior and posterior parts of the sphenethmoid are cartilaginous in *Smilisca*. In both species the sphenethmoid diverges dorsomedially to produce a frontoparietal fontanelle. In *Tripriion* the fontanelle is obscured by the medial growth of the frontoparietals, whereas in *Smilisca* the fontanelle remains exposed, covered only by connective tissue, in which secondary calcification occurs in large adults.

The Otic and Occipital Regions

The otic process is the most anterior otic structure in *Tripriion*; it lies at the posterior level of the optic foramen. The otic process almost immediately

merges with the pseudobasal process and then separates from it at the anterior level of the oculomotor foramen, where the otic process gives rise to the crista parotica dorsally. The cornu principalis of the hyale diverges ventrally at this level. By contrast, the most anterior otic structure in *Smilisca* is the anterior edge of the otic capsule, which lies at the anterior level of the oculomotor foramen. The anterior part of the pseudobasal process appears anterior to the otic process at the posterior level of the oculomotor foramen. The otic process merges immediately with the pseudobasal process and then diverges to form the crista parotica dorsally. The cornu principalis of the hyale does not diverge from the pseudobasal process until the level of the anterior acoustic foramen.

The anterior edge of the otic capsule lies at the anterior level of the prootic foramen in *Tripriion*. The crista parotica joins the medial edge of the otic capsule just posterior to this level. The crista joins the otic capsule at a corresponding level in *Smilisca*. At the posterior level of the prootic foramen, the pars externa plectri and pars ascendens plectri appear in *Tripriion*, whereas these do not appear in *Smilisca* until a level just anterior to the posterior acoustic foramen. The pars media plectri appears between the prootic and anterior acoustic foramina in *Tripriion* and between the anterior and posterior acoustic foramina in *Smilisca*. In both *Tripriion* and *Smilisca* the operculum appears at the level of the posterior acoustic foramen.

In *Tripriion* the otic region is heavily ossified; only the anterior part of the tectum synoticum, crista parotica, pars externa plectri, pars interna plectri, pars ascendens plectri, operculum, and ventrolateral ledge of the otic capsule are cartilaginous. By contrast, the otic region of *Smilisca* is largely unossified. The pars media plectri is ossified, as it is in *Tripriion*, but additional ossification is restricted to perichondral and endochondral ossification occurring in the sides of the neurocranium and the dorsum of the otic capsule, plus a small amount in the floor of the neurocranium. The remaining parts of the otic region are cartilaginous.

The Bursa Angularis Oris

The bursa angularis oris is located in the same place in both *Tripriion* and *Smilisca*. However, the structure seems to be more highly organized in *Smilisca*; the bursa has a distinct central lumen, whereas in *Tripriion* the gland is represented only by a mass of unorganized lymphoid tissue.

The Articular Region

The only obvious difference in the articular regions of the two genera is that the maxillary extensively overlaps the quadratojugal in *Tripriion*, whereas it only barely overlaps it in *Smilisca*.

Discussion

The differences between the crania of *Smilisca* and *Tripriion* can be grouped into three categories: proportions; degrees of ossification of both endochondral and dermal elements; and the absence, reduction, or addition of elements.

The proportional differences are the most complex and difficult to interpret. The existence of a longer and more extensive olfactory

region in *Tripriion*, as compared with *Smilisca*, is suggested by the forward projection of the nasal cavities and cartilaginous structures anterior to the nasal cavities into the prenasal bone. The correspondingly identical positions of the posterior termini of the nasal cavities in both species precludes the idea that these structures merely have been shifted anteriorly in *Tripriion*; rather, the size of the nasal structures seems to have adjusted to correspond to the anterior position of the external nares and the anterior rotation of the premaxillary into the prenasal.

Like the olfactory region, the otic region extends over a proportionately greater distance in *Tripriion* than in *Smilisca*. The various cranial nerve foramina have been used as an index to the positions of the otic structures. This method, although not wholly satisfactory, is the most practical with the kinds of material and techniques available. The otic and pseudobasal processes and crista parotica project farther anteriorly in *Tripriion* than in *Smilisca*. The first of these elements appears at the posterior edge of the optic foramen. The anteriormost otic structure of *Smilisca* is the anterior edge of the otic capsule at the anterior level of the oculomotor foramen. This structure is followed by the pseudobasal and otic processes and crista parotica, respectively. The posteriormost otic structure, the operculum, appears at the level of the posterior acoustic foramen in both species. The posterior otic structures terminate at approximately the same level in *Tripriion* and *Smilisca*, whereas the anterior otic elements appear farther anteriorly in *Tripriion* than in *Smilisca*, and in the former the crista parotica and plectral apparatus are oriented anterolaterally. Perhaps these features in *Tripriion* are the result of internal adjustments to compensate for and balance the posterodorsal development of the heavy occipital crests.

Internal supportive structures tend to be reduced in *Tripriion*. The alary cartilage, tectum nasi, planum terminale, and planum antorbitale are much reduced in size in comparison with *Smilisca*. In *Tripriion* the palatine is present only as a vestige and the pterygoid does not brace the mandibular and suspensorial regions against the otic region of the cranium. These internal reductions contrast sharply with the addition of the prenasal and dermal sphenethmoid externally, and the otherwise extensive ossification in *Tripriion*, as compared with *Smilisca*. There is considerably less cartilage involved in the olfactory and otic regions of *Tripriion*. Many cartilaginous structures of *Tripriion* are reduced in size, and those which are not reduced, such as the nasal septum and solum nasi, are more

heavily ossified. Thus, in comparison with *Smilisca*, the skull of *Tripriion* is characterized by small cartilaginous elements and the absence of large blocks of cartilage.

By far the most striking contrast between *Tripriion* and *Smilisca* is the extensive ossification of external dermal bones in *Tripriion*, in which there is a proximal proliferation of bone so that the cranium is completely roofed. Furthermore, the paired dermal elements, such as the nasals and frontoparietals, converge on one another, and all dermal elements articulate with adjacent bones. In *Smilisca*, by comparison, only the posterior parts of the frontoparietals converge with one another, and the squamosal and frontoparietal are the only adjacent dermal elements which articulate with one another. *Tripriion* is characterized by distal proliferations of bone which result in wide spinose labial flanges, extensive supraorbital shelves, and exostosed bone over the entire surface of the skull. *Smilisca* lacks distal proliferation of bone, except for the small supraorbital flange of the frontoparietal.

DEVELOPMENT OF THE OSTEOCRANIUM OF *Tripriion petasatus*

In the following description each bone is discussed separately. Membrane bones are treated first and are followed by cartilage bones. Bones are mentioned in the order of their appearance as accurately as this order could be ascertained from examination of available specimens. Four progressive stages of development of the skull are shown schematically in Figures 30 and 31. The stage in which cranial elements appear is depicted in Figure 33. Larval stages are those defined by Gosner (1960). Post-metamorphic stages represent successively more advanced specimens.

The Membrane Bones

Frontoparietal.—The frontoparietal first appears as a long rod of bone medial to the eye of the larva. There is no evidence of more than one center of ossification. Ossification spreads medially, anteriorly, and posteriorly from the initial center of growth. Bone proliferation seems to be most rapid in the posterior area where the paired frontoparietals first meet medially. The supraorbital flange develops along the lateral edge of the frontoparietal and appears between Post-metamorphic Stages 3 and 4, just prior to the advent of integumentary-cranial co-ossification of the frontoparietal.

Nasal.—The first center of ossification of the nasal is located dorsolaterally. The bone expands most rapidly anteriorly and ventrally; posteromedial and medial ossification progresses more slowly. Between Post-metamorphic Stages 3 and 4, the nasal develops a supraorbital process which expands posteriorly, lateral to the frontoparietal. At the same time integumentary-cranial co-ossification appears along the margin of the nasal bordering the orbit. Co-ossification

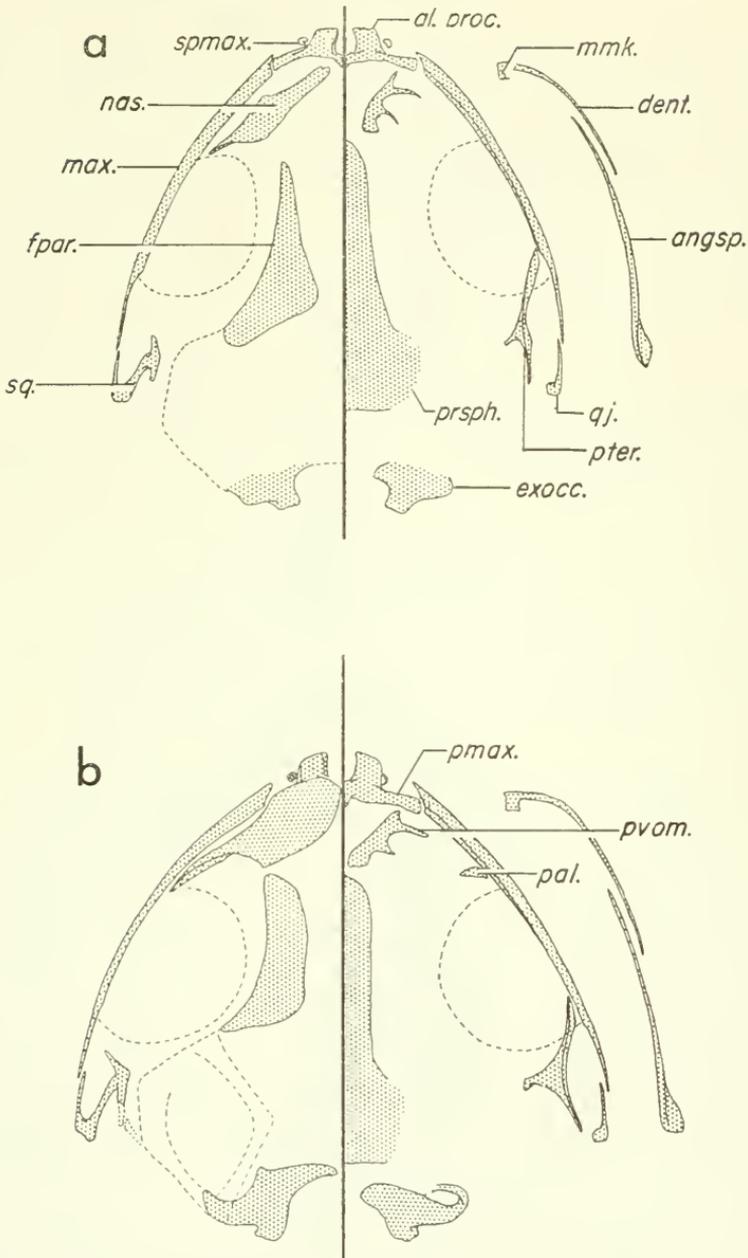


FIG. 30. Skulls of young *Triprion petasatus*. Dorsal and ventral views on right and left sides respectively of heavy median line. Right half of lower jaw shown to right of each skull. (a) recently metamorphosed young (KU 92639), snout-vent length 12.6 mm. approximately $\times 20$; (b) young (KU 92638), snout-vent length 14.1 mm. approximately $\times 18$. Abbreviations: *al. proc.*, alary process of premaxillary; *angsp.*, angulosplenic; *col.*, columella; *dent.*, dentary; *exocc.*, exoccipital; *fpar.*, frontoparietal; *max.*, maxillary; *mmk.*, mentomeckelian; *nas.*, nasal; *pal.*, palatine; *pmax.*, premaxillary; *prsph.*, parasphenoid; *pter.*, pterygoid; *pvom.*, prevomer; *qj.*, quadratojugal; *spmax.*, septomaxillary; *sq.*, squamosal.

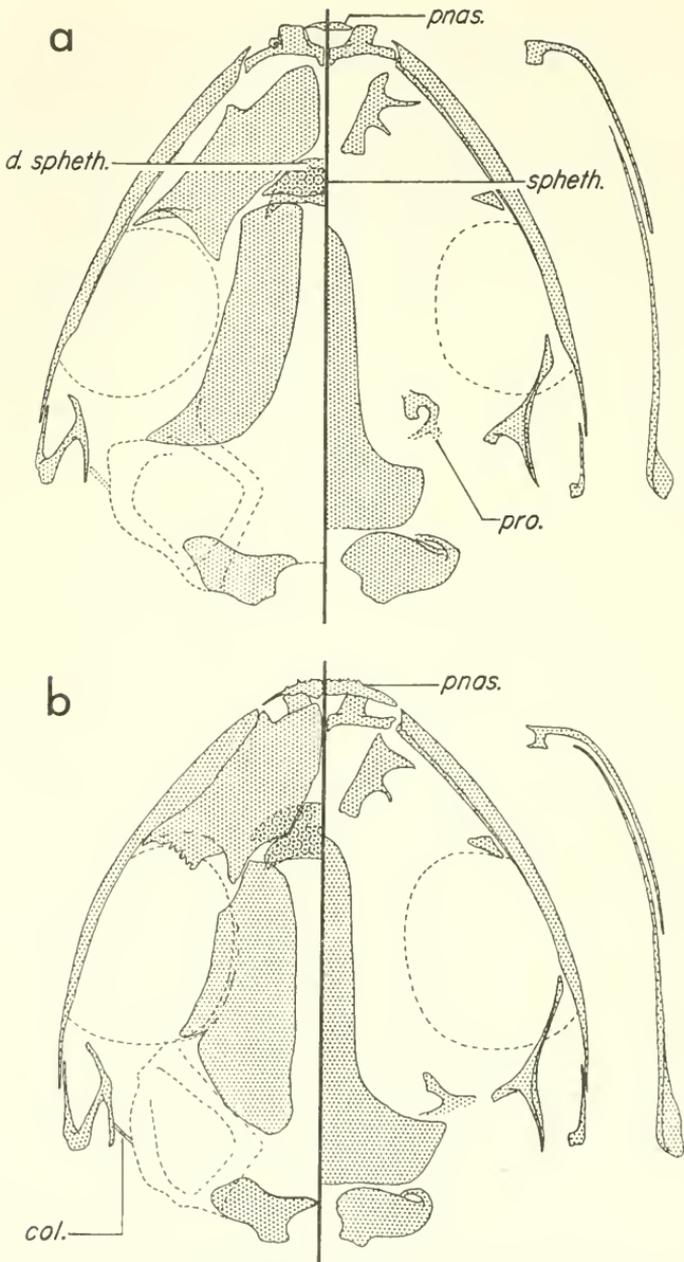


FIG. 31. Skulls of young *Tripurion petasatus*. Dorsal and ventral views on right and left sides respectively, of heavy median line. Right half of lower jaw shown to right of each skull. (a) young (KU 92637), snout-vent length of 15.5 mm. approximately $\times 15$; (b) young (KU 92636), snout-vent length 17.5 mm. Abbreviations: *col.*, columella; *d. spheth.*, dermal sphenethmoid; *pnas.*, prenasal; *pro.*, prootic; *spheth.*, sphenethmoid. Refer to Fig. 30 for identification of other structures.

spreads over the entire surface of the nasal but proliferates most rapidly at the anterior edge of the orbit and in the canthal region. The accelerated growth of the former area gives rise to the serrate or spinose flange continuous with the supraorbital flange of the frontoparietal; these two elements, with the squamosal posteriorly, completely encase the eye of the adult frog. The rapid proliferation of bone in the canthal region results in the well-defined canthal ridge extending from the external nares and termination in the spinose preorbital knob of the mature specimen.

Septomaxillary.—The septomaxillary appears dorsally between the anterior end of the nasal and the alary process of the premaxillary. The bone is extremely small and is obscured from view early in development by growth of adjacent bones; thus, little is known about it.

Premaxillary.—The premaxillary appears early, as a small bone of the same form found in the adult. Besides over-all increase in size, two changes are noticeable. The first of these is the development of palatine processes on the posterior edge of the premaxillary. The second change, the more subtle and at the same time the more striking change, is the apparent forward rotation of the premaxillary. In early post-metamorphic specimens, the premaxillary lies in a position common to many anurans, wherein the alary process is slightly convex anteriorly and forms approximately a ninety-degree angle with the parietal plane of the skull. In subsequent post-metamorphic stages the premaxillary rotates so that the alary process projects anteriorly in association with the developing prenasal. In the adult frog the alary process lies within the prenasal. The premaxillary is not involved in integumentary-cranial co-ossification.

Maxillary.—Early changes in the maxillary involve the lengthening of the bone anteriorly and posteriorly. The bone extends forward, anterior to the level of the premaxillary, and posteriorly, to lie lateral to the developing quadratojugal. Soon after Post-metamorphic Stage 5 the maxillary fuses with the quadratojugal. Fusion commences at the posterior extremity of the maxillary and progresses anteriorly in the area of overlap between the maxillary and quadratojugal. A second early center of ossification lies in the anterior part of the maxillary and produces the pars facialis of the maxillary which articulates with the nasal dorsolaterally. Integumentary-cranial co-ossification appears after Post-metamorphic Stage 5 on the dorsum of the maxillary at the level of the articulation of the developing pterygoid and maxillary. Co-ossification progresses anteriorly, covering the pars facialis and the remaining dorsal surface. A rapid proliferation of bone along the dorsolateral margin of the maxillary results in the heavy, spinose maxillary flange characteristic of the adult frog.

Squamosal.—The ventral arm of the squamosal develops first. By Post-metamorphic Stage 1 it is attached to the quadratojugal ventrally. Subsequent areas of ossification are centered dorsally on the squamosal. The posterior arm increases in length first, followed by the anterior arm growing toward the maxillary anteroventrally. At the same time, bone proliferates dorsomedially so that the squamosal ultimately articulates with the frontoparietal dorsal to the prootic. Integumentary-cranial co-ossification commences in the latter region initially, and then spreads along the developing anterior arm.

Parasphenoid.—The parasphenoid appears early as a thin plate of ossification located centrally on the venter of the skull. Ossification seems to progress at an equal rate in all directions. The anterior end is completed first, followed by the lateral wings and the posterior part underlying the exoccipital and prootic. Apparently the odontoids develop at a late stage in the development of the skull.

Pterygoid.—The pterygoid develops rather slowly. Proximal parts of the bone appear first and the principal areas of early ossification involve the anterior and posterior rami; the medial ramus is the last part of the pterygoid to ossify, and never establishes contact with the prootic.

Angulosplenic.—The angulosplenic arises on the posteromedial part of Meckel's cartilage and grows both anteriorly and posteriorly. In later development the posterior parts of the angulosplenic and dentary fuse. The anterior part of the angulosplenic remains separated from the dentary and mentomeckelian by Meckel's cartilage.

Dentary.—The dentary appears anterior and lateral to Meckel's cartilage. A small proliferation of bone unites the dentary to the developing mentomeckelian. The greatest amount of ossification takes place posteriorly to lengthen the dentary and eventually unite it to the angulosplenic.

Quadratojugal.—The quadratojugal develops in association with the quadrate cartilage. It first appears around the cartilage and then ossifies anteriorly and extends along the medial surface of the maxillary for a short distance. The quadratojugal is not involved in integumentary-cranial co-ossification because the maxillary completely covers external parts of the bone.

Palatine.—Development of the palatine is foreshortened. It arises as a small sliver of bone oriented perpendicularly to the maxillary. Subsequent ossification widens the palatine in an anterior-posterior direction. The palatine remains very small and unattached to either the sphenethmoid or maxillary.

Prevomer.—The prevomer develops slowly. In early stages it consists of four radiating pieces of bone located medial to the internal nares. Later, the central part of the bone ossifies and extremities of the bone lengthen, so that in an adult specimen the prevomer is in contact with the premaxillary anteriorly and forms the anterior and part of the posterior margin of the internal nares. Prevomerine dentition does not appear until Post-metamorphic Stage 2, after the development of maxillary and premaxillary dentition.

Prenasal.—The rudimentary prenasal (Fig. 32a) is a small triangular piece of bone which lies anterior to the alary processes of the premaxillary. Proliferation of bone advances most rapidly in lateral areas (Fig. 32 b-e) and somewhat more slowly in a ventral direction. Integumentary-cranial co-ossification is well advanced by Post-metamorphic Stage 3 and is centrally located on the prenasal. Co-ossification advances rapidly to develop anteriorly projecting spines in a manner similar to that describing the development of the maxillary flange. However, growth of the prenasal relative to that of the maxillary flange is more prolonged and rapid. As the prenasal extends anteriorly, one must assume that a secondary resorption of the bone is taking place internally to form the internal prenasal cavities which accommodate the alary processes of the premaxillary as described for the adult frog. The ventral part of the prenasal is not involved in co-ossification. The prenasal expands until it is

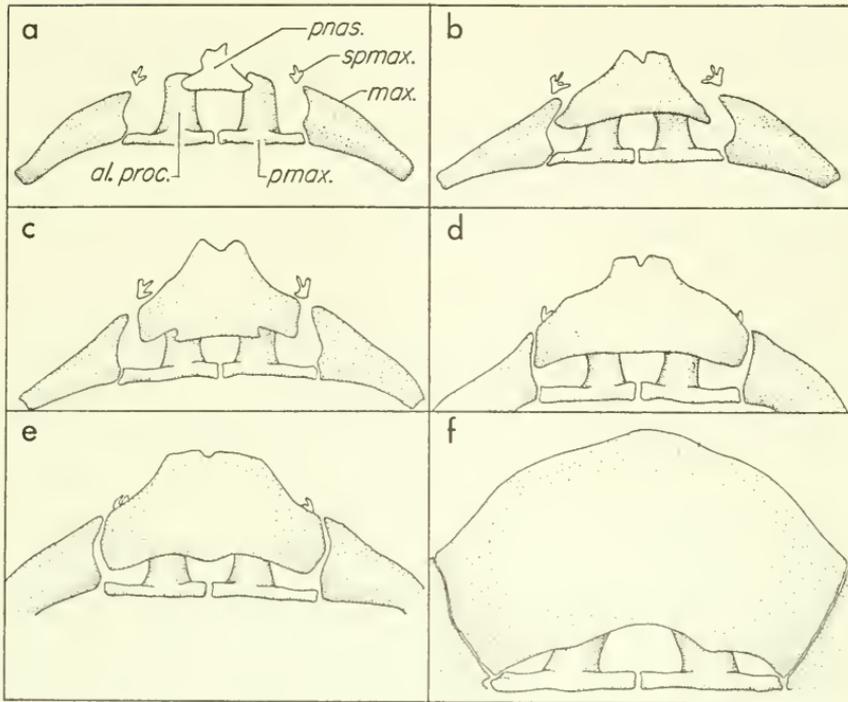


FIG. 32. Development of the prenasal bone in *Triprion petasatus*: (a) young (KU 92637), snout-vent length 15.5 mm. $\times 13$; (b) young (KU 92635), snout-vent length 16.9 mm. $\times 13$; (c) young (KU 92636), snout-vent length 17.5 mm. $\times 13$; (d) young (KU 92634), snout-vent length 19.3 mm. $\times 13$; (e) young (KU 92632), snout-vent length 20.3 mm. $\times 13$; (f) young adult (KU 71744), snout-vent length 50.9 mm. $\times 8$. Abbreviations: *al. proc.*, alary process of premaxillary; *max.*, maxillary; *pmax.*, premaxillary; *pnas.*, prenasal; *spmax.*, septomaxillary.

narrowly separated from the premaxillary posteroventrally and in very close association with the maxillary laterally.

Dermal Sphenethmoid.—The dermal sphenethmoid is first visible as a delicate plate of ossification between the nasals and frontoparietals, overlying and discrete from the developing ossification of the endochondral sphenethmoid. The dermal sphenethmoid is initially ossified in the dense connective tissue layer of the lower dermis of the skin overlying the endochondral sphenethmoid. Subsequent ossification of the endochondral sphenethmoid unites it to the dermal sphenethmoid, and co-ossification of the latter results in the characteristically sculptured surface of the adult bone.

The Cartilage Bones

Exoccipital.—The rudiment of the exoccipital probably appears between Larval Stages 43 and 45 since the exoccipital is well-formed by Post-metamorphic Stage 1. Subsequent bone proliferation closes the occipital arch and perichondral ossification appears in the basal plate and tectum synoticum. The exoccipital is not involved in integumentary-cranial co-ossification.

Mentomeckelian.—The mentomeckelian ossifies very early. The anterior part of the cartilage is replaced by bone initially and is fused with the adjacent dentary. Bone proliferation progresses posteriorly. The mentomeckelian remains separated from the angulosplenic by Meckel's cartilage.

Columella.—Bone first appears distally in the columella and ossification advances proximally.

Prootic.—The prootic is the last of the cranial bones to appear. It arises at the posterior border of the prootic foramen; ossification progresses over the otic capsule.

COMPARATIVE DEVELOPMENT OF THE OSTEOCRANIUM

Comparison of the development of the osteocrania in anurans is difficult due to the lack of information about most species. The most comprehensive study on osteocranial development is that by Erdmann (1933) on *Rana temporaria*. Incomplete observations are available for *Eleutherodactylus nubicola* (Lynn, 1942), *Pseudacris triseriata triseriata* (Stokely and List, 1954), *Hyla septentrionalis* (Trueb, 1966) and *Smilisca baudini* (Duellman and Trueb, 1966). By contrast, there is a relative abundance of descriptive material available on the anuran chondrocranium (reviewed by de Beer, 1937).

The disproportionate amounts of information available on chondro- and osteocranial anuran development doubtlessly are a reflection of the difficulties encountered in post-metamorphic developmental studies. Anuran larvae are generally easily obtained and reared through desired developmental stages, whereas obtaining and rearing young frogs is appreciably more difficult. There are standardized larval stages whereby larvae can be categorized by degree of development without recourse to size or age. But once metamorphosis is reached there are no such criteria and thus no standards of comparison. Both size and age have been used as indices to post-metamorphic development. It has been shown previously (Trueb, 1966; and Duellman and Trueb, 1966) that size is an unreliable estimator of degree of development. Age, as utilized by Stokely and List (1954), is of value assuming one has a source of living specimens and adequate laboratory facilities.

Comparison of the appearance of cranial elements among *Smilisca baudini*, *Tripurion petasatus*, and *Hyla septentrionalis* is made in Figure 33. In view of the preceding discussion, it is obvious that the post-metamorphic stages designated in the figure are not strictly definable in precise terms as are the larval stages; in reality, the post-metamorphic stages simply represent conditions of progressive cranial development within each species. Thus there is only an approximate correlation between post-metamorphic stages of the different species. Consequently, the graph is most useful for observations on the sequence of bone development.

There seems to be little variation in the order of appearance of the cartilage bones. The exoccipital is the first cartilage-replacement bone to ossify; it appears in late larval stages in *Smilisca* and *Pseudacris* and in early post-metamorphic stages in *Tripurion* and *Hyla septentrionalis*. The exoccipital is followed by the mentomeckelian in each case; in *Tripurion* this bone appears at about the same time as the exoccipital, whereas in the other three genera it appears much later in post-metamorphic development, after most dermal elements have ossified. The columella, sphenethmoid, and prootic appear after the mento-

meckelian in rapid succession in *Triprion*. The sequence of ossification of these three structures is unknown in *Smilisca*. In *Hyla septentrionalis* the sphenethmoid and prootic precede the columella, whereas in *Pseudacris* the prootic precedes the sphenethmoid and columella.

The sequence of ossification of dermal bones is less well ordered and somewhat more complicated. In each of the four genera, the frontoparietal is among the first bones to appear during larval stages. In *Smilisca* the frontoparietal, septomaxillary and parasphenoid (all present in Larval Stage 40), are followed by the premaxillary, maxillary, dentary, squamosal, angulosplenic, and the maxillary and premaxillary dentition. These bones, as a group, are all present in Larval Stage 44. By contrast, only one to three dermal bones appear before metamorphosis in the other three genera. In *Triprion* the frontoparietal is followed by the nasal, which does not appear until early post-metamorphic stages in *Pseudacris*, *Smilisca*, and *Hyla septentrionalis*. In *H. septentrionalis* the frontoparietal and septomaxillary ossify during advanced larval stages and in *Pseudacris* the frontoparietal, premaxillary, and "nasal cartilage (calcification)" (? = septomaxillary) appear before metamorphosis.

There are few post-metamorphic cranial additions in *Smilisca*. The nasal, pterygoid, and prevomerine dentition are followed by ossification of the prevomer, quadratojugal, and palatine. This pattern contrasts sharply with the remaining three genera in which most dermal bones ossify during metamorphosis or early post-metamorphic stages. In *Triprion* all dermal bones and dentition except the prevomer, prevomerine dentition, dermal sphenethmoid, and prenasal appear during metamorphosis. Development is somewhat less rapid in *Hyla septentrionalis*. Most bones appear during metamorphosis except the palatine, and the quadratojugal and prevomerine dentition; the latter structures ossify subsequent to the appearance of the palatine. The pattern is similar in *Pseudacris*; however, the majority of bones appearing early are followed by the quadratojugal first and then the palatine and parasphenoid.

Some interesting deviations in the sequence of ossification exist among dermal bones of these four genera. The prevomer appears during or shortly after metamorphosis in all genera except *Smilisca* in which it is one of the last bones to ossify. The prevomer and prevomerine dentition appear at the same time in *Triprion*. In *Smilisca* prevomerine dentition appears before complete ossification of the bone, and by contrast the prevomer is well ossified in *Hyla septentrionalis* before the appearance of its dentition. The parasphenoid is among the earliest bones to ossify in *Smilisca*, *Triprion*, and *Hyla septentrionalis*, but in *Pseudacris* it is one of the last. The quadratojugal appears late in development in all genera except *Triprion*.

The sequences of ossification in these four genera compare favorably with the pattern described for *Rana temporaria* with two exceptions. The prootic appears before the mentomeckelian, and the nasal appears quite later in development of *Rana*. The pattern of development of *Rana* more closely resembles that of *Pseudacris*, *Triprion*, and *Hyla septentrionalis* than *Smilisca*, in that only the parasphenoid, frontoparietal, premaxillary, and exoccipital appear before metamorphosis. The meager data available for *Eleutherodactylus nubicola* suggest that it is quite different from the preceding genera discussed. If hatching in *Eleutherodactylus* is considered to be more or less equivalent to metamorphosis in other anurans, then *E. nubicola* is similar to *Smilisca* in the

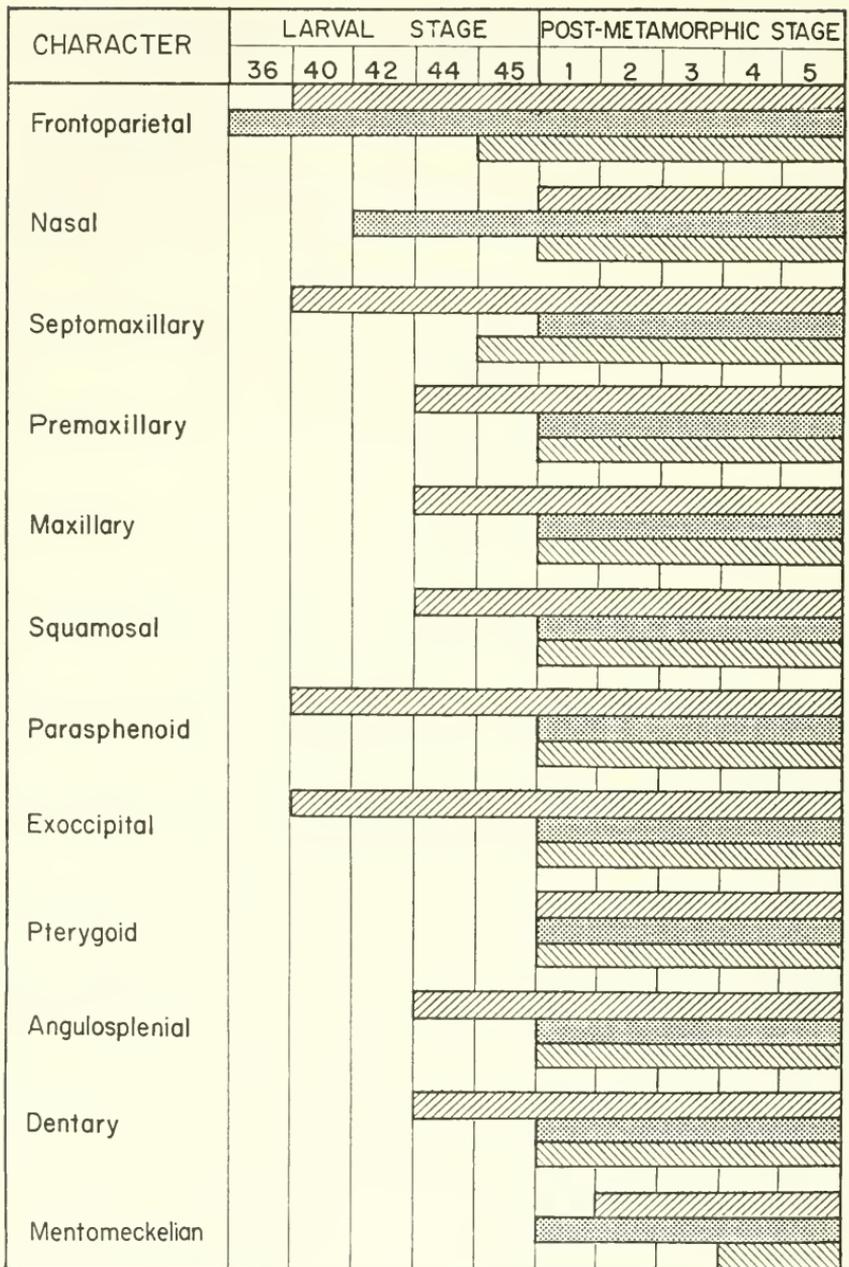


FIG. 33, first segment. The order of occurrence of cranial ossifications in the skulls of three hylid frogs. In each group of three bars, the uppermost bar (cross-hatching) represents *Smilisca baudini*, the middle bar (dots), *Tripriorion petasatus*, and the lower bar (cross-hatching), *Hyla septentrionalis*.

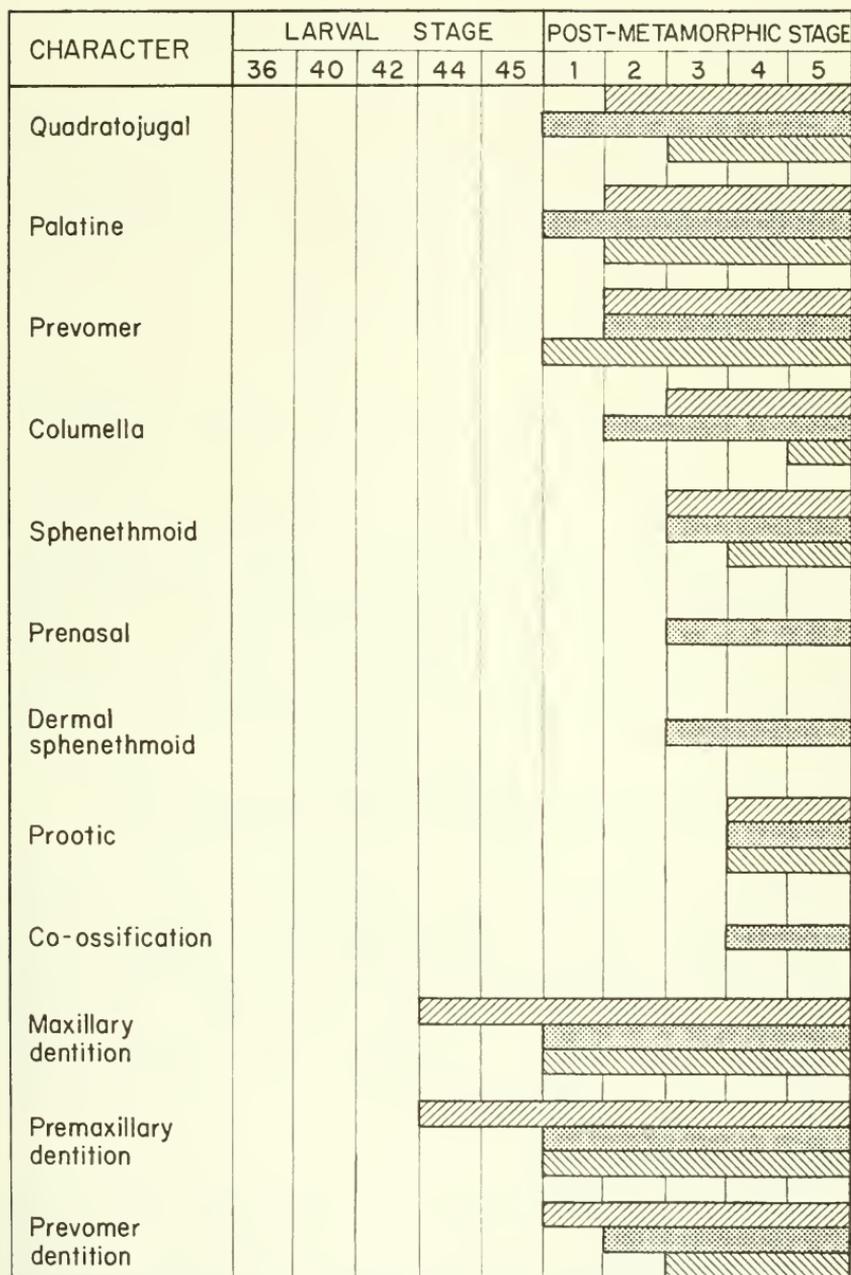


FIG. 33, second segment. Legend on facing page.

early larval development of dermal bones. However, it differs from *Smilisca* in the appearance of the angulosphenial, squamosal, and parasphenoid before the premaxillary, dentary, and frontoparietal, respectively.

Obviously, there is a great deal more flexibility in the development of dermal cranial elements as compared with cartilage bones. Moreover, it is interesting to note that the dermal elements which appear the latest in development in the hylid genera discussed are those structures which are most often reduced or absent among hylids. For example, the pterygoid often lacks bony articulations with the articular region posteriorly and the prootic medially. I know of no case in which the prevomer has been lost, but it is not unusual for the bone to lack teeth. The palatine is reduced in some frogs, notably in *Tripriion*. The quadratojugal is probably the most common cranial structure to be reduced or totally lost among hylids.

As one would expect, addition of the dermal sphenethmoid to the crania of *Hyla septentrionalis* and *Tripriion* occurs following the initial ossification of all other dermal bones. The prenasal appears in *Tripriion* with the dermal sphenethmoid. Subsequent to the development of all dermal bones, integumentary-cranial co-ossification commences on their surfaces. The development of co-ossification generally corresponds to original centers of ossification and follows the pattern of proliferation of dermal bone. The process of co-ossification is the same in *Tripriion* as it is in *Hyla septentrionalis*, which has been described by Trueb (1966). Co-ossification starts relatively earlier in *Tripriion* than in *H. septentrionalis*, and co-ossification together with the expansive distal proliferation of dermal bones creates the highly contoured skull characteristic of *Tripriion*. This sequence of events suggests that the bizarre cranial modifications of *Tripriion*, and probably the other casque-headed hylids, are evolutionarily recent specializations, rather than primitive characters.

THE OCCURRENCE OF THE CASQUE-HEADED CO-OSSIFIED CRANIUM WITHIN THE FAMILY HYLIDAE

The occurrence of integumentary-cranial co-ossification and/or the development of a casque is widespread in the family Hylidae. One or both conditions are characteristic of the following genera: *Amphignathodon*, *Anotheca*, *Aparasphenodon*, *Corythomantis*, *Diaglena*, *Hemiphractus*, *Nyctimantis*, *Osteocephalus*, *Pternohyla*, *Tetrapriion*, *Trachycephalus*, and *Tripriion*. Also included are some species of *Hyla* (*brunnea*, *dominicensis*, *fimbrimembra*, *lichenata*, *miliaria*, and *septentrionalis*) and *Gastrotheca* (*weinlandi*, *fulvorufa*, *nicefori*, and *ovifera*).

Members of the genus *Hemiphractus* are characterized by extremely bizarre skulls which are heavily casqued. The skin of the skull is not co-ossified with the underlying bone; thus, the osteology of this group is not pertinent to the problem at hand. In fact, the cranium of *Hemipharctus* is unlike that of any other hylid; perhaps further study will show that the frogs in this genus represent an early phyletic divergence from other hylids.

The skulls of two species of fringe-limbed hylids (*Hyla fimbriembra* and *H. miliaria*) seem to be co-ossified in preserved specimens. Examination of a skull of *Hyla miliaria* reveals that the cranium of this species is not co-ossified. Radiographs of *Hyla fimbriembra* show the presence of numerous osteoderms; these are characteristic of adults of both *H. miliaria* and *H. fimbriembra*. Their presence renders the skin of the cranium immovable and thus simulates the co-ossified condition. It is probable that osteoderms represent one of the first adaptive steps in the evolution of a co-ossified cranium. The fringe-limbed hylids are represented by so few specimens that sufficient material is not available to pursue studies of the cranium.

Anotheca, *Nyctimantis*, and *Amphignathodon*, *Gastrotheca*, and possibly *Flectonotus* seem to form a natural group of genera within the Hylidae. This group displays similarity in the external morphology of its members, their life histories, and their tendency towards arboreal habits. The skulls are casqued and co-ossified in all of these frogs, except some species of *Gastrotheca*. It is possible that these comprise a group in which the casque-headed, co-ossified condition has been derived independently. However, specimens necessary to the evolution of this hypothesis were not available to the present study. The remaining genera of casque-headed, co-ossified hylids are treated in this paper.

My studies on the cranial morphology provided evidence which necessitates certain modifications in the existing generic classification of the casque-headed, co-ossified hylids. In the following account of cranial osteology, data are presented which support the generic synopsis given below. The genera are listed alphabetically, and generic synonyms are given chronologically. In the lists of included species, synonyms are given in brackets.

Synopsis of the Genera

Aparasphenodon Miranda-Ribeiro

Aparasphenodon Miranda-Ribeiro, 1920:86 [Type species, *Aparasphenodon brunoi* Miranda-Ribeiro, 1920:87, by monotypy].

Diagnosis.—Skull longer than broad; snout, in dorsal view, narrow, acuminate; canthal ridges distinct, anteriorly concave; surface configuration of dermal roofing bones consisting of reticulate network of ridges in low relief and prominent patterns of radial ridges; prenasal present; alary processes of premaxillaries concealed by prenasal, anteriorly inclined; internasal absent; palatines present; dermal sphenethmoid present; vocal sac single, median, subgular.

Range.—Coastal region of southeastern Brazil and (?) upper Orinoco Basin of Venezuela.

Included Species.—*A. brunoi* Miranda-Ribeiro, 1920 [*Corythomantis adspersa* Lutz, 1926; *Corythomantis apicalis* Miranda-Ribeiro, 1920], (?) *Corythomantis venezolana* Mertens, 1950.

Remarks.—Carvalho (1941) pointed out that *Corythomantis adspersa* and *C. apicalis* are names based on juveniles of *Aparasphenodon brunoi*. Mertens (1950) named *Corythomantis venezolana* from San Fernando de Atabapo, Venezuela. I have examined photographs and radiographs of the unique holotype. Although it is not possible to discern the exact nature of the cranial elements from radiographs, a prenasal bone and palatines seem to be present (both absent in *Corythomantis*). The canthal ridges are distinct (indistinct in *Corythomantis*) and anteriorly concave. Furthermore, the shape of the snout and the configuration of the dermal roofing bones are reminiscent of those of *Aparasphenodon brunoi*.

Corythomantis Boulenger

Corythomantis Boulenger, 1896:405 [Type species, *Corythomantis greeningi* Boulenger, 1896:405, by monotypy].

Diagnosis.—Skull longer than broad; snout in dorsal view moderately narrow but rounded; canthal ridges indistinct; surface configuration of dermal roofing bones consisting of reticulate network of ridges in low relief; prenasal absent; alary processes of premaxillaries concealed by nasals, anteriorly inclined; internasal absent; palatines absent; dermal sphenethmoid present; vocal sac single, median, subgular.

Range.—Xeric region of northeastern Brazil.

Included Species.—*C. greeningi* Boulenger, 1896 [*C. schubarti*, Miranda-Ribeiro, 1937].

Remarks.—Carvalho (1941) placed *C. schubarti* in the synonymy of *C. greeningi*.

Osteocephalus Steindachner

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

Diagnosis.—Skull broader than long; snout in dorsal view broad, truncate; canthal ridges distinct, not anteriorly concave; surface configuration of dermal roofing bones consisting of poorly-developed ridges; prenasal absent; alary processes of premaxillaries exposed, not co-ossified, not anteriorly inclined; internasal absent; palatines present; dermal sphenethmoid present, poorly developed; vocal sacs paired, lateral, behind angles of jaws.

Range.—Amazon Basin.

Included Species.—*O. lepieuri* (Duméril and Bibron, 1841) [*O. planiceps* Cope, 1874]; *O. taurinus* Steindachner, 1862 [*O. flavolineatus* Steindachner, 1862].

Remarks.—Goin (1961) noted that eight or ten species probably are included in this genus. Until they have been adequately studied, I hesitate to include any species in the genus other than those that I have examined.

Pternohyla Boulenger

Pternohyla Boulenger, 1882:326 [Type species, *Pternohyla fodiens* Boulenger, 1882:326, by monotypy].

Diagnosis.—Skull broader than long; snout in dorsal view broadly rounded; canthal ridges indistinct; surface configuration of dermal roofing bones consisting of network of prominent bony spines; prenasal absent; alary processes of premaxillaries exposed, co-ossified or not, not anteriorly inclined; internasal present (*P. fodiens*) or absent (*P. dentata*); palatines present; dermal sphenethmoid absent; vocal sac bilobed, subgular.

Range.—Extreme southwestern Arizona in the United States, southward at low and moderate elevations to Michoacán, México.

Included Species.—*P. dentata* Smith, 1957; *P. fodiens* Boulenger, 1882 [*Hyla rudis* Mocquard, 1899].

Remarks.—Kellogg (1932) showed that the type of *Hyla rudis* Mocquard is a juvenile of *Pternohyla fodiens*.

Trachycephalus Tschudi

Trachycephalus Tschudi, 1838:74 [Type species, *Trachycephalus nigromaculatus* Tschudi, 1838:74, by monotypy].

Tetraprion Stejneger and Test, 1891:167 [Type species, *Tetraprion jordani* Stejneger and Test, 1891:167, by original designation].

Diagnosis.—Skull as long as broad or slightly longer than broad; snout in dorsal view rounded with medial notch; canthal ridges distinct, not anteriorly concave; surface configuration and dermal roofing bones consisting of reticulate network of ridges and patterns of radial ridges in moderate relief; prenasal absent; alary processes of premaxillaries exposed, expanded, co-ossified, not anteriorly inclined; internasal absent; palatines present; dermal sphenethmoid present; vocal sacs paired, lateral, behind angles of jaws.

Range.—Northeastern Brazil southward to eastern Argentina in the La Plata Delta; Pacific slopes of Colombia and Ecuador.

Included Species.—*T. atlas* Bokermann, 1966; *T. jordani* (Stejneger and Test, 1891); *T. nigromaculatus* Tschudi, 1838 [*T. geographicus* Duméril and Bibron, 1841; *T. marmoratus* Steindachner, 1864; *T. occipitalis* Fitzinger, 1864; *Hyla angustifrons* Werner, 1893]; *T. siemersi* (Mertens, 1937).

Remarks.—In the original description of *Tetraprion jordani* Stejneger and Test (1891:168) assigned the frog generic status because “. . . it differs from all known *Hylidae* in possessing teeth on the palatines.” Subsequent authors (Rivero, 1961; Peters, 1955; Smith, 1957; and Myers, 1942) discussed the generic relationships but unaccountably overlooked the striking resemblance of *Tetraprion* to *Trachycephalus nigromaculatus* Tschudi, 1838. Both frogs have palatine odontoids; those of *Trachycephalus* are better developed than those of *Tetraprion*. *Trachycephalus* lacks parasphenoid odontoids, but bears a prominent ventral ridge on the parasphenoid. The basic structure of the skulls of both genera is nearly identical. In both frogs the medial rami of the pterygoids fail to articulate with the prootics, and the squamosal arches are incomplete. The

alary processes of the premaxillaries are expanded and co-ossified. Because the processes do not fuse medially, there appears to be a medial premaxillary "notch." The general appearance of the dorsal aspects of the skulls is similar. *Tetraprion* has carried the process of co-ossification and expansion of dermal bones somewhat further than *Trachycephalus*; thus the maxillaries and premaxillaries are more extensive and heavily sculptured, and the frontoparietals terminate posteriorly in a moderate, upturned occipital crest. Both frogs share the unusual character of having paired, lateral vocal sacs located behind the angles of the jaws. In view of the foregoing evidence it seems only reasonable to place *Tetraprion* in the generic synonymy of *Trachycephalus*.

Tripriion Cope

Pharyngodon Cope, 1865:193 [Type species, *Pharyngodon petasatus* Cope, 1865:193, by monotypy; preoccupied by *Pharyngodon* Diesing, 1860 (Nemathelminthes)].

Tripriion Cope, 1866:127 [Substitute name for *Pharyngodon* Cope, 1865, preoccupied].

Diaglana Cope, 1887:12 [Type species, *Tripriion spatulatus* Günther, 1882:279, by original designation].

Diagnosis.—Skull longer than broad; snout in dorsal view moderately acuminate; canthal ridges distinct anteriorly concave; surface configuration of dermal roofing bones consisting of extremely fine reticulate network of ridges and patterns of radial ridges; prenasal present; alary processes of premaxillaries concealed by prenasal, anteriorly inclined; internasal absent; palatines present, reduced; dermal sphenethmoid present (*T. petasatus*) or absent (*T. spatulatus*); vocal sac bilobed (*T. petasatus*) or single (*T. spatulatus*), subgular.

Range.—Disjunct; Pacific lowlands from Sinaloa to Oaxaca, México; Yucatan Peninsula of México, and northern Guatemala.

Included Species.—*T. petasatus* Cope, 1865; *T. spatulatus* Günther, 1882 [*Diaglana reticulata* Taylor, 1942].

Remarks.—Cope (1887:12) proposed the generic name *Diaglana* for *Tripriion spatulatus* Günther, 1882, and diagnosed *Diaglana* as differing from *Tripriion* (*T. petasatus* sole included species) ". . . in having a transverse instead of vertical pupil." Taylor (1942) named *Diaglana reticulata*, but Duellman (1968) provided evidence that *D. reticulata* and *D. spatulata* are conspecific. The skulls of *Tripriion* and *Diaglana* are very similar in general appearance. The skull of *Tripriion* is more depressed centrally than is that of *Diaglana*; the canthal ridges terminate posterior to the external nares, whereas they terminate anterior to the external nares in *Diaglana*; the prenasal is dorsally concave in *Tripriion* and nearly flat in *Diaglana* and *Tripriion* has a dermal sphenethmoid which is absent in *Diaglana*. In all other respects, both internal and external, the skulls of the two genera are nearly identical. Duellman and Klaas (1964) demonstrated that the pupil of *Tripriion petasatus* is horizontally elliptical. In view of the latter information, and the morphological similarities of the two frogs, *Diaglana* should be a generic synonym of *Tripriion*. The geographic complementarity of their ranges is in agreement with this conclusion.

Cranial Morphology of *Hyla septentrionalis*

The skull of *Hyla septentrionalis* is broader than long (Pl. 4a, b); the snout in dorsal view is slightly truncate. The dermal roofing bones are moderately to heavily casqued and partly co-ossified. The dorsal surfaces of the dermal bones are rugose and in some places fused with the overlying skin. *Hyla septentrionalis* lacks a prenasal and internasal. There are no labial flanges nor is there an occipital crest. A dermal sphenethmoid is present. The frontoparietals bear a broad supraorbital flange which is not conspicuously upturned; the frontoparietal usually does not cover the entire crista parotica posterolaterally. The prevomerine teeth are straight (see Table 1) or slightly curved (see Table 1). The anterior arm of the squamosal usually does not articulate with the maxillary. The vocal sac is single, median and subgular. The external morphology of the skull of *Hyla septentrionalis* has been described (Trueb, 1966); the following account is concerned only with the internal cranial anatomy.

The Olfactory Region.—The anterior end of the septum nasi appears between the alary processes of the premaxillaries (Fig. 34). The inferior prenasal cartilage lies along the posterior surface of the alary process of the premaxillary (Fig. 34). The superior prenasal cartilage is massive and closely associated with the alary cartilage. The anterior end of the superior prenasal cartilage lies adjacent to the posterodorsal tip of the alary process of the premaxillary and is posterolaterally connected to the alary cartilage. At successive levels posterior to the level of the premaxillary, the solum nasi appears, the foramina for the ramus externus narius and ramus medius narius enter the solum, the alary cartilage fuses with the septum nasi, and the anterior end of the cavum medium appears. The anterior end of the cavum inferius lies posteroventral to the cavum medium and anterior to the anterior level of the cavum principale (Fig. 35). The inferior prenasal cartilage fuses with the solum nasi at the level of the anterior margin of the external naris. The tectum nasi is well developed and a crista subnasalis is present. The first ossification of the nasal region is perichondral ossification of the septum nasi at the mid-level of the olfactory eminence. In posterior sections, the ventral part of the solum ossifies first. At the level of the anterior margin of the internal naris, the dorsal part of the septum begins to ossify. The septum and solum nasi are completely ossified anterior to the posterior margins of the internal nares, and are synosteotically united with the sphenethmoid posteriorly.

The anterior end of the septomaxillary is broad and thin and lies dorsolateral to the cavum medium (Fig. 36). The septomaxillary expands ventrolaterally around the lateral end of the cavum medium. The ventrolateral flange of the septomaxillary bifurcates from the broad anterior ramus and expands posteromedially ventral to the cavum medium. In subsequent sections, the anterodorsal ramus of the septomaxillary thickens and then bifurcates into a medial ramus associated with the lamina superior and a lateral ramus. Posterior to the bifurcation, the medial ramus diminishes in size, whereas the lateral ramus develops a high dorsal crest and fuses with the ventral ramus posterior to the divergence of the nasolacrimal duct from the cavum medium.

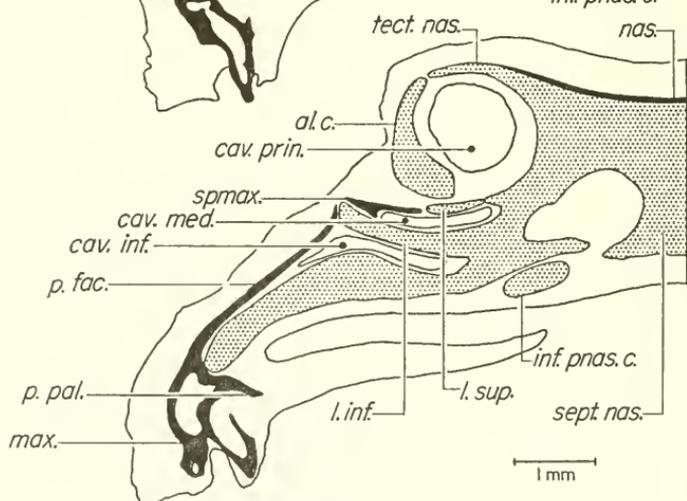
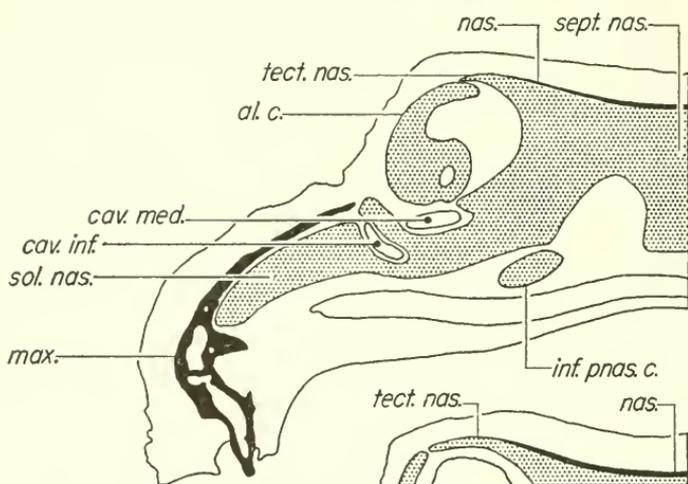
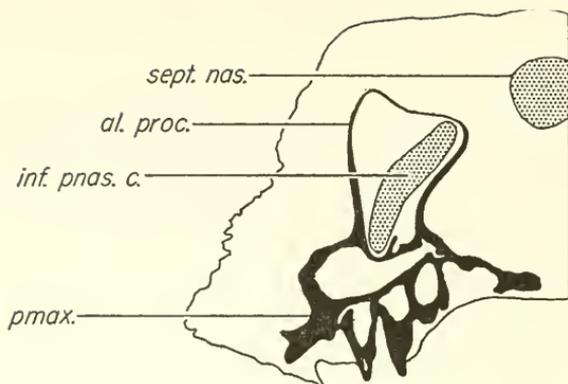
The Sphenethmoid and Orbital Region.—The sphenethmoid is in synosteotic continuity with the septum nasi anteriorly. At the level of the orbitonasal foramen (Fig. 37), the sphenethmoid is entirely bony except for the distal tip of

TABLE 1.—Geographical and Morphological Characters of Casque-headed, Co-ossified Hylids and Related Forms. Symbols and Abbreviations: (—), absent; (+), present; (//), not concave anteriorly; () , concave anteriorly; (R), reduced; (I) Type I septomaxillary; (II) Type II septomaxillary; exp., expanded; mod., moderate.

SPECIES	DISTRIBUTION	Vocal Sac	Internasal	Prenasal	Dermal sphenethmoid	Prevermerine teeth	Palatine	Septomaxillary	Bifurcate cavum principale	Anterior acoustic foramen	Posterior acoustic foramen	Quadratojugal	Labial flange	Canthal ridges
<i>Hyla septentrionalis</i>	Cuba, Bahamas, Isle of Pines, Florida.	single, median.	—	—	+))	+	II	—	+	+	+	—	/
<i>Hyla brunnea</i>	Jamaica	single, median.	—	—	+	C	+	(?)	—	+	+	+	—	/
<i>Hyla dominicensis</i>	Hispaniola	single, median.	—	—	+)	+	(?)	—	+	+	+	—	/
<i>Phrynohyas ventulosa</i>	Pacific and Atlantic lowlands of México to Argentina.	paired, lateral.	—	—	—))	+	II	—	+	+	+	—	—
<i>Osteocephalus taurinus</i>	Wet forests of interior and northern South America.	paired, lateral.	—	—	+	∩	+	II	—	+	+	+	—	/
<i>Trachycephalus nigromaculatus</i>	Southeastern Brazil.	paired, lateral.	—	—	+))	+	II	—	+	+	+	mod.	/
<i>Trachycephalus atlas</i>	Bahia, Brazil.	paired, lateral.	—	—	+))	+	(?)	—	+	+	+	mod.	/
<i>Trachycephalus jordani</i>	Pacific slopes of Colombia and Ecuador.	paired, lateral.	—	—	+))	+	II	—	+	+	+	mod.	/

TABLE 1.—Concluded

SPECIES	DISTRIBUTION	Vocal Sac	Internasal	Prenasal	Dermal sphenethmoid	Prevomerine teeth	Palatine	Septomaxillary	Bifurcate cavum principale	Anterior acoustic foramen	Posterior acoustic foramen	Quadratofugal	Labial flange	Canthal ridges
<i>Corythomantis greeningi</i>	Caatinga of Brazil.	single, median.	-	-	+	<	-	II	-	+	+	R	mod.	-
<i>Aparasphenodon brunoi</i>	Restinga of south-eastern Brazil.	single, median.	-	+	+	∩	R	II	-	+	-	R	mod.	/
<i>Tripurion spatulatus</i>	Lowlands of western México.	single, median.	-	+	-	<	R	I	+	+	+	+	exp.	/
<i>Tripurion peltatus</i>	Yucatan Peninsula and northern Guatemala.	single, bilobed.	-	+	+	<	R	I	+	+	+	+	exp.	/
<i>Pternohyla dentata</i>	Lowlands and moderate elevations of western México.	single, bilobed.	+	-	-	<	+	I	+	+	+	+	mod.	-
<i>Pternohyla fodiens</i>	Río Santiago Basin of Mexican Plateau.	single, bilobed.	+	-	-	<	+	I	+	+	-	+	mod.	-
<i>Smilisca baudini</i>	Pacific and Atlantic lowlands of México to Costa Rica.	single, bilobed.	-	-	-	-	+	I	+	+	+	+	-	-



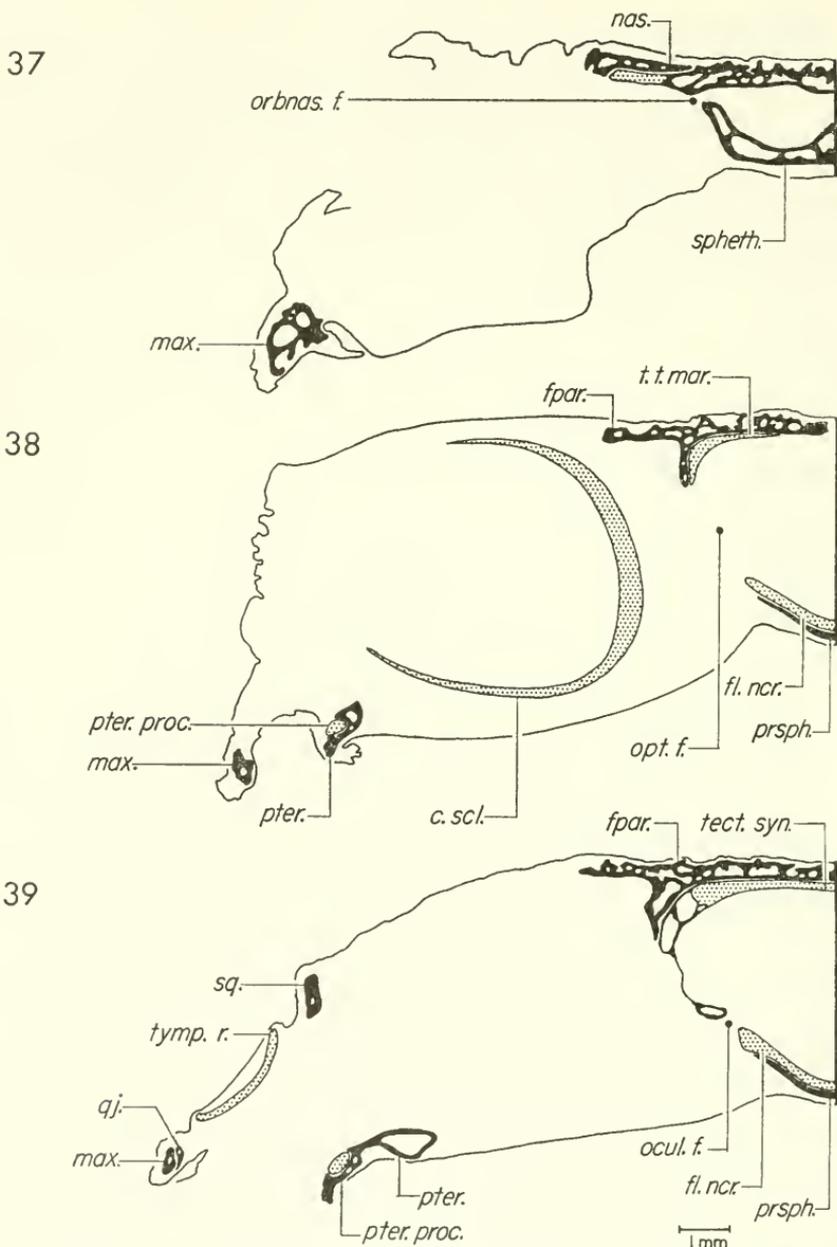
FIGS. 34-36. Transverse sections through the anterior end of the skull of *Hyla septentrionalis* (KU 89930): (34) level of alary process of premaxillary; (35) anterior level of cavum medium; (36) anterior levels of cavum principale and septomaxillary. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *cav. inf.*, cavum inferius; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *nas.*, nasal; *p. fac.*, pars facialis of maxillary; *p. pal.*, pars palatina of maxillary; *pmax.*, premaxillary; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spmax.*, septomaxillary; *tect. nas.*, tectum nasi.

the anterolateral wing, which is cartilaginous. In posterior sections, the cartilage expands into a broad supraorbital shelf which is detached from the bony parts of the sphenethmoid in the mid-part of the orbit. Posterior to the dermal sphenethmoid, the roof of the endochondral sphenethmoid splits to form the frontoparietal fontanelle ventral to the frontoparietals. Anteriorly, the margins of the fontanelle are bony. Cartilage appears laterally in the sphenethmoid in the posterior part of the orbit. In subsequent sections, bone disappears dorso-laterally and cartilage appears at the margins of the optic foramen. A short distance anterior to and at the level of, the optic foramen, the sphenethmoid is completely cartilaginous.

The bursa angularis oris is moderately well developed. It lies between the pterygoid and maxillary in the posterior part of the orbit. The anterior end of the bursa is a mass of lymphoid tissue, which is loosely encapsulated in connective tissue. A short, central lumen of small diameter precedes the simple, longitudinal aperture connecting the gland with the oral cavity; another small, central lumen appears near the end of the bursa.

The Otic and Occipital Regions.—The posterior margins of the optic foramen (Fig. 38) are formed in bone by the perichondral and dorsolateral endochondral ossification of the prootic, and the lamina perpendicularis of the frontoparietal. The trochlear nerve utilizes the optic foramen but is separated dorsally from the optic nerve by connective tissue. The oculomotor foramen (Fig. 39) lies just posterior and ventral to the optic foramen. The dorsal margin of the oculomotor foramen is bony, whereas the anteroventral edge is cartilaginous; posteroventrally, the margin is ossified. A thick bridge of bone separates the oculomotor foramen from the more posterior prootic foramen (Fig. 40). The margins of the prootic foramen are bony. Posteriorly, the anterior acoustic foramen (Fig. 41) lies in bone anteriorly and posteroventrally, and in cartilage posterodorsally. The anterior acoustic foramen is narrowly separated by cartilage and bone (perichondral ossification) from the posterior acoustic foramen (Fig. 42). The posterior acoustic foramen is bordered by bone on all but the anterior margin. The jugular foramen lies in bone a short distance posterior to the posterior acoustic foramen.

The most anterior part of the otic region is the pseudobasal process, the anterior end of which lies at the posterior level of the oculomotor foramen. In posterior sections, the pseudobasal process enlarges and expands medially (Fig. 40). At the anterior level of the prootic foramen, the otic process lies medially adjacent to the squamosal dorsolaterally. The otic process extends postero-ventrally, and fuses with the dorsolateral corner of the pseudobasal process. Posteriorly, the otic process loses its connection with the pseudobasal process and expands medially to fuse with the otic capsule and form the crista parotica (Fig. 41). The pseudobasal process fuses medially with the otic capsule at the posterior margin of the prootic foramen. Just posterior to the latter level, the cornu principalis of the hyale diverges posteroventrally from the ventro-lateral edge of the otic capsule. The pars externa plectri lies at the level of the anterior acoustic foramen. A short distance posterior the medial part of the pars media plectri appears, and is followed by the pars interna plectri (Fig. 42). The pars ascendens plectri and the distal part of the pars media plectri lie at the posterior margin of the anterior acoustic foramen. The mid-part of the pars media plectri and the posterior end of the pars externa plectri lie im-



FIGS. 37-39. Transverse sections through the skull of *Hyla septentrionalis* (KU 89930) at levels of the cranial nerve foramina: (37) level of orbitonasal foramen; (38) level of optic foramen; (39) level of oculomotor foramen. Abbreviations: *c. scl.*, cartilaginous sclera; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *nas.*, nasal; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *orbnas. f.*, orbitonasal foramen; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *spheth.*, sphenethmoid; *sq.*, squamosal; *t. t. mar.*, taenia tecti marginalis; *tect. syn.*, tectum synoticum, *tym. r.*, tympanic ring.

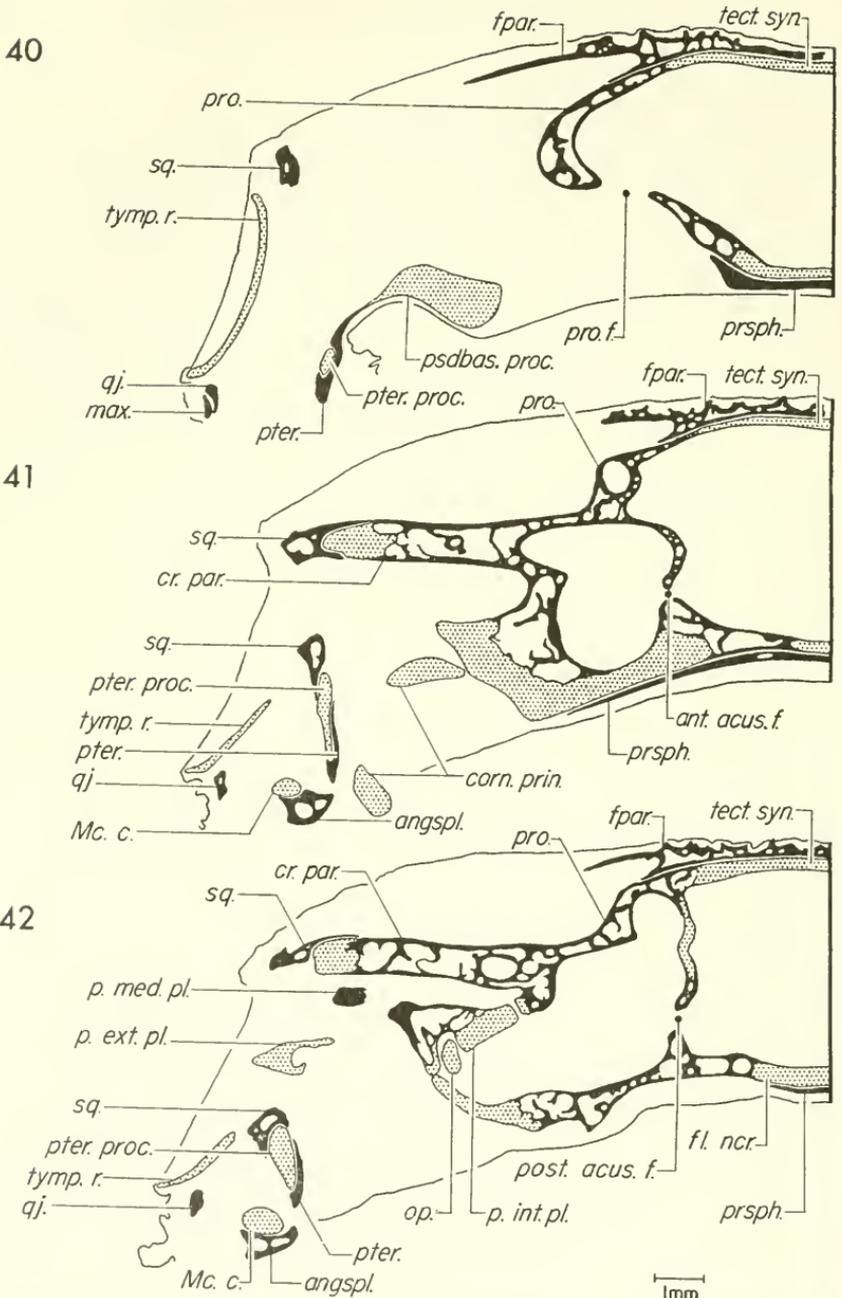
mediately posterior to the anterior acoustic foramen and terminates anterior to the posterior margin of the juglar foramen.

At the posterior level of the optic foramen, the prootic is ossified only laterally around the margins of the foramen. Dorsally, the tectum synoticum (Fig. 39) forms the posterior border of the frontoparietal fontanelle and the roof of the neurocranium. Ventrally, the floor of the neurocranium is cartilaginous. Posteriorly, ossification invades the cartilage of the prootic. At the anterior level of the prootic foramen, the tectum synoticum and the ventromedial part of the floor of the neurocranium are cartilaginous. Posteriorly, ossification invades the cartilage of the prootic. At the anterior level of the prootic foramen, the tectum synoticum and the ventromedial part of the floor of the neurocranium are cartilaginous. At the level of the anterior acoustic foramen posteriorly, the roof is cartilaginous. Ventrally, the cartilaginous floor of the neurocranium is restricted to a narrow medial strip which is flanked laterally by bone; laterally adjacent to the bone is cartilage which forms the lateral and ventrolateral parts of the otic capsule. Posteriorly, at the level of the jugular foramen, cartilage diminishes and is replaced by bone except laterally, dorsomedially and ventromedially. The pars externa plectri, pars interna plectri, pars ascendens plectri and operculum are cartilaginous. The distal tip of the crista parotica is cartilaginous. The pars media plectri is bony.

The Articular Region.—Anterior to the articular region, Meckel's cartilage lies dorsolateral to the angulosplenial bone. Posteriorly, the cartilage enlarges and moves into a position dorsomedial to the angulosplenial. The quadrate process first appears flanked by the ventral arm of the squamosal dorsally and the medial ramus of the pterygoid medially at the anterior level of the operculum. Slightly posterior, ossification invades the cartilage of the quadrate process. At approximately the mid-level of the operculum, the quadratojugal fuses with the ossification of the quadrate process. At the posterior level of the jugular foramen, the quadrate process loses its ossification; in subsequent sections the pterygoid and squamosal terminate.

Remarks.—There is considerable variation in the development of dermal roofing bones in *Hyla septentrionalis* (Pl. 4a, b). Typically, adult females are more heavily ossified than males. The most striking differences between adult males and females are the fusion of the anterior arm of the squamosal with the maxillary, and the articulation of the posterolateral corners of the frontoparietal with the squamosal in the females. Moreover, some large females bear palatine and parasphenoid odontoids which are not usually characteristic of males. The prevomerine dentigerous processes are slightly curved in some large females.

Hyla septentrionalis is a member of a group of large West Indian tree frogs composed of *Hyla vasta*, *H. brunnea*, *H. lichenata*, and *H. dominicensis*. *Hyla vasta* is one of the largest and is the most divergent osteologically; the skull is not casqued or co-ossified. However, the general shape and structure of the skull is similar to a young *Hyla septentrionalis* before extensive dermal modifications develop. The maxillary is robust and bears a large pars facialis. The nasals are moderately large and articulate firmly with the posterior process of the pars facialis of the maxillary. The sphenethmoid is well ossified. The frontoparietals do not converge medially; thus, a frontoparietal fontanelle is exposed dorsally. The squamosal is moderately weak; the anterior arm does not articulate with the maxillary. The pterygoid is robust and articulates firmly with the



FIGS. 40-42. Transverse sections through the skull of *Hyla septentrionalis* (KU 89930) at levels of cranial nerve foramina: (40) level of prootic foramen; (41) level of anterior acoustic foramen; (42) level of posterior acoustic foramen. Abbreviations: *angspl.*, angulosplenic; *ant. acus. f.*, anterior acoustic foramen; *corn. prin.*, cornu principalis; *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *op.*, operculum; *p. ext. pl.*, pars externa plectri; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *post. acus. f.*, posterior acoustic foramen; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *psdbas. proc.*, pseudobasal process; *qj.*, quadratojugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tym. r.*, tympanic ring.

prootic. The parasphenoid does not bear odontoids. Anteriorly, the palatines are moderately developed; they bear an inconspicuous and smooth posteroventral ridge. The prevomers are well developed; the posterior dentigerous part of the prevomer is massive and only slightly curved. (see Table 1).

Externally, the skull of *Hyla dominicensis* is almost indistinguishable from that of *Hyla septentrionalis*. The skull is heavily casqued and partly or wholly co-ossified. The dermal sphenethmoid is proportionally somewhat larger than the dermal sphenethmoid of *H. septentrionalis*; thus, the length of the medial convergence of the nasals anterior to the sphenethmoid is noticeably shorter in *H. dominicensis*. Posteriorly, the frontoparietals extend over, and curve posteroventrally, around the occipital region. The posterior arm of the squamosal is short and very poorly developed. Ventrally, *H. dominicensis* lacks the firm articulation of the medial branch of the pterygoid with the prootic, which is characteristic of *H. septentrionalis* also. Like *H. vasta*, *H. dominicensis* bears a smooth parasphenoid and palatine with smooth posteroventral ridges. The dentigerous process of the prevomers are less massive than those of *H. vasta* and about equal in development to those of *H. septentrionalis*; the dentigerous processes are slightly curved (see Table 1).

Hyla brunnea is a large frog, approaching *H. lichenata* in size. The skull has a well developed casque, is partly co-ossified, and is easily distinguished from those of *H. vasta*, *H. septentrionalis*, and *H. dominicensis* by the shape of the snout. In dorsal view the snout of *H. brunnea* is acuminate and protuberant, whereas the snouts of the other species are rounded or truncate. Osteologically, the shape of the snout in *H. brunnea* is due to the projection of the nasals anteriorly between the external nares. The nasals bear more distinct canthal ridges than in *H. septentrionalis*, *H. dominicensis*, and *H. vasta*; the condition of the canthal ridges accentuates the pointed shape of the snout. In lateral view, the alary processes of the premaxillary of *H. brunnea* are inclined slightly anteriorly, whereas in the other three species, the alary processes are vertical or inclined slightly posteriorly. The dermal sphenethmoid is proportionally slightly smaller than the dermal sphenethmoids of *H. septentrionalis*, and *H. dominicensis*. The frontoparietal is well developed. The frontoparietal extends posterolaterally to the posterior arm of the squamosal; posteriorly it extends over and curves posteroventrally around the occipital region as the frontoparietal does in *H. dominicensis*. The anterior arm of the squamosal does not articulate with the maxillary. The posterior arm of the squamosal is better developed than that of *H. dominicensis*, but not as well developed as that of *H. septentrionalis*. The ventral arm of the squamosal is robust. The pterygoid is robust; its medial arm articulates with the prootic. The parasphenoid bears small, inconspicuous odontoids and the palatine a conspicuous and smooth ventral ridge. The prevomers are large and well ossified. The dentigerous processes of the prevomers are strongly curved. (see Table 1).

There are no skeletal preparations of *Hyla lichenata* available for examination. Dunn (1926:123) suggested that *H. lichenata* is more closely related to *H. brunnea* than to *H. dominicensis* and *H. septentrionalis* because ". . . the Jamaican species [*Hyla lichenata*, *marianae*, and *wilderi*] all agree with *brunnea* in the prominent and terminal nostrils, which is the only essential feature differentiating the primitive Jamaican form from the primitive Hispaniolan *dominicensis*. The Hispaniolan species [*Hyla vasta*, *heilprini*, and *pulchrilineata*] agree with *dominicensis* in this feature." Dunn's statement "prominent and

terminal nostrils" is more satisfactorily interpreted by the structure of the snout and anterior end of the skull in *H. brunnea*. If the external shape of the snout of *H. lichenata* closely resembles that of *H. brunnea*, it seems logical to assume that structurally these two species are similar and that both probably differ similarly from *H. dominicensis*, *septentrionalis*, and *vasta*. *Hyla lichenata* is a larger frog than *H. brunnea*. The skull is heavily casqued and completely co-ossified. Thus as Dunn (1926:124) suggested, *H. lichenata* may be "an overgrown *brunnea*."

Cranial Morphology of *Osteocephalus taurinus*

The skull of *Osteocephalus taurinus* (Pl. 5a, b) is slightly broader than long, or as broad as long. The snout in dorsal view is moderately truncate. Most of the dorsal surfaces of the skull are rugose. The overlying skin is thin and characterized by a thin layer of dense connective tissue, the presence of which precludes the complete development of integumentary-cranial co-ossification. The development of rugosities on the surface of dermal bones and the presence of a poorly developed, dense, connective tissue layer overlying the bone suggest that the lower part of the connective tissue has been transformed into membranous bone. Thus, co-ossification is partial or incomplete in *Osteocephalus*, and the skin is freely movable on the surface of the head. *Osteocephalus* lacks a prenasal and internasal. There are no labial flanges or an occipital crest. A dermal sphenethmoid is present. The frontoparietals bear a small, upturned flange; the frontoparietal does not extend over the crista parotica posterolaterally. The prevomerine teeth are angled (see Table 1). The anterior arm of the squamosal extends less than one-half the distance to the maxillary. The vocal sacs are paired, lateral, and located behind the angles of the jaws.

The Olfactory Region.—The premaxillaries are narrowly separated medially by connective tissue. Laterally, the premaxillary is separated from the pars palatina and pars dentalis of the maxillary by an area of dense connective tissue. An extremely small and inconspicuous palatine process is present postero-medially on the premaxillary. The alary processes of the premaxillaries are widely separated medially. They are inclined posteriorly at approximately an 80-degree angle. The processes are straight and approximately two and one-half times as long as the depth of the pars dentalis of the premaxillary.

In ventral view (Pl. 5b), the prevomer lies lateral to the mid-line of the skull, and ventral to the solum nasi and sphenethmoid. The anterior end of the prevomer lies posterior to the premaxillary. The posterior, dentigerous part of the prevomer is angled (see Table 1). The prevomer bears well developed lateral wings that form the anterior, medial, and posteromedial margins of the internal naris. Internally, the prevomer bears a small dorsal extension that supports the olfactory eminence.

The palatine is a narrow, thin bone which lies posterior to the internal naris. The distal end is slightly expanded and is lodged in connective tissue dorsal to the pars palatina of the maxillary and adjacent to the anterior maxillary process. The delicate proximal end lies ventral to the lateral edge of the sphenethmoid and is separated from the sphenethmoid by a thin layer of connective tissue. The palatine bears a small posteroventral ridge which has an irregular surface.

The nasal is moderately large (Pl. 5a). Anteriorly, the nasal lies dorsally adjacent to the tips of the alary processes of the premaxillary. The nasal arches

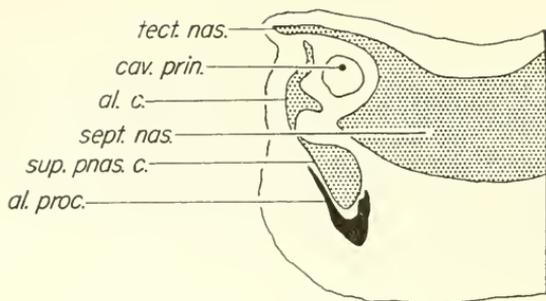
posterodorsally over the external naris and terminates posteroventrally in a slim maxillary process. The maxillary process articulates with the posterior process of the pars facialis of the maxillary. The nasals converge anteromedially to the dorsally exposed part of the sphenethmoid. Posterolaterally the nasal articulates with the frontoparietal and posteromedially with the dermal sphenethmoid. The dorsal surface of the nasal is slightly rugose. The canthal ridge is distinct; it extends along the lateral edge of the bone to the anterodorsal corner of the orbit. The margins of the nasal are smooth.

The maxillary is well developed but not robust. It does not bear a labial flange and the outer surface of the bone is smooth. The maxillary bears a well developed pars facialis anterior to the orbit; all margins of the pars facialis are free except for the posterior process; the latter articulates with the maxillary process of the nasal to form a bony anterior margin to the orbit. Medially, the pars palatina of the maxillary is small and extends the length of the bone dorsal to the pars dentalis. The maxillary articulates firmly with the quadratojugal posteriorly and terminates laterally adjacent to the quadratojugal at the level of the jugular foramen.

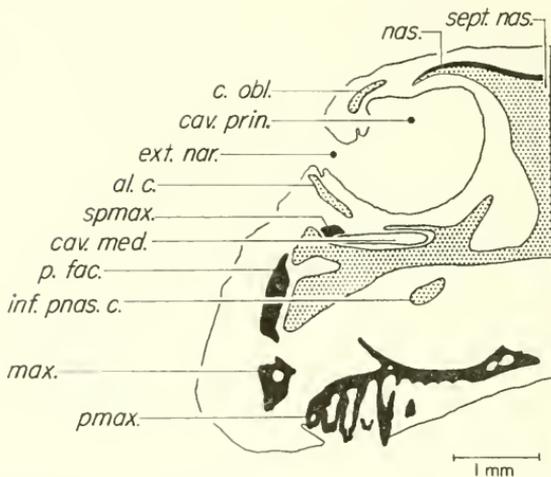
The anterior end of the septum nasi appears between the alary processes of the premaxillaries. Slightly posterior, the anterolateral corners of the tectum nasi appear dorsal to the alary processes; in subsequent sections, the tectum expands medially and fuses with the septum nasi posterior to the dorsal part of the alary process (Fig. 43). The anterior end of the superior prenasal cartilage lies adjacent to the posterodorsal surface of the alary process. In posterior sections, the superior prenasal cartilage extends dorsally and fuses with the anteroventral surface of the alary cartilage (Fig. 43). The anterior end of the alary cartilage lies just posterior and ventrolateral to the anterior corner of the tectum nasi. Posteriorly, the alary cartilage expands ventromedially and fuses with the solum nasi for a short distance to completely encase the anterior end of the cavum principale in cartilage. At the level of the foramen for the ramus externus and medius narius the alary cartilage loses its connection with the solum nasi, gradually diminishes in size and terminates at the posterior margin of the external naris. The anterior end of the inferior prenasal cartilage lies at the base of the posterior surface of the alary process of the premaxillary. From its anterior tip, the prenasal cartilage extends posterodorsally and fuses with the solum nasi at the level of the planum terminale. A crista subnasalis is present. The anterior end of the cavum principale (Fig. 43) lies between the alary cartilage and septum nasi, anterior to the level of the pars dentalis of the premaxillary. The cavum medium (Fig. 44) appears posteriorly at the level of the external naris and pars dentalis of the premaxillary just posterior to the foramen ramus externus and medius narius. The anterolateral recess of the cavum inferius appears ventrolateral to the cavum medium; the medial recess appears slightly posterior to the lateral recess, at the level of the palatine process of the premaxillary.

The nasal region is only moderately ossified. There is a gap between the anterior end of the prevomer and the premaxillary; the anterolateral and lateral margin of the nasal does not articulate with the pars facialis of the maxillary. The anterior level of perichondral ossification of the septum nasi lies at the anterior end of the prevomer, or near the posterior terminus of the planum terminale. Posterior to this level, ossification increases gradually in the dorsal part of the septum, and progresses in a posteroventral direction. At the level

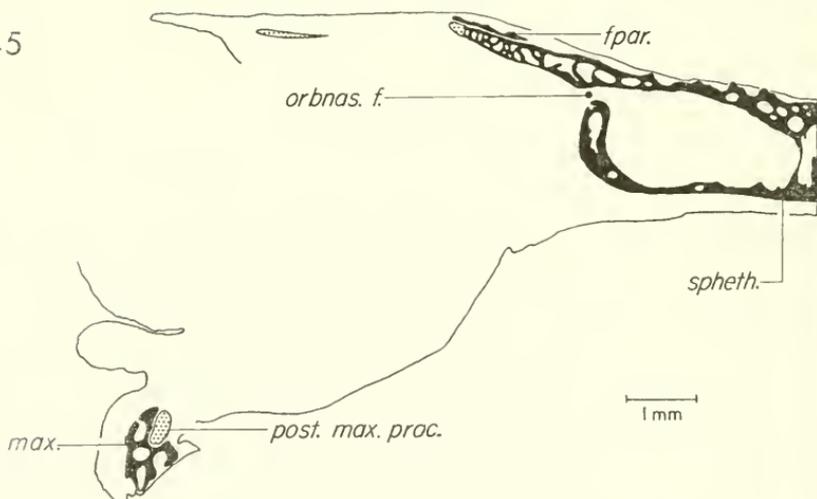
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FIGS. 43-45. Transverse sections through the anterior end of the skull of *Osteocephalus taurinus* (KU 92243): (43) level of alary process of premaxillary; (44) anterior level of cavum medium and septomaxillary; (45) level of orbitonasal foramen. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *c. obl.*, cartilago obliquus; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *ext. nar.*, external nares; *inf. pnas. c.*, inferior prenasal cartilage; *max.*, maxillary; *nas.*, nasal; *orbnas. f.*, orbitonasal foramen; *p. fac.*, pars facialis of maxillary; *pmax.*, premaxillary; *post. max. proc.*, posterior maxillary process; *sept. nas.*, septum nasi; *spheth.*, sphenethmoid; *spmax.*, septomaxillary; *sup. pnas. c.*, superior prenasal cartilage; *tect. nas.*, tectum nasi.

of the anterior margin of the internal nares, the septum nasi is completely ossified. The solum is ossified a short distance posterior to the anterior margin of the internal nares.

The anterior ramus of the septomaxillary is broad and thin and lies dorso-lateral to the cavum medium. It expands medially first, and comes to lie between the lamina superior and lamina inferior. In subsequent sections, the septomaxillary extends posterolaterally around the lateral end and ventrolateral edge of the cavum medium. The ventral ramus thus formed loses its lateral connection with the dorsal, anterior ramus. In sections posterior to this bifurcation, the horizontally-oriented anterior ramus develops a high dorsal flange, the dorsal ramus of the septomaxillary. A short distance posterior to the appearance of the dorsal ramus, the dorsal part of the septomaxillary bifurcates into medial and lateral rami. The former is associated with the distal edge of the lamina superior, and the latter bears the dorsal ramus. In more posterior sections, the medial ramus diminishes in size whereas the lateral ramus turns approximately 90 degrees from a vertical to a more dorsal, horizontal orientation to accommodate the confluence of the cava medium and principale. Slightly posterior to the latter level, the medial ramus of the septomaxillary terminates and the distal part of the cavum medium diverges laterally as the nasolacrimal duct. The dorsal and ventral rami of the septomaxillary then fuse, diminish in size and terminate in a short distance.

The Sphenethmoid and Orbital Region.—The frontoparietals converge medially throughout their lengths posterior to the dermal sphenethmoid (Pl. 5a). Anteriorly, the frontoparietal articulates with the posterior margin of the dermal sphenethmoid medially and the posterior margin of the nasal laterally. The frontoparietal forms a narrow, upturned supraorbital shelf or flange laterally; the flange extends posteriorly over the prootic and terminates at the posterior margin of the frontoparietal dorsal to the exoccipital. The frontoparietal does not bear an occipital crest posteriorly, and it does not extend laterally over the crista parotica. The dorsal surface of the frontoparietal is slightly rugose but the overlying skin is not fused with the bone below. The distal margins of the frontoparietal are smooth.

The dermal sphenethmoid is pentagonal in shape; the anterior end is acuminate and the posterior end is flat. The bone lies posteromedial to the nasals and anteromedial to the frontoparietals. The dorsal surface of the dermal sphenethmoid is moderately rugose and bears a reticulate pattern of bony ridges, but the overlying skin is not fused with the bone below. The dorsally exposed sphenethmoid is confluent with the underlying endochondral sphenethmoid as previously described for *Tripurion petasatus* and *Hyla septentrionalis*.

The endochondral sphenethmoid is in synosteotic continuity with the septum nasi anteriorly. Posterior to the transition zone between the planum antorbitale and the sphenethmoid, the sphenethmoid is completely bony (Fig. 45). Cartilage appears at the distal tip of the anterolateral wing of the sphenethmoid a short distance anterior to the level of the orbitonasal foramen; this cartilage expands laterally in posterior sections and terminates posteriorly at the level of the articulation of the nasal and frontoparietal. The margins of the orbitonasal foramen are bony (Fig. 45). Posterior to the terminus of the dermal sphenethmoid, the roof of the endochondral sphenethmoid splits to form the frontoparietal fontanelle ventral to the frontoparietals. Anteriorly, the margins of the

fontanelle are bony; posteriorly, near the level of the optic foramen, the margins of the foramen are cartilaginous (*taenia tecta marginalis*) (Fig. 46). At the same level, cartilage appears in the dorsolateral parts of the sphenethmoid, and a short distance posterior, in the floor of the sphenethmoid.

The anterior end of the parasphenoid (Pl. 5b) lies at a level between the orbitonasal foramen and the posterior terminus of the dermal sphenethmoid. The parasphenoid lies ventral to the sphenethmoid and prootic and forms a bony bridge of support for the neurocranial floor at the level of the synchondrotic union of the sphenethmoid and prootic. The parasphenoid is narrowly separated from dorsally adjacent bones and cartilages by dense connective tissue. Posteriorly and ventral to the prootic, the bone bears a delicate and inconspicuous odontoid structure.

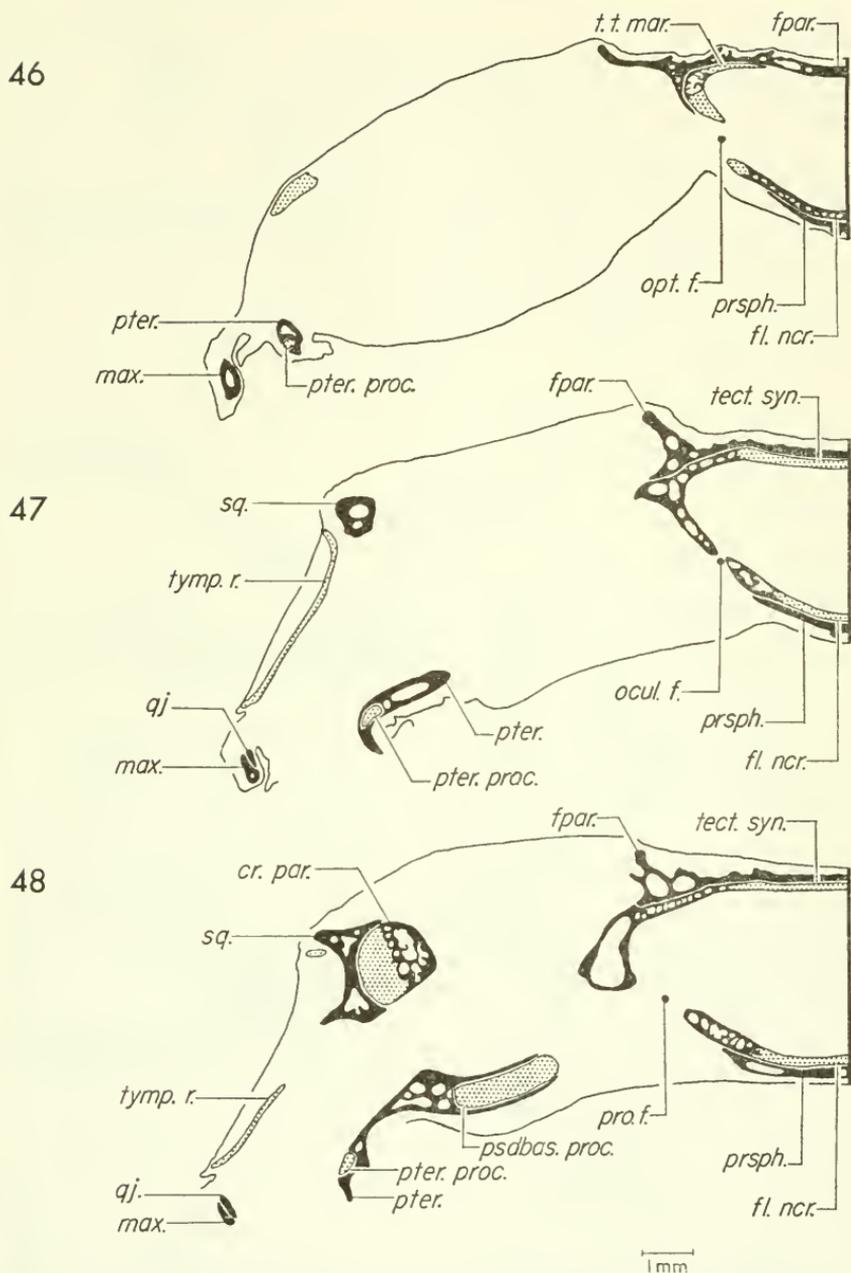
The bursa angularis oris is well developed; it lies in the posterior part of the orbit parallel to the length of the jaw and between the maxillary and pterygoid bones. The lymphoid tissue of the gland is encased in a connective tissue capsule. The bursa is tubular and closed at the anterior end. A short distance posteriorly, a longitudinal aperture opens from the central lumen of the bursa into the oral cavity. At the latter level, the lumen of the gland loses its smooth surface and forms plicae and folds internally.

The Otic and Occipital Regions.—The squamosal is a moderately delicate bone. The anterior arm is slender and extends less than one-half the distance from the dorsal union of the three squamosal arms to the maxillary. The posterior arm of the squamosal is longer than the anterior arm. In dorsal view, the posterior arm articulates medially and broadly overlaps the crista parotica. The ventral arm is delicate; posteroventrally, it lies between the posterior ramus of the pterygoid medially and the quadratojugal laterally. The surfaces of the squamosal are smooth and not co-ossified.

The pterygoid (Pl. 5b) is robust. The anterior ramus is only moderately long; its anterior end lies adjacent to the posterior maxillary process at approximately the mid-level of the orbit. The medial ramus is long, well developed, and articulates firmly with the anteroventral corner of the otic capsule ventrally. The posterior ramus articulates with the ventral half of the ventral arm of the squamosal.

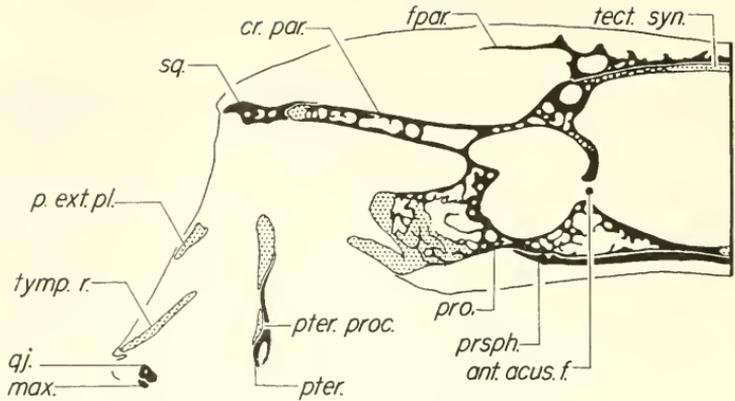
The quadratojugal is long and slender. The anterior end of the quadratojugal articulates medially with the maxillary at the mid-level between the optic and oculomotor foramina. Just posterior to the terminus of the maxillary, the ossification of the quadratojugal invades the cartilage of the quadrate process.

The anterior margin of the optic foramen (Fig. 46) is bony. Dorsally, the lamina perpendicularis of the frontoparietal forms a bony margin, whereas ventrally, the edge of the foramen is cartilaginous. Posteriorly, the prootic forms a bony margin to the optic foramen. The trochlear foramen lies dorsally adjacent to the lamina perpendicularis at the frontoparietal within the bony margins of the optic foramen. The trochlear and optic nerves are separated by connective tissue. The oculomotor foramen (Fig. 47) lies posterior and ventral to the optic foramen and a short distance anterior to the prootic foramen (Fig. 48). The margins of the oculomotor and prootic foramina are bony. There are two acoustic foramina (Figs. 49-50); both have bony margins. The jugular foramen (Fig. 51) is formed in bone posteriorly.

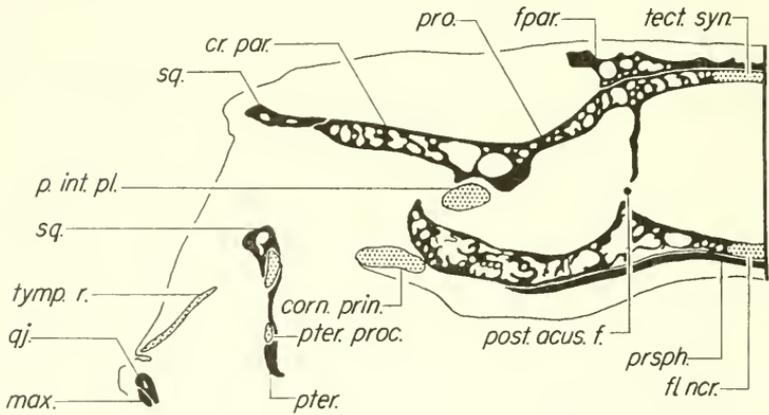


FIGS. 46-48. Transverse sections through skull of *Osteocephalus taurinus* (KU 92243) at levels of cranial nerve foramina: (46) level of optic foramen; (47) level of oculomotor foramen; (48) level of prootic foramen. Abbreviations: *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *psdbas. proc.*, pseudo-basal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *sq.*, squamosal; *t. t. mar.*, taenia tecti marginalis; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

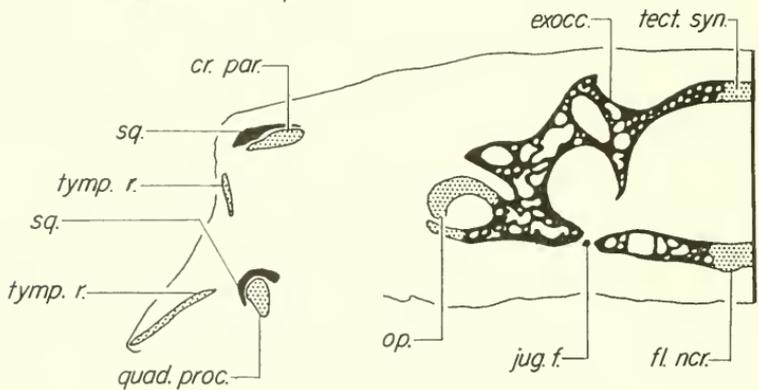
49



50



51



1 mm

FIGS. 49-51. Transverse sections through the skull of *Osteocephalus taurinus* (KU 92243) at levels of cranial nerve foramina: (49) level of anterior acoustic foramen; (50) level of posterior acoustic foramen; (51) level of jugular foramen. Abbreviations: *ant. acus. f.*, anterior acoustic foramen; *corn. prin.*, cornu principalis; *cr. par.*, crista parotica; *exocc.*, exoccipital; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *jug. f.*, jugular foramen; *max.*, maxillary; *op.*, operculum; *p. ext. pl.*, pars externa plectri; *post. acus. f.*, posterior acoustic foramen; *pro.*, prootic; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *quad. proc.*, quadratojugal process; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

The antermost part of the otic region is the dorsolateral corner of the otic process which lies medially adjacent to the posterior arm of the squamosal at a level just posterior to the oculomotor foramen (Fig. 48). At the posterior margin of the prootic foramen, the crista parotica is complete and the pterygoid and pseudobasal process are fused to the ventral part of the otic capsule; the otic process is fused to the ventral part of the otic capsule; the otic process is fused to the pseudobasal process ventrally for a short distance at this level. The pars ascendens plectri, pars externa plectri, pars interna plectri, and cornu principalis of the hyale lie at the level of the anterior acoustic foramen. The pars media plectri lies at the level of the posterior acoustic foramen. The operculum lies at the posterior level of the posterior acoustic foramen (Fig. 50) and terminates posterior to the jugular foramen.

At the posterior level of the optic foramen, the prootic is ossified laterally; the tectum synoticum and the floor of the neurocranium are cartilaginous. In posterior sections, ossification progresses ventrolaterally and invades the neurocranial floor. At the posterior margin of the prootic foramen, bone has replaced the lateral parts of the tectum synoticum; the otic capsule is completely ossified except for the ventrolateral corner, and only a narrow ventromedial strip of the neurocranial floor remains cartilaginous. Posteriorly, the tectum becomes increasingly ossified until only a narrow dorsomedial strip remains at the posterior margin of the posterior acoustic foramen. The ventrolateral edge of the otic capsule is cartilaginous posterior to the terminus of the operculum. The distal tip of the crista parotica, the pars ascendens plectri, pars externa plectri, pars interna plectri, and operculum are cartilaginous, whereas the pars media plectri is bony.

The Articular Region.—Anterior to the articular region, Meckel's cartilage lies lateral to the angulosplenic bone. Posteriorly, at the level of the operculum, the cartilage assumes a position dorsal to the angulosplenic bone, enlarges slightly in size and becomes partly ossified. At the posterior level of the jugular foramen, the quadrate process is cartilaginous, and bordered dorsally by the ventral arm of the squamosal and medially by the posterior ramus of the pterygoid; at this level, the quadratojugal lies ventrolateral to the quadrate process. A short distance posterior, bone invades the cartilage of the quadrate process. The quadratojugal does not fuse with the ossified quadrate process until the mid-level of the occipital condyles. At the posterior levels of the occipital condyles, the ventral arm of the squamosal and the posterior ramus of the pterygoid terminate. Posteriorly, the quadrate process loses its ossification.

Remarks.—The morphology of *Osteocephalus* is similar to that of the widespread (México to Argentina) lowland species, *Phrynohyas venulosa* (compare Fig. 52a, b and Pl. 5a, b). Both species have paried, lateral vocal sacs behind the angles of the jaws. Cranially, the differences between the two species are minor. The septomaxillary of *Phrynohyas* is like that described for *Tripurion* and *Smilisca* and differs from that of *Osteocephalus*; the ventral ramus of the septomaxillary is not attached to the anterolateral corner of the septomaxillary. The dermal roofing bones are expanded; the nasals are nearly indential to those of *Osteocephalus*, but the frontoparietals lack a supraorbital flange. The dorsum of the skull of *Phrynohyas* is not co-ossified; consequently, a dermal sphenethmoid is absent. Both species lack a complete squamosal arch. The posterior arm of the squamosal of *Osteocephalus* bears a broader articulation with the crista parotica than in *Phrynohyas*.

Ventrally (compare Fig. 52b and Pl. 5b), the most noticeable difference between the two species is the shape of the dentigerous processes of the premaxillaries. The processes are large in both species; they are slightly curved in *Phrynohyas* and angular in *Osteocephalus*. The palatine of *Osteocephalus* bears minute denticulations laterally, whereas the palatine of *Phrynohyas* is smooth; the palatines are otherwise the same. *Osteocephalus* bears an exceptionally small rugosity, consisting of two or three odontoid-like structures, near the base of the parasphenoid; the parasphenoid of *Phrynohyas* is edentate. In both species, the basal wings of the parasphenoid are posteriorly inclined. The pterygoids of *Osteocephalus* and *Phrynohyas* bear medial rami which articulate firmly with the prootics; the anterior rami of the pterygoids terminate adjacent to the maxillary in the mid-orbital region. The bursa angularis oris of *Phrynohyas* is like that of *Osteocephalus*.

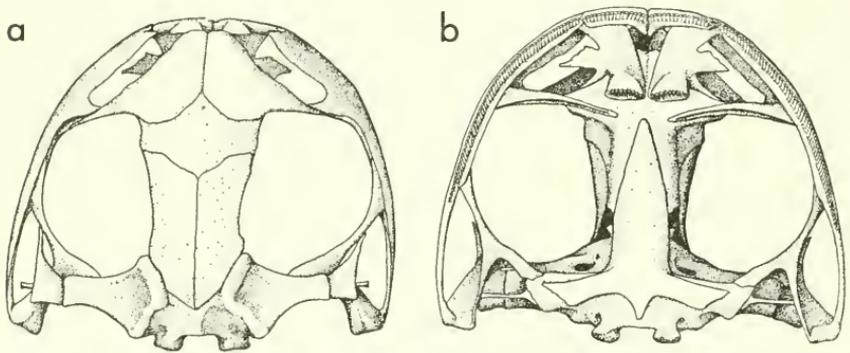


FIG. 52. Skull of *Phrynohyas venulosa* (KU 68177) $\times 2.6$: (a) dorsal view; (b) ventral view.

Cranial Morphology of *Trachycephalus nigromaculatus*

The skull of *Trachycephalus* is as long as wide (Pl. 6a). The snout in dorsal view is truncate and bears a medial "notch." All dorsal surfaces of the dermal bones are sculptured into rugosities and prominent, irregular ridges. The distal margins of dermal bones are rugose or spinose; distal spines are best developed in the orbital and occipital regions. The skull of *Trachycephalus* is characterized by the absence of a prenasal, the presence of a dermal sphenethmoid, and the lack of labial flanges on the maxillary and premaxillary. The pars facialis of the maxillary articulates only with the ventrolateral corner of the nasal. The dorsal surface of the dermal bones are extremely rugose. The prevomerine teeth are straight. The palatine and parasphenoid bear odontoid structures. The vocal sacs are paired, lateral, and located behind the angles of the jaws.

The Olfactory Region.—The premaxillaries are robust and lie anteromedial to the maxillaries. The alary processes of the premaxillaries are greatly expanded and co-ossified anteriorly. Anterodorsally, the alary process articulates with the anterior tip of the nasal. Dorsomedially, the process forms the anterior margin of the external nares. Laterally, the alary process articulates with the pars facialis of the maxillary, and medially the processes articulate with one

another. The alary processes are concave posteriorly and are oriented approximately vertically. The pars palatina of the premaxillary is well developed and the posteromedial palatine process is conspicuous.

In ventral view (Pl. 6b), the prevomer lies lateral to the midline of the skull and ventral to the solum nasi and sphenethmoid. The anterior end of the prevomer lies dorsolateral to the premaxillary. The prevomer bears well developed lateral wings which form the anterior and medial margins of the internal naris. The prevomers converge medially just anterior to the prevomerine teeth; the dentigenous processes are slightly curved in a transverse plane. Internally, the prevomer provides bony support for the olfactory eminence. The prevomer is separated from the sphenethmoid and the solum nasi by a thin layer of dense connective tissue.

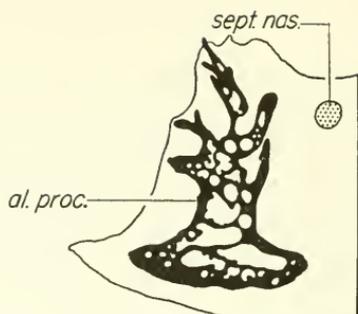
The palatine is a robust bone which lies posterior to the internal naris. The broad, distal end is lodged in connective tissue dorsal to the pars palatina of the maxillary and adjacent to the anterior maxillary process. The proximal end is pointed and lies ventral to the sphenethmoid and posterior to the prevomer. The palatine is separated from the sphenethmoid by a thin layer of dense connective tissue. The palatine bears a series of odontoids along a prominent ventral ridge.

The nasals are large. The anterior end of the nasal is blunt and articulates with the dorsal margin of the alary process of the premaxillary. Laterally the nasal arches over the external nares and articulates posteriorly and ventrolaterally with the pars facialis of the maxillary at the corner of the orbit. The nasal forms the anterior margin of the orbit. It articulates with the frontoparietal dorsolaterally and the dorsally exposed dermal sphenethmoid dorsomedially. The nasals converge medially anterior to the dermal sphenethmoid. The canthal ridge is distinct. The ridge extends from the anterior end of the nasal along the lateral margin to the anterodorsal corner of the orbit. The entire surface of the nasal is involved in the integumentary-cranial co-ossification. Dorsally, near the orbit, the surface of the nasal is rugose. The rest of the nasal is marked by prominent bony ridges. The ridges are rough and form a radial pattern from the rugose area.

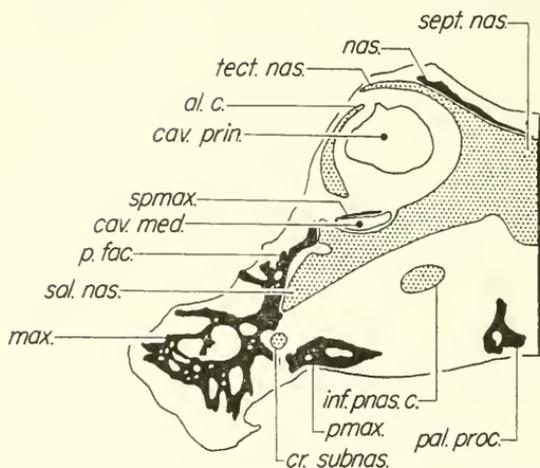
The maxillary is moderately robust, but lacks a labial flange. The pars facialis of the maxillary is well developed. It is largest anterior to the orbit. Anteriorly, the pars facialis articulates with the alary process of the premaxillary and forms the ventral margin of the external naris. Posterior to the external naris, the dorsal edge of the pars facialis is free; it articulates with the maxillary process of the nasal at the anterior margin of the orbit. The pars facialis diminishes in size ventral to the orbit, but it is conspicuous along the entire length of the maxillary. The pars palatina of the maxillary is well developed and extends from the anterior end of the bone posteriorly to the level of termination of the pars dentalis. Posteriorly, the maxillary firmly articulates with the quadratojugal which lies medial adjacent to the maxillary. The outer surface of the maxillary is co-ossified and highly rugose. There is an indistinct pattern of irregular bony ridges which radiate dorsally and anteriorly from the lower margin of the maxillary anterior to the orbit. Posterior and ventral to the orbit the outer surface of the maxillary is smooth, but the dorsal margin bears a series of small spines.

The anterior end of the septum nasi (Fig. 53) lies anterior to the nasals between the dorsomedial corners of the alary processes of the premaxillaries.

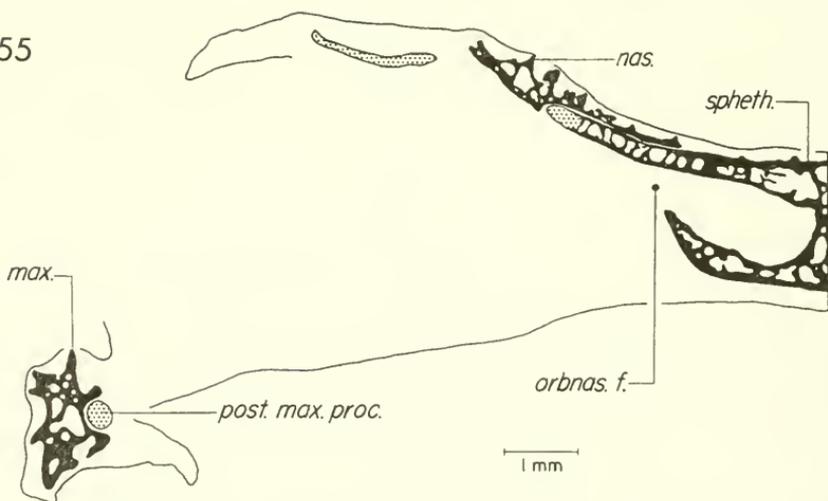
53



54



55



FIGS. 53-55. Transverse sections through the anterior end of the skull of *Trachycephalus nigromaculatus* (KU 100353): (53) level of the alary process of the premaxillary; (54) anterior level of cavum medium and septomaxillary; (55) level of orbitonasal foramen. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *ant. max. proc.*, anterior maxillary process; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *cr. subnas.*, crista subnasalis; *inf. pnas. c.*, inferior prenasal cartilage; *max.*, maxillary; *nas.*, nasal; *orbnas. f.*, orbitonasal foramen; *p. fac.*, pars facialis of maxillary; *pal. proc.*, palatine process of premaxillary; *pmax.*, premaxillary; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spheth.*, sphenethmoid; *sprmax.*, septomaxillary; *tect. nas.*, tectum nasi.

In subsequent sections, the inferior prenasal cartilage appears ventromedially at the base of the alary process. The anterior end of the superior prenasal cartilage lies adjacent to the posterodorsal surface of the alary process and is closely associated with the alary cartilage which emerges as an arcuate shaped cartilage from the dorsolateral corner of the massive superior prenasal cartilage. The tectum nasi appears posterior and dorsal to the anterior end of the alary cartilage. The tectum fuses medially with the septum nasi posterior to the alary process. The anterior end of the cavum principale lies ventral to the anterior end of the nasal at the posterior level of the pars dentalis of the premaxillary. The cavum is completely surrounded by the cartilage of the alary cartilage, the tectum, septum, and solum nasi. A short distance posterior, at the anterior level of the palatine process of the premaxillary (Fig. 54), the anterior end of the cavum medium appears ventral to the cavum principale. The anterior end of the cavum medium lies dorsal to the solum nasi instead of appearing within the cartilage as it usually does. In sections posterior to the anterior end of the cavum, the lamina superior appears as a small rod of cartilage dorsomedial to the cavum medium. Anteriorly, the lamina superior is disjunct from the crista intermedia at the posterior level of the palatine process of the premaxillary. The anterolateral recess of the cavum inferius appears in sections slightly posterior to the anterior end of the cavum medium; there is no anteromedial recess.

There is an unusual amount of ossification in the nasal region in the form of perichondral ossification of the nasal cartilages. The anterior end of the septum nasi, the inferior prenasal cartilage and the tectum nasi are perichondrally ossified. Farther posterior, the lateral margin of the alary cartilage is ossified and the entire dorsum and venter of the internasal septum posterior to the alary process of the premaxillary. The dorsal perichondral ossification of the septum nasi is replaced posteriorly by the nasal. At the anterior level of the septomaxillary and lamina superior, ossification appears in the membranous connective tissue overlying the cavum medium. The latter ossification is associated posteriorly with the venter of the lamina superior, and persists until the posterior level of the septomaxillary. Perichondral ossification of the venter of the solum disappears at the anterior end of the prevomer. At the level of the planum terminale, the septum nasi is perichondrally ossified dorsally, dorsolaterally, and ventrolaterally. Endochondral ossification lies in the dorsal part of the septum at the posterior level of the planum terminale. Posterior to this level, ossification spreads from the dorsal part of the septum ventrally. At the mid-level of the olfactory eminence, anterior to the internal naris, the entire septum is ossified, whereas the solum is cartilaginous. Shortly posterior to the anterior margin of the internal naris, ossification appears in the solum; the solum nasi is completely ossified at approximately the mid-level of the internal naris. The septum nasi is synosteotically united with the sphenethmoid posteriorly.

The anterior end of the septomaxillary (Fig. 54) is a thin bone horizontally oriented dorsal to the cavum medium. The septomaxillary expands laterally above, and then around, the cavum medium in posterior sections. The part of the septomaxillary lateral to the cavum terminates leaving the ventral ramus disjunct from the anterior ramus. Just posterior to this point, the anterior ramus of the septomaxillary diverges into a lateral and medial rami. The former develops a dorsal ramus. Somewhat posterior, at the level of the fusion of the

superior prenasal cartilage and solum nasi, the dorsal and ventral rami of the septomaxillary fuse and separate the newly formed nasolacrimal duct from the posterior part of the cavum medium. As the nasolacrimal duct diverges farther from the cavum in posterior sections, the ventral ramus diminishes in size and the septum becomes thicker and shorter vertically. The medial and lateral rami terminate, leaving only the dorsal ramus and the small ventral remainder of the septum. The latter gradually diminish in size and disappear.

The Sphenethmoid and Orbital Region.—The frontoparietals converge medially throughout their lengths. Anteriorly, the frontoparietal articulates with the nasal laterally and the dermal sphenethmoid medially. Anterolaterally, the frontoparietal forms a supraorbital shelf. Posterolaterally, the frontoparietal articulates with the anterior and posterior arms of the squamosal. Posteriorly, the frontoparietal terminates in spinose processes, but there is no occipital crest. Ventrally, the frontoparietal is attached to the exoccipital; it bridges the crista parotica from the exoccipital to the squamosal. The entire dorsal surface of the frontoparietal is involved in integumentary–cranial co-ossification. Medially, the bone is rugose. From the central rugosity, irregular bony ridges radiate out toward the distal margins of the bone. The outer edges of the bone bear series of small spines.

The dermal sphenethmoid (Pl. 6a) is a triangular shaped bone, centrally located at the anterior level of the orbit; the bone lies posteromedial to the nasals and anteromedial to the frontoparietals. The dermal sphenethmoid is completely involved in integumentary–cranial co-ossification. The dorsal surface of the bone is rugose. The dorsally exposed dermal sphenethmoid is confluent with the underlying endochondral sphenethmoid as previously described for *Tripriion petasatus*, *Hyla septentrionalis*, and *Osteocephalus taurinus*.

The endochondral sphenethmoid is in synosteotic continuity with the septum nasi anteriorly. The margins of the orbitonasal foramen are bony (Fig. 55). At the level of the foramen, the sphenethmoid is completely bony except for the distal tip of the anterolateral wing. Posteriorly, this tip expands distally to form a broad supraorbital shelf ventral to the nasal (Fig. 55). The cartilage diminishes in size and disappears posterior to the level of the frontoparietal–nasal articulation. In sections posterior to the dermal sphenethmoid, the roof of the endochondral sphenethmoid splits to form the frontoparietal fontanelle ventral to the frontoparietals. Posterolaterally, the margins of the fontanelle are formed by the cartilaginous taenia tecta marginalis. The cartilaginous tectum synoticum forms the posterior border of the fontanelle; the latter lies slightly anterior to the level of the optic foramen. Posterior to the level of the supraorbital, cartilaginous flange, cartilage appears again in the sphenethmoid at the level of the bursa angularis oris in the posterior part of the orbit. The cartilage lies in the dorsolateral corners of the braincase; in subsequent posterior sections, the cartilage spreads ventrally. At the level of the optic foramen, the sphenethmoid is composed entirely of cartilage except for a thin layer of internal perichondral ossification which lines the neurocranium.

The parasphenoid (Pl. 6b) is a robust bone which lies ventral to the sphenethmoid and prootic and forms a bony bridge between the two bones at the level of the optic foramen. The parasphenoid is separated from overlying bones by a thin layer of connective tissue. The acuminate anterior end of the parasphenoid lies posterior to the level of the orbitonasal foramen. Posteriorly, the

the parasphenoid widens and finally terminates in a broad, robust base ventral to the prootic. The parasphenoid bears a well developed longitudinal ventral ridge extending from a level slightly posterior to the anterior tip of the parasphenoid to a level slightly anterior to the optic foramen. Although the ridge is prominent, it is completely smooth and even, and thus bears little resemblance to similarly placed odontoid structures of other genera.

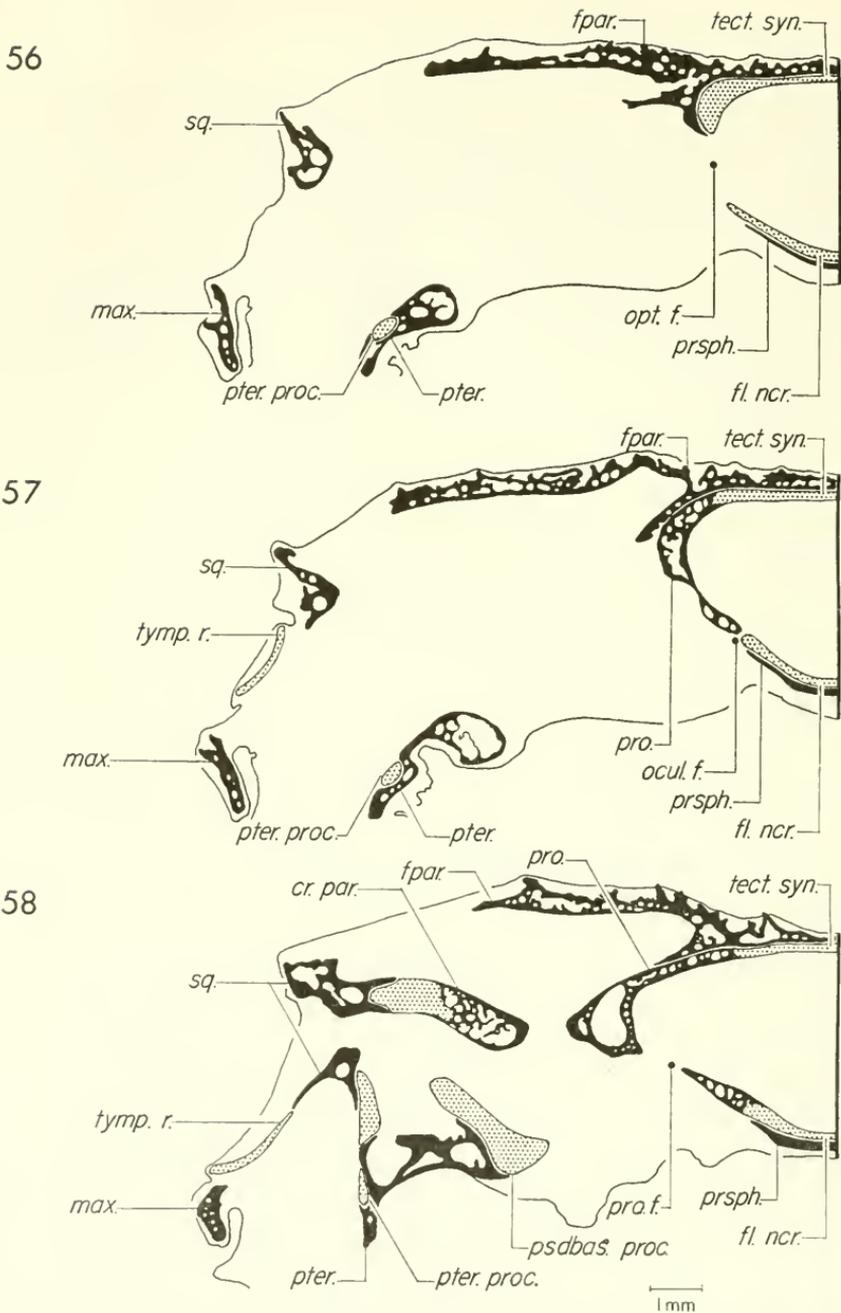
The bursa angularis oris is well developed and lies in the posterior part of the orbit. The bursa is tube-shaped and lies parallel to the jaw between the maxillary and pterygoid bones. Anteriorly, the bursa is a solid mass of lymphoid tissue. There is no central lumen within the bursa anterior to the level of the longitudinal aperture of the bursa into the oral cavity. The structure of the bursa angularis oris resembles that of *Triprion petasatus*.

The Otic and Orbital Regions.—In dorsal view (Pl. 6a), the squamosal is a long bone which extends from the posterior edge of the orbit, along the posterolateral margin of the frontoparietal to a level posterior to the posterior edge of the frontoparietal. The dorsal and lateral surfaces of the squamosal are ossified and highly rugose and spiny. The anterior arm of the squamosal is robust; it forms a part of the posterior margin of the orbit. Ventrally, the anterior arm terminates dorsal to the maxillary; it is connected to the maxillary by connective tissue but does not articulate with the maxillary. The posterior arm of the squamosal is as robust as the anterior arm and longer. The posterior arm articulates with the frontoparietal and crista parotica and extends posterior to these structures to the level of the posteroventral end of the ventral arm of the squamosal. The ventral arm of the squamosal is moderately robust. Ventrally, it terminates between the quadratojugal laterally and the pterygoid medially, and dorsal to the quadrate process.

The pterygoid is moderately robust. The anterior ramus lies adjacent to the posterior maxillary process at a level just posterior to the orbitonasal foramen. Posteriorly the pterygoid and pterygoid process diverge from the maxillary. The medial ramus is short, poorly developed and does not articulate with the prootic medially. The posterior ramus is robust; it articulates with the quadrate process and ventral arm of the squamosal posteriorly.

The quadratojugal is well developed. The anterior end lies medially adjacent to the maxillary at the level of the optic foramen. The quadratojugal increases in size posteriorly, whereas the maxillary diminishes in size. Posteriorly, the ossification of the quadratojugal invades the cartilage of the quadrate process.

The margins of the optic foramen (Fig. 56) are bony and formed by the lamina perpendicularis of the frontoparietal and perichondral ossification of the sphenethmoid and prootic. The trochlear foramen lies dorsally adjacent to the lamina perpendicularis of the frontoparietal, within the bony margins of the optic foramen. The trochlear and optic foramina are separated by connective tissue. The oculomotor foramen (Fig. 57) lies posteroventral to the optic foramen. Anterodorsally, the margins are bony and formed by the prootic. Ventrally, the margins are formed of bone (the parasphenoid and perichondral ossification of the floor of the neurocranium) and cartilage. The prootic foramen (Fig. 58) lies a short distance posterior and slightly dorsal to the oculomotor foramen; the two foramina are separated by connective tissue. The dorsal, ventral, and posterior margins of the prootic foramen are bony. The anterior acoustic foramen (Fig. 59) lies a short distance posterior to the prootic foramen.



FIGS. 56-58. Transverse sections through the skull of *Trachycephalus nigromaculatus* (KU 100353) at levels of cranial nerve foramina: (56) level of optic foramen; (57) level of oculomotor foramen; (58) level of prootic foramen. Abbreviations: *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

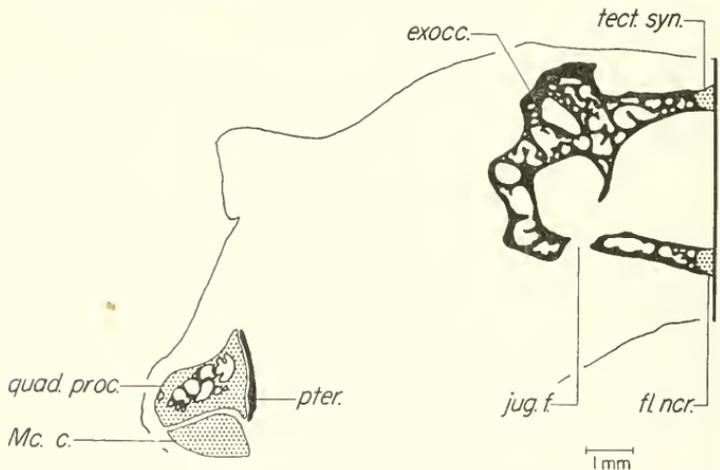
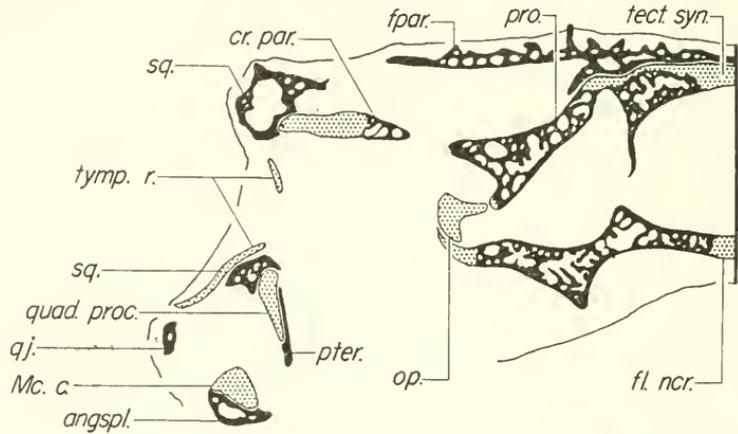
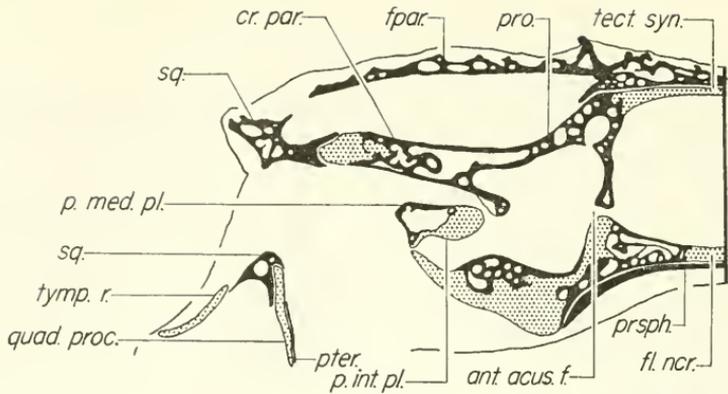
men. The margins of the foramen are bony although only a thin bridge of bone separates the anterior acoustic foramen from the more posterior-lying posterior acoustic foramen (Fig. 60). The margins of the posteroventral jugular foramen (Fig. 61) are bony.

The pseudobasal process (Fig. 57) appears at the level of the optic foramen. The process lies ventrolateral to the neurocranium and increases in size posteriorly. The anterior end of the otic process lies encased in the anterior arm of the squamosal at the level of the oculomotor foramen. Posteriorly, both the otic and pseudobasal process expand medially. The otic process also extends posteroventrally to fuse with the pseudobasal process at the anterior level of the prootic foramen. At the mid-level of the prootic foramen the lateral block of cartilage formed by the otic and pseudobasal process is differentiated into the crista parotica dorsally (Fig. 58), the lateral edge of the otic capsule medially, and a lateral piece of cartilage which is continuous with the pterygoid process a short distance posteriorly. At the posterior level of the prootic foramen, the crista parotica extends from the dorsal head of the squamosal to the otic capsule medially and the cornu principalis of the hyale diverges postero-laterally from the ventrolateral edge of the otic capsule or pseudobasal process. Posterior to the level of the prootic foramen, the ventral edge of the otic capsule is complete.

The pars interna plectri, pars externa plectri, and the pars media plectri appear between the levels of the prootic and anterior acoustic foramen. The appearance of the pars externa plectri is followed by the appearances of the medial part of the pars media plectri and the pars interna plectri respectively. Posterior to the anterior level of the pars interna plectri, the distal parts of the pars media plectri appear. The anterior end of the operculum closes the foramen ovale. The posterior terminus of the operculum lies a short distance posterior to the posterior acoustic foramen. It is quite likely that a pars ascendens plectri is present also, but its position and nature cannot be determined from the specimen.

At the posterior level of the optic foramen, the prootic is ossified dorso-laterally; the tectum synoticum and the floor of the neurocranium are cartilaginous. Posteriorly, ossification invades the tectum synoticum and the floor of the neurocranium. At the level of the anterior acoustic foramen, the tectum synoticum and the ventromedial part of the floor of the neurocranium is cartilaginous. The ventral part of the otic capsule is cartilaginous with perichondral ossification. Bone invades cartilage posteriorly. At the level of the jugular foramen, the cranium is bony except for small dorso- and ventromedial pieces and the dorsum of the otic capsule. The distal end of the crista parotica is cartilaginous. The pars externa plectri, pars interna plectri, and operculum are cartilaginous, whereas the pars media plectri is bony.

The Articular Region.—Anterior to the articular region, Meckel's cartilage lies dorsolateral to the angulosplenic bone. Posteriorly, the cartilage assumes a position dorsal to the angulosplenic bone and then enlarges and comes to lie in close association with the posterior ramus of the pterygoid, the ventral arm of the squamosal and the quadrate process. The quadratojugal ossification invades the cartilage of the quadrate process at a level just anterior to the jugular foramen; the intrusive ossification and quadratojugal terminate a short distance posterior to the jugular foramen. At this level the ventral arm of the squamosal



FIGS. 59-61. Transverse sections through the skull of *Trachycephalus nigromaculatus* (KU 100353) at levels of cranial nerve foramina: (59) level of anterior acoustic foramen; (60) level of posterior acoustic foramen; (61) level of jugular foramen. Abbreviations: *angspl.*, angulosplenic; *ant. acus. f.*, anterior acoustic foramen; *cr. par.*, crista parotica; *exocc.*, exoccipital; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *jug. f.*, jugular foramen; *Mc. c.*, Meckel's cartilage; *op.*, operculum; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *post. acus. f.*, posterior acoustic foramen; *pro.*, prootic; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadrate jugal; *quad. proc.*, quadrate process; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

and the posterior ramus of the pterygoid flank the quadrate process dorsolaterally and dorsomedially, respectively. Meckel's cartilage, which lies ventral to the quadrate process, is underlain by the angulosplenial bone.

Cranial Morphology of *Trachycephalus jordani*

The skull of *Trachycephalus jordani* is only slightly longer than wide (Pl. 7a). The snout, in dorsal view, is truncate and bears a small medial "notch." All dorsal surfaces of the skull are involved in integumentary-cranial co-ossification. Dorsally, all dermal bones are sculptured in irregular rugosities and patterns of fine radial ridges. The distal margins of all dermal bones bear series of fine, denticulate spines. The posterior edge of the frontoparietal bears a moderately developed occipital crest. The skull of *Trachycephalus jordani* is characterized by its width and broadly rounded snout. A dermal sphenethmoid is present. The prenasal and internasal are absent, but the premaxillaries are heavily co-ossified and protrude anteriorly. The labial flanges are narrow. The prevomerine teeth are curved (see Table 1), and the palatine and parasphenoid bear well developed odontoid structures. The vocal sacs are paired, lateral and located behind the angles of the jaw.

This description is based on examination of the two available skeletal preparations. The attempt to make serial sections of one of the dried skulls was only moderately successful; thus, the following account is incomplete and is principally limited to the bony parts of the skull. Description of the septomaxillary, and the cartilaginous and other soft anatomical features of the cranium of *Trachycephalus jordani* is based on the examination of serial sections of a juvenile specimen.

The Olfactory Region.—The premaxillaries lie anterior to the nasals and anteromedial to the maxillaries. The alary process of the premaxillary is greatly enlarged and totally co-ossified. Ventrolaterally, the alary process articulates with the pars facialis of the maxillary; dorsally, it meets the anterior tip of the nasal. Between the two latter articulations, the alary process forms the bony anterior margin of the external naris. Medially, the alary process is narrowly separated by connective tissue from the adjacent process. The anterior surface of the process is spinose. The development of spines is heaviest near the base of the alary process. The latter results in the protrusion of a narrow labial flange anterodorsal to the pars dentalis of the premaxillary; this flange is continuous with a similar structure on the maxillary. The premaxillary bears an inconspicuous pars palatina and a moderately well developed palatine process.

In ventral view (Pl. 7b), the prevomer is large, lies lateral to the mid-line of the skull, and ventral to the solum nasi and sphenethmoid. The anterior end of the prevomer lies dorsal to the pars dentalis of the premaxillary and maxillary. The posterior dentigerous part of the prevomer is curved posterolaterally from the midline of the bone toward the palatine (see Table 1). The prevomer bears well developed lateral wings that form the anterior, medial, and posteromedial margins of the internal nares. Internally, the prevomer provides a bony support for the olfactory eminence.

The palatine is a moderately well developed bone which lies posterior to the internal nares. The broad, distal end is lodged in connective tissue dorsal to the pars palatina of the maxillary. The delicate, pointed proximal end lies ventral to the lateral edge of the sphenethmoid. The palatine bears a delicate postero-

ventral ridge with a serrate edge of fine denticulations; the ridge extends from the lateral edge of the sphenethmoid to the distal end of the palatine.

The nasal is extremely large. Anteriorly, the nasal terminates at the dorsal tip of the alary process of the premaxillary; the nasal forms the dorsal and posterior bony margins of the external naris. Laterally, the nasal lies closely adjacent to, but does not articulate with, the pars facialis of the maxillary; posterolaterally, it forms the bony anterior margin and anterior part of the supraorbital flange of the orbit. The nasals converge anteromedially to the dermal sphenethmoid. The posterior margin of the nasal articulates with the dermal sphenethmoid medially and the frontoparietal laterally. The dorsal surface of the nasal is completely involved in integumentary-cranial co-ossification. The nasal bears a well developed canthal ridge extending from the dorsal margin of the external naris to the anterodorsal corner of the orbit. The posterior part of the canthal ridge is rugose and pitted; bony ridges radiate from this area over the entire surface of the nasal.

The maxillary is moderately well developed. It bears a narrow labial flange throughout its length. All dorsal and lateral surfaces of the bone are co-ossified. The outer edge of the maxillary bears a series of small, spinose protuberances like those of the alary process of the premaxillary. The pars facialis bears prominent ridges. The pars facialis is well developed over the length of the maxillary. It is largest anterior to the orbit; ventral to the orbit, the pars facialis diminishes in size but it is still conspicuous. Medially, the maxillary bears a moderately developed pars palatina extending the length of the bone dorsal to the pars dentalis; the pars dentalis is best developed anterior to the orbit. Posteriorly, the quadratojugal lies medial to the maxillary. The posterior terminus of the maxillary lies just anterior to the articulation of the quadratojugal and ventral arm of the squamosal.

The anterior end of the septum nasi lies anterior to the nasals between the alary processes of the premaxillaries. In subsequent sections, the septum expands laterally posterior to the alary processes and the alary cartilage differentiates laterally from the septum. The superior prenasal cartilage lies adjacent to the posterodorsal surface of the alary process and ventromedial to the alary cartilage with which it is fused for a short distance. The tectum nasi appears at the same level at which the alary cartilage differentiates from the solum and is fused with the solum throughout its length. The anterior end of the cavum principale appears at a level near the base of the alary process and anterior to the pars dentalis of the premaxillary. The cavum is completely surrounded by the alary cartilage, the tectum nasi, solum nasi, and septum nasi. The anterior end of the cavum medium lies at the level of the external nares and the bases of the alary processes of the premaxillaries. The cavum medium appears within the cartilage of the solum nasi instead of dorsal to it, as the cavum does in *T. nigromaculatus*. The anterolateral recess of the cavum inferius lies ventrolateral to the cavum medium at the level of the posterior border of the external naris and anterior to the pars dentalis of the premaxillary. The inferior prenasal cartilage is well developed but short. It extends from the base of the alary process of the premaxillary posterodorsally to fuse with the solum nasi at the level of the pars dentalis of the premaxillary.

The anterior end of the septomaxillary lies dorsolateral to the cavum medium. In subsequent sections, the bone expands around the lateral edge of the cavum.

The anterior ramus bifurcates into lateral and medial branches at the level of the posterior margin of the external naris. The lateral branch bears a well developed dorsal ramus which appears just posterior to the divergence of the medial and lateral rami and just anterior to the separation of the lateral and ventral rami. Slightly anterior to the fusion of the inferior prenasal cartilage with the solum nasi, the dorsal and ventral rami of the septomaxillary unite to separate the nasolacrimal duct from the cavum medium. As the nasolacrimal duct diverges farther from the cavum in posterior sections, the ventral ramus diminishes in size and the septum becomes thicker and depressed. The medial and lateral rami terminate, leaving only the dorsal ramus and the small ventral remainder of the septum which gradually diminish in size and disappear.

The Sphenethmoid and Orbital Region.—The frontoparietal articulates anteriorly with the posterior margins of the dermal sphenethmoid and nasal. Laterally, the frontoparietal forms the posterior part of the supraorbital shelf and posterolaterally, it lies adjacent to the squamosal. The frontoparietals converge medially posterior to the dermal sphenethmoid. The posterior margin of the frontoparietal terminates in a small, spinose occipital crest. Ventral to the occipital crest, the frontoparietal lies dorsally adjacent to the exoccipital; laterally, it bridges the prootic from the exoccipital to the squamosal. The posterolateral corner of the frontoparietal bears a weak articulation with the posterior arm of the squamosal. The dorsal surface of the frontoparietal is involved in integumentary-cranial co-ossification. Medially, the bone is rugose and pitted. Peripheral parts of the frontoparietal bear bony radial ridges which are most prominent posteriorly.

The dermal sphenethmoid is large and centrally located between the nasals and frontoparietals. The dorsal surface of the bone is completely co-ossified and marked by a pattern of bony ridges, which radiate from the center of the bone. The dorsally exposed dermal sphenethmoid is confluent with the underlying endochondral sphenethmoid as described for *Triprion petasatus*, *Hyla septentrionalis*, *Osteocephalus taurinus*, and *Trachycephalus nigromaculatus*.

The endochondral sphenethmoid is in synostotic continuity with the septum nasi anteriorly. The sphenethmoid is entirely ossified at the level of the orbitonasal foramen. The structure of the sphenethmoid in sections just posterior to the level of the orbitonasal foramen suggests that some cartilage is present at the distal tip of the anterolateral wing of the sphenethmoid. Just posterior to the terminus of the dermal sphenethmoid, the roof of the endochondral sphenethmoid splits to form the frontoparietal fontanelle ventral to the frontoparietals. The fontanelle extends posteriorly to approximately the level of the optic foramen. Some cartilage appears in the sphenethmoid near its posterior terminus, but perichondral ossification is always well developed.

The anterior end of the parasphenoid lies at a level posterior to the orbitonasal foramen. The parasphenoid is moderately developed; it lies ventral to the sphenethmoid and prootic. The ventral surface of the parasphenoid bears a long, well developed series of odontoids.

The bursa angularis is well developed and lies in the posterior part of the orbit. The bursa is tubular and lies parallel to the jaw between the maxillary and pterygoid bones. Anteriorly, the gland is a mass of lymphoid tissue. Just anterior to the level of the longitudinal aperture of the bursa connecting the gland with the oral cavity, a central lumen of small diameter appears. The

structure of the bursa is almost identical to that of *Trachycephalus nigromaculatus*.

The Otic and Occipital Regions.—In dorsal view the squamosal is a slim bone which extends from the posterior edge of the orbit to the level of the occipital crest. The dorsal and lateral surfaces of the squamosal are spinose and co-ossified. The anterior arm of the squamosal is robust. It does not articulate with the maxillary ventrally, although it lies dorsally adjacent to the maxillary. The posterior arm of the squamosal is equal to length to the anterior arm; it terminates posteroventrally to the posterolateral corner of the frontoparietal. The posterior arm lies laterally adjacent to the frontoparietal; ventral to the frontoparietal, the post-squamosal arm articulates with the crista parotica. The ventral arm of the squamosal is moderately robust. It extends posteroventrally from the mid-point of the arc formed by the anterior and posterior arms of the squamosal and articulates with the pterygoid and quadratojugal ventrally.

The pterygoid is robust. The anterior end of the anterior ramus extends posteriorly adjacent to the maxillary. At a level anterior to the posterior end of the pars dentalis of the maxillary, the pterygoid diverges medially from the maxillary. The posterior ramus of the pterygoid articulates with the ventral arm of the squamosal. The medial ramus is strong and articulates firmly with the prootic.

The quadratojugal is well developed. The anterior end lies medially, adjacent to the maxillary, at a level slightly anterior to the oculomotor foramen. The quadratojugal increases in size posteriorly, whereas the maxillary gradually diminishes in size. Posteriorly, the ossification of the quadratojugal invades the cartilage of the quadrate process.

The trochlear foramen lies dorsally adjacent to the lamina perpendicularis of the frontoparietal and within the bony margins of the optic foramen. The trochlear and optic nerves are separated by connective tissue. The oculomotor foramen lies posteroventral to the optic foramen, and is only narrowly separated from the posterodorsal prootic foramen. There are two acoustic foramina. The jugular foramen lies a short distance posterior to the posterior acoustic foramen. The otic and occipital regions of *T. jordani* are doubtless very well ossified. The specimen utilized for the description of the internal morphology, olfactory, otic and occipital regions is immature; thus, definitive treatment of the morphology of these areas must be postponed until suitable material is available for study.

The pseudobasal and otic processes appear at the anterior level of the oculomotor foramen. In posterior sections, the otic process expands greatly in size and fuses ventrally with the pseudobasal process at the anterior level of the prootic foramen. In subsequent sections, at the level of the prootic foramen, the otic process joins the otic capsule medially, forming the crista parotica, and diverges ventrally from the pseudobasal process. A short distance posterior to the prootic foramen, the pseudobasal process joins the ventral part of the otic capsule medially.

The pars ascendens plectri, pars externa plectri, and distal part of the pars media plectri lie slightly anterior to the level of the anterior acoustic foramen. The medial parts of the pars media plectri and the pars externa plectri lie at the level of the anterior acoustic foramen. The anterior end of the operculum lies between the levels of the two acoustic foramina. The operculum increases in

size in posterior sections, and at the level of the posterior acoustic foramen has replaced the pars interna plectri and closed the foramen ovale. The operculum terminates anterior to the level of the jugular foramen.

The Articular Region.—Anterior to the articular region, Meckel's cartilage lies dorsolateral to the angulosplenic bone. Posteriorly, the cartilage assumes a position dorsal to the angulosplenic bone and then enlarges and comes to lie in close association with the posterior ramus of the pterygoid, the ventral arm of the squamosal, and the quadrate process. The quadratojugal ossification invades the cartilage of the quadrate process at a level just anterior to the posterior acoustic foramen. The intrusive ossification and quadratojugal terminate a short distance posterior to the posterior acoustic foramen. At this level, the posterior terminus of the ventral arm of the squamosal and the posterior ramus of the pterygoid flank the quadrate process dorsolaterally and dorsomedially, respectively. Meckel's cartilage lies ventral to the quadrate process and is underlain by the arcuate angulosplenic bone.

Cranial Morphology of *Corythomantis greeningi*

The skull of *Corythomantis* is longer than wide (Pl. 8a, b). The snout, in dorsal view, is moderately narrow, but rounded terminally. The dorsal surfaces of the skull are involved in integumentary-cranial co-ossification. The development of co-ossified tissue varies on the dorsal surface of the cranium. Skin overlying dorsolateral parts of the skull is typical of co-ossified tissue; it has a thin epidermal layer which is underlain by loose connective tissue, and it lacks a lower, dense connective tissue layer. Skin overlying dorsomedial parts of the skull is histologically transitional between normal and co-ossified tissue. Some dense connective tissue occurs in the dermis; it is irregular in thickness, poorly organized, and separated from the underlying dermal bones. Dorsally, all dermal bones are sculpted in a pattern of low, reticulate ridges (Pl. 8a). The distal margins of dermal roofing bones and the squamosals and maxillary terminate in spinose protuberances. The skull of *Corythomantis* is characterized by the presence of a dermal sphenethmoid, an extremely reduced quadratojugal, and extensive nasals. The prenasal and palatine bones are absent, and the parasphenoid is poorly developed. The vocal sac is single, median, and subgular.

The Olfactory Region.—The premaxillaries (Pl. 8b) are small and lie posterior to the anterior ends of the nasals and maxillaries. The lateral corner of the pars dentalis of the premaxillary is covered by the maxillary and the anterior surface of the alary process of the premaxillary is covered by the nasal. The rest of the bone is externally exposed and not involved in integumentary-cranial co-ossification. The premaxillaries are separated medially from one another and laterally from the maxillaries by dense connective tissue. Ventromedially, each premaxillary bears a small, inconspicuous palatine process. The alary process of the premaxillary is anterodorsally oriented and about one and one-half times as long as the depth of the pars dentalis of the premaxillary. The process is slightly convex anteriorly and in contact with the superior prenasal cartilage dorsally.

In ventral view (Pl. 8b) the prevomer lies lateral to the midline of the skull and ventral to the solum nasi and sphenethmoid. The anterior end of the prevomer is associated with the ventrolateral surface of the solum nasi dorsal to

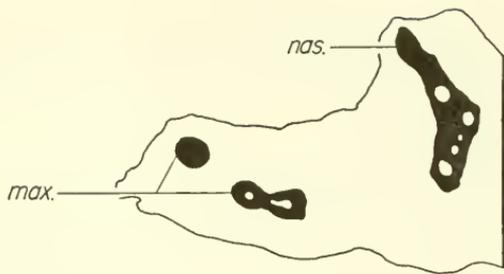
the pars palatina and pars dentalis of the maxillary and premaxillary; the prevomer is separated from the latter bones by dense connective tissue. The prevomer bears delicate anterolateral and posterolateral processes which form the anterior, medial, and posterior margins of the internal nares. The dentigerous processes of the prevomer are small and oriented at a slight angle (see Table 1) to the midline of the skull. Posteriorly the prevomer provides bony support for the olfactory eminence and articulates with the sphenethmoid.

The nasals (Pl. 8a) are extremely large. Anteriorly, the nasal terminates in spinose protuberances at the tip of the snout anteromedial to the maxillaries and premaxillaries. The nasals converge medially from their anterior termini posterior to the anterior tip of the dermal sphenethmoid. The ventrolateral margin of the nasal articulates with the pars facialis of the maxillary except where the former forms the anterior, medial, and posterior margins of the external nares. Posterolaterally, the nasal forms the bony anterior margin of the orbit. The posterior margin of the nasal articulates with the frontoparietal and the posteromedial margin with the dermal sphenethmoid. The dorsal surface of the nasal is completely involved in integumentary-cranial co-ossification. The nasal bears a moderately developed canthal ridge. The ridge extends from the anterodorsal corner of the orbit to the tip of the snout and is best developed anteriorly. The entire surface of the nasal is marked by a reticulate network of low bony ridges. The orbital margin of the nasal terminates in a slight, upturned flange bearing small, denticulate spines.

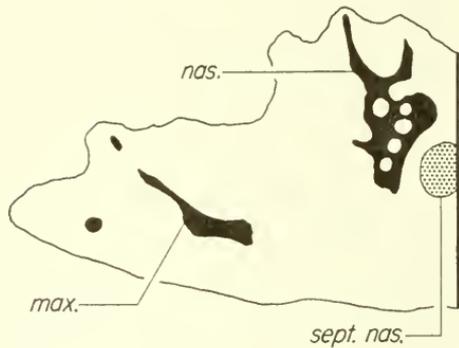
The maxillary is moderately robust. Anterior to the orbit the maxillary bears a shallow flange of spinose protuberances which decrease greatly in size ventral and posterior to the orbit. The dorsal surface of the maxillary is involved in integumentary-cranial co-ossification and is marked by a reticulate network of low, bony ridges. Medially, the maxillary bears a pars palatina dorsal to the pars dentalis. The pars palatina is best developed anterior to the orbit; ventral to the orbit, the pars palatina is barely evident. Dorsal to the pars palatina and anterior to the orbit, the maxillary bears a moderately developed pars facialis. The latter articulates with the nasal except where it forms the ventral margin to the external nares. Posteriorly, the pars facialis terminates at the anterior margin of the orbit which is formed by the nasal. The maxillary is exceptionally long; it terminates posteriorly adjacent to the posteroventral terminus of the ventral arm of the squamosal.

The anterior end of the septum nasi appears between the nasals anterior to the alary processes of the premaxillary (Figs. 62-63). The tectum nasi appears dorsolateral to the septum at the anterior end of the alary process, in subsequent sections, the septum nasi and tectum nasi fuse. A short distance posterior to the appearance of the tectum, the superior prenasal cartilage is present on the posterodorsal face of the alary cartilage (Fig. 64); the prenasal cartilage is joined laterally to the alary cartilage. The anterior end of the cavum principale lies anterior to the level of the pars dentalis of the premaxillary; the cavum (Fig. 64) is encased by the septum nasi and tectum nasi laterally and the alary cartilage laterally and ventrally. The superior prenasal cartilage fuses with the solum nasi at the level of the anterior margin of the external nares. Just posterior to the latter level, the anterior end of the cavum medium appears ventral to the cavum principale and septomaxillary. At the same level, the cartilago obliquus appears along the posteromedial surface of the alary process of

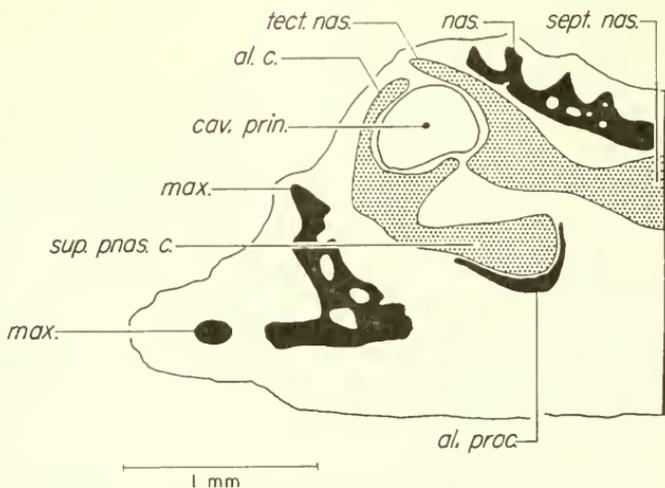
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FIGS. 62-64. Transverse sections through the anterior end of the skull of *Corythomantis greeningi* (KU 92222): (62) anterior level of nasal and maxillary; (63) anterior level of septum nasi; (64) level of cavum principale and alary process of premaxillary. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *cav. prin.*, cavum principale; *max.*, maxillary; *nas.*, nasal; *sept. nas.*, septum nasi; *sup. pnas. c.*, superior prenasal cartilage; *tect. nas.*, tectum nasi.

the premaxillary. The anterior end of the cavum inferius lies in the lateral part of the solum nasi at the level of the pars dentalis of the premaxillary. The crista subnasalis is absent. The septum nasi is ossified at the anterior level of the olfactory eminence. Ossification of the solum nasi occurs at the level of the internal naris.

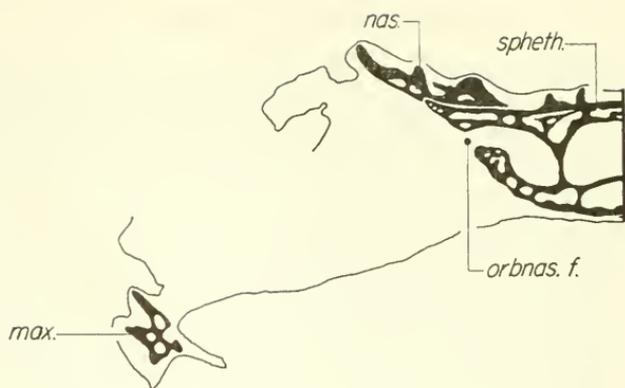
The anterior end of the septomaxillary is a delicate, arcuate-shaped bone which is horizontally oriented and lies ventrolateral to the cavum principale at the anterior level of the external naris. The anterior ramus increases in size and bifurcates medially to accommodate the lateral part of the cavum medium. In posterior sections, a slim, dorsal ramus appears. At the same level, the ventral part of the septomaxillary diverges from the anterior ramus, the latter being separated from the former by the cavum medium. The anterior ramus bifurcates into medial and lateral rami at the level of the appearance of the dorsal ramus. Posterior to the divergence of the nasolacrimal duct from the cavum medium, the ventral ramus of the septomaxillary fuses with the robust dorsal and lateral rami.

The Sphenethmoid and Orbital Region.—The frontoparietals (Pl. 8a) converge medially throughout their lengths. Anteriorly the frontoparietal articulates with the nasal; anteromedially, the frontoparietal articulates with the posterior margin of the dermal sphenethmoid. Anterolaterally, the frontoparietal extends over the orbit as a narrow shelf. The posterior margin terminates in a small, upturned, spinose occipital crest. Ventral to the crest, the frontoparietal is attached to the exoccipital; laterally, it bridges the prootic from the exoccipital to the posterior arm of the squamosal. The entire dorsal surface of the frontoparietal is involved in integumentary–cranial co-ossification. The outer margins of the bone are marked by series of small, denticulate spines; the rest of the dorsal surfaces are covered by a fine reticulate network of bony ridges.

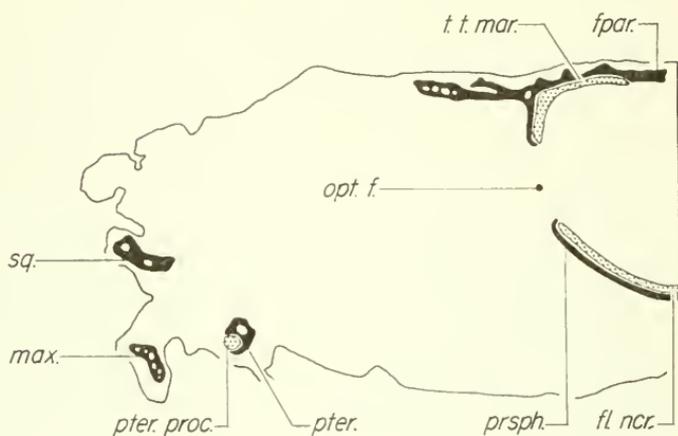
The dermal sphenethmoid (Pl. 8a) is a triangular-shaped bone centrally located at the anterior level of the orbit; the bone lies posteromedial to the nasals and anteromedial to the frontoparietals. The dermal sphenethmoid is completely involved in integumentary–cranial co-ossification and the dorsal surface of the bone is marked by a reticulate network of bony ridges. The dorsally exposed dermal sphenethmoid is confluent with the underlying endochondral sphenethmoid as is described for *Triprion petasatus* and *Hyla septentrionalis*.

Anteriorly the endochondral sphenethmoid is in synosteotic continuity with the septum nasi. It is separated from the overlying nasals and frontoparietals by a thin layer of dense connective tissue. Posterior to the planum, the sphenethmoid is completely bony; the margins of the orbitonasal foramen are bony (Fig. 65). Cartilage appears at the distal tip of the anterolateral wing of the sphenethmoid at the level of the articulation of the frontoparietal and nasal. The cartilage expands distally to form a broad supraorbital shelf. The supraorbital cartilage extends, from the sphenethmoid, ventral to the frontoparietal, laterally over the dorsal surface of the eye. The cartilage gradually diminishes in size in posterior sections. Just posterior to the terminus of the dermal sphenethmoid, the roof of the endochondral sphenethmoid splits to form the frontoparietal fontanelle ventral to the frontoparietals. The fontanelle extends posteriorly to the level of the optic foramen. At the latter level, the posterior margin of the fontanelle is formed by the tectum synoticum. A second area of cartilage is

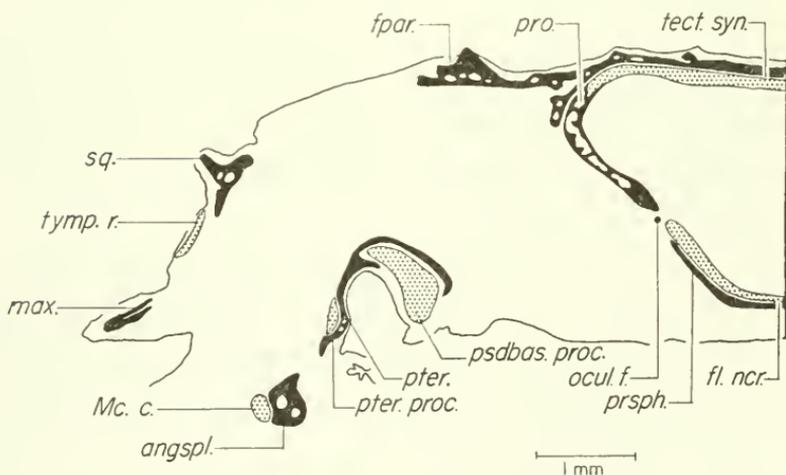
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FIGS. 65-67. Transverse sections through the skull of *Corythomantis greeningi* (KU 92222) at levels of cranial nerve foramina: (65) level of orbitonasal foramen; (66) level of optic foramen; (67) level of oculomotor foramen. Abbreviations: *angsp.*, angulospl. (angsp.); *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *nas.*, nasal; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *orbnas. f.*, orbitonasal foramen; *pro.*, prootic; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *spheth.*, sphenethmoid; *sq.*, squamosal; *t. t. mar.*, taenia tecti marginalis; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

found in the sphenethmoid at the posterior level of the orbit. The cartilage appears as the taenia tecta marginalis forming the lateral margins of the frontoparietal fontanelle. In subsequent sections, the amount of cartilage present increases; at a level anterior to the optic foramen, the entire sphenethmoid is cartilaginous.

The anterior end of the parasphenoid (Pl. 8b) lies at a level just posterior to the trochlear foramen. The parasphenoid is extremely thin and poorly developed; it lies ventral to the sphenethmoid and prootic and forms a weak bridge of support for the cartilaginous neurocranial floor. The parasphenoid is separated from adjacent bones by an exceedingly thin layer of connective tissue which is better developed anteriorly than posteriorly. The ventral surface of the parasphenoid is smooth and does not bear any odontoid structures.

The bursa angularis oris is very well developed and lies in the posterior part of the orbit. The bursa is tube-shaped and lies parallel to the jaw between the maxillary and pterygoid bones. The gland consists of a mass of lymphoid tissue loosely encased in connective tissue. The bursa is closed at the anterior and posterior ends but it bears a central lumen which lies parallel to the length of the gland. At approximately the mid-length of the bursa, the central lumen opens to the mouth.

The Otic and Occipital Regions.—In dorsal view (Pl. 8a), the squamosal is an arcuate bone which extends posteriorly from the posterior edge of the orbit to the level of the occipital crest. The dorsolateral margin of the squamosal bears a series of small, denticulate spines and is involved in integumentary-cranial co-ossification. The anterior arm of the squamosal is moderately robust. It forms part of the posterior margin of the orbit and terminates ventrally on the dorsal surface of the maxillary. The articulation of the anterior arm of the squamosal on the maxillary is loose; the two bones are separated by dense connective tissue. The posterior arm of the squamosal is shorter than the anterior arm; the former terminates at the posterolateral corner of the frontoparietal. The posterior arm articulates medially with the frontoparietal or is separated from the latter by connective tissue. The ventral arm of the squamosal extends posteroventrally from the mid-point of the arc formed by the anterior and posterior arms of the squamosal; posteroventrally, the terminus lies dorsal to the quadrate process between the posterior ramus of the pterygoid and the posterior end of the maxillary.

The pterygoid is well developed (Pl. 8b). The anterior end of the anterior ramus lies at a level just posterior to that of the orbitonasal foramen. The anterior ramus extends posteriorly adjacent to the maxillary and posterior maxillary process. At a level slightly anterior to the posterior end of the pars dentalis of the maxillary, the pterygoid and pterygoid process diverge medially from the maxillary. The posterior ramus articulates with the quadrate process and ventral arm of the squamosal. The medial ramus is strong and articulates firmly with the ventral ledge of the otic capsule.

The quadratojugal is small and poorly developed. The anterior end (Fig. 68) lies midway between the levels of the prootic foramen and anterior acoustic foramen. Anteriorly, the quadratojugal is a small rod of bone lying medial to the maxillary and separated from the latter by an extensive layer of dense connective tissue. In subsequent posterior sections, the bone increases slightly in size and becomes involved in ossification of the quadrate process at the

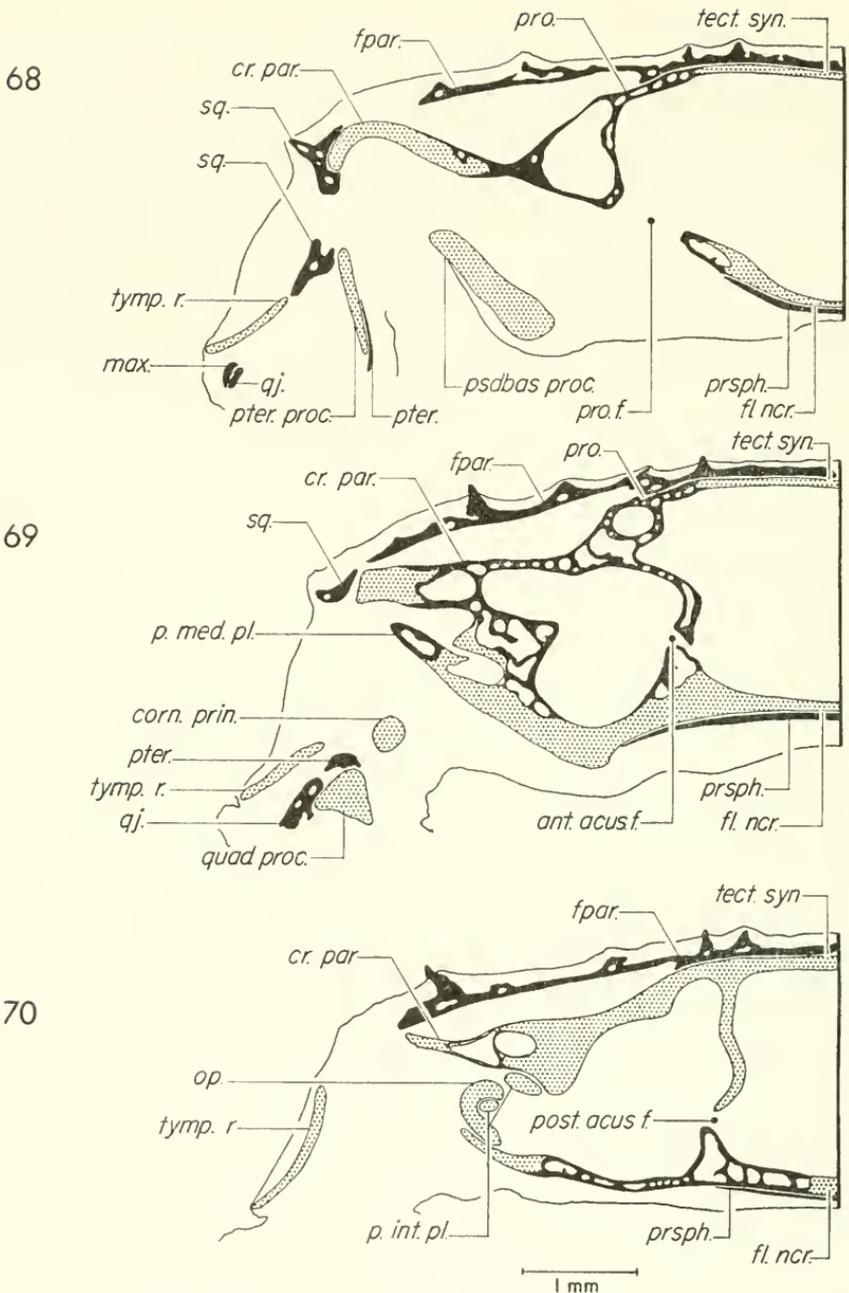
anterior level of the posterior acoustic foramen. The posterior terminus of the quadratojugal lies at the mid-level of the posterior acoustic foramen.

The anterior, dorsal, and ventral margins of the optic foramen (Fig. 66) are bony and formed by the lamina perpendicularis dorsally and the parasphenoid ventrally; posteriorly the bony margin of the foramen is formed by the prootic. The trochlear foramen lies dorsally adjacent to the prootic in the posterodorsal part of the optic foramen. The optic and trochlear foramina are separated by connective tissue. The oculomotor foramen (Fig. 67) lies posterior and slightly ventral to the optic foramen. The margins of the oculomotor foramen are bony. The prootic foramen (Fig. 68) lies immediately posterior and slightly dorsal to the oculomotor foramen. The margins of the prootic foramen are bony. There are two acoustic foramina. The anterior acoustic foramen (Fig. 69) lies at the level of the pars media plectri and is bordered by bone. The anterodorsal margin of the posterior acoustic foramen (Fig. 70) lying at the level of the pars interna plectri and anterior end of the operculum, is cartilaginous, whereas the ventral and posterior margins of the foramen are bony. The margins of the jugular foramen, posteriorly, are bony.

The pseudobasal process (Fig. 67) appears at the anterior level of the prootic foramen. The process lies lateral to the neurocranium and slightly posterior to its appearance, the pseudobasal process expands dorsolaterally into the otic process. The otic process lies medially adjacent to the anterior arm of the squamosal. For a short distance, the otic process is continuous with the pseudobasal process ventromedially and the pterygoid process ventrolaterally. The otic process diverges from the pseudobasal process at the mid-level of the prootic foramen. At a slightly posterior level, the otic process is separated from the pterygoid process by the squamosal; at the same level, the otic process joins the otic capsule medially to form the crista parotica (Fig. 68). Just posterior to the latter fusion, the cornu principalis of the hyale diverges laterally from the pseudobasal process.

The pars externa and pars ascendens plectri are cartilaginous and appear just anterior to the level of the anterior acoustic foramen. At the level of the anterior acoustic foramen and the fusion of the pars ascendens and pars externa plectri, the pars media plectri appears distally, fused to the dorsum of the pars externa plectri. Laterally, the pars media plectri is cartilaginous; medially, it is bony. In subsequent sections, the bony pars media plectri moves medially; at the anterior margin of the posterior acoustic foramen, the pars media plectri fuses with the lateral edge of the otic capsule. The pars interna plectri is cartilaginous and lies posteromedial to the pars media plectri. The cartilaginous operculum appears just posterior, at the mid-level of the posterior acoustic foramen (Fig. 70) and terminates posterior to the posterior acoustic foramen.

At the posterior level of the optic foramen, the prootic is ossified only peripherally at the margins of the foramen; the floor and roof of the neurocranium are cartilaginous. In posterior sections, ossification progresses from the level of the optic foramen dorsomedially in the neurocranium. At the level of the prootic foramen, the sides of the braincase are ossified, but the floor of the neurocranium and the tectum synoticum dorsally are cartilaginous. The tectum synoticum is cartilaginous throughout its length, whereas a moderate invasion of bone occurs in the neurocranial floor. At the terminus of the cranium, the ventromedial part of the neurocranial floor is cartilaginous. The pars externa plectri,



FIGS. 68-70. Transverse sections through the skull of *Corythomantis greeningi* (KU 92222) at levels of cranial nerve foramina: (68) level of prootic foramen; (69) level of anterior acoustic foramen; (70) level of posterior acoustic foramen. Abbreviations: *ant. acus. f.*, anterior acoustic foramen; *corn. prin.*, cornu principalis; *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *op.*, operculum; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *post. acus. f.*, posterior acoustic foramen; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *psdbas. proc.*, pseudo-basal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *quad. proc.*, quadrate process; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

pars ascendens plectri, pars interna plectri, and operculum are cartilaginous. The distal and medial tips of the pars media plectri are cartilaginous; centrally, the bone is well ossified. The distal part of the crista parotica, adjacent to the squamosal, is cartilaginous; medially, the crista parotica and the dorsal part of the otic capsule are ossified, whereas the otic capsule floor is cartilaginous. Posteriorly, ossification decreases in dorsal parts of the otic capsule and increases in ventral parts. At the level of the posterior acoustic foramen, only the distal tip and part of the floor of the otic capsule are ossified. At the level of the jugular foramen, the skull is bony with the exceptions of the dorso- and ventromedial parts of the braincase and the posterodorsal part of the otic capsule.

The Articular Region.—Anterior to the articular region, Meckel's cartilage lies dorsolateral to the angulosplenic bone. Posteriorly, the cartilage assumes a position dorsal to the angulosplenic bone and then enlarges and comes to lie in close association with the posterior ramus of the pterygoid, the ventral arm of the squamosal, and the quadrate process at the posterior level of the pars media plectri. At the level of the posterior acoustic foramen, the ossification of the quadratojugal invades the cartilage of the quadrate process. The quadratojugal, maxillary, and posterior ramus of the pterygoid terminate at the posterior margin of the posterior acoustic foramen. At a slightly posterior level the squamosal terminates; the disappearance of the latter is followed by the termination of the quadrate process. Meckel's cartilage persists a short distance posteriorly.

Remarks.—The only variation noted among three males of *Corythomantis greeningi* was in the posterior development of the frontoparietal. The smallest specimen (11.2 mm. head length) shows the least development of this bone. The posterior margin of the frontoparietal bears no occipital crest and does not articulate with the bony part of the exoccipital. Posterolaterally, the frontoparietal bears a flange which extends over the anteromedial part of the crista parotica but does not articulate with the squamosal. A slightly larger individual (13.3 mm. head length) has a better developed frontoparietal. The frontoparietal articulates with the exoccipital posteriorly, but does not terminate in an upturned flange; lateral development of the frontoparietal is unchanged from the condition of the smaller specimen. The third specimen (head length 14.1 mm.) is fully developed.

The skull of *Corythomantis greeningi* bears a clear resemblance to a species (Fig. 71a) known from Jacareacanga, Pará Province, Brazil (represented by specimens in the collections of the University of Kansas and of Werner C. A. Bokerman, São Paulo, Brazil), which is an undescribed member of the species complex called *Hyla rubra*. The skull of this species differs from that of *Hyla rubra* (Fig. 71b) from Jacareacanga in the following aspects: the skull is longer in proportion to its width than in *H. rubra*; the sphenethmoid is rounded anteriorly, whereas it is truncate in *H. rubra*; the anterior arm of the squamosal articulates with the maxillary, whereas in *H. rubra* it does not; and the parasphenoid is poorly developed.

Comparison of plate 8a and figure 71a shows the similarity of *Corythomantis greeningi* to this unnamed species of the *Hyla rubra* group. The shapes and proportions of the two skulls resemble one another. Both have extensive squamosals, poorly developed parasphenoids, and pterygoids having medial

rami which articulate with the prootic. There is a poorly developed palatine in the unnamed species and no palatine in *C. greeningi*. Internally, the cranial structures of these species resemble one another in general pattern, and notable similarities occur in the structure of the septomaxillary and the bursa angularis oris. The primary difference noted in internal structure is the presence of the crista subnasalis in the unnamed species. Externally, this species resembles *Hyla rubra* in size, character of the feet and general appearance. Osteologically, the long, narrow skull has a small prootic region and extremely large nasals; these characters relate this frog to the *Hyla rubra* group.

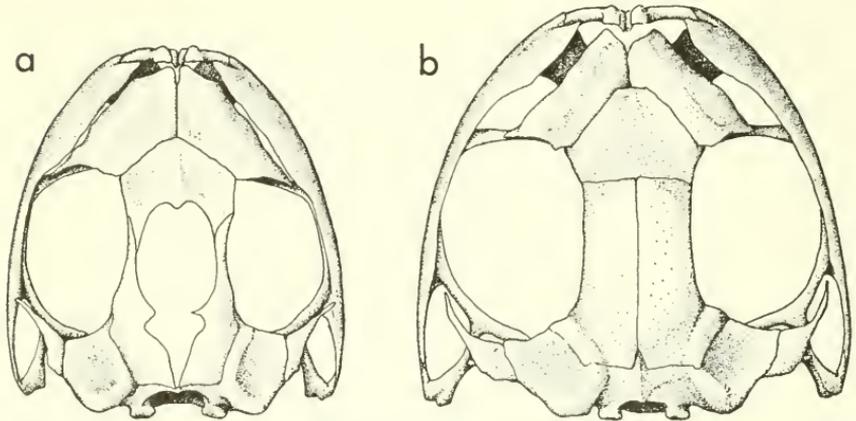


FIG. 71. Dorsal views of skulls of *Hyla rubra*, $\times 4.5$: (a) KU 92151 from Jacareacanga, Para, Brazil; (b) KU 104411 from Santa Cecilia, Napo, Ecuador.

Cranial Morphology of *Aparasphenodon brunoi*

The skull of *Aparasphenodon brunoi* is longer than wide (Pl. 9a). The snout, in dorsal view, is narrow and acuminate. All dorsal surfaces of the skull are involved in integumentary-cranial co-ossification. Dorsally, all dermal bones are sculptured in patterns of pronounced parallel ridges. The termination of these ridges at the distal margins of all dermal bones results in delicate series of extremely small spinules. The latter are best developed on the outer edge of the maxillary, the canthal ridge near the orbit, on the nasal and frontoparietal at the margin of the orbit and at the posterior edge of the frontoparietals. *Aparasphenodon* lacks a well developed occipital crest. The skull of *Aparasphenodon* is characterized by an acuminate snout; the presence of a dermal sphenethmoid and prenasal, a moderate labial flange on the maxillary, angled vomerine teeth (see Table 1), and the presence of a prominent anteroventral crest on the base of the parasphenoid. The vocal sac is single, median, and subgular.

The Olfactory Region.—The prenasal (Pl. 9a) lies anterior to the premaxillaries and nasals and between the anterior ends of the maxillaries. The bone is flat ventrally; dorsally, it bears a broad medial ridge marked with longitudinal, parallel ridges. The anterior tip of the prenasal bears a group of short spines. The prenasal lacks a labial flange. Posterolaterally, the prenasal articulates with the maxillary; posteromedially, it articulates with the anterior margins of the

nasals, except where it forms the anterior margin of the external nares. Ventrally, the prenasal is not co-ossified. It articulates posterolaterally with the labial flanges of the maxillaries. The ventromedial margin of the prenasal is free and lies anterior to the medial articulation of the premaxillaries. Internally, the anterior end of the prenasal contains many small cavities. A short distance posterior to the anterior end a single, central cavity appears which houses the anterior end of the septum nasi. In subsequent sections, the anterolateral corners of the tectum nasi appear laterally, adjacent to the prenasal. Slightly posterior, the dorsal and ventral parts of the prenasal split to form the external nares; at this level the external part of the tectum nasi fuses medially with the septum nasi. Posterior to the fusion of the tectum and septum nasi, the prenasal consists of an upper plate of bone overlying the septum and tectum nasi dorso-medially and a lower plate of bone underlying the nasal cartilages and alary processes of the premaxillary. Ventrally, the prenasal is separated from the maxillary by dense connective tissue. Dorsomedially, the prenasal overlaps the nasals posteriorly.

The premaxillaries (Pl. 9b) lie posterior to the prenasal and the anterior ends of the labial flanges of the maxillary. Dense connective tissue separates the maxillary from the anterolateral edges and lateral corners of the premaxillaries. The premaxillaries are narrowly separated medially by connective tissue. A small, inconspicuous palatine process is present posteromedially on the premaxillary. The alary process of the premaxillary is long, dorsally concave, and inclined anteriorly at approximately a 45-degree angle. The process is straight and lies just dorsal to the ventral plate of the prenasal. The anterior end of the alary process lies at the level of the anterior bony margin of the external nares.

In ventral view (Pl. 9b), the prevomer lies lateral to the midline of the skull, and ventral to the solum nasi and sphenethmoid. The anterolateral corner of the prevomer lies dorsal to the pars dentalis of the premaxillary and the labial flange of the maxillary. At the level of the palatine process of the premaxillary, the crista subnasalis diverges from the solum nasi and the prevomer thickens around the lateral edge of the solum to form a robust bony support for the olfactory eminence. The prevomer bears well developed lateral wings that form the anterior and medial margins of the internal nares. The prevomerine dentigerous processes are large and form an angular pattern (see Table 1).

The palatine is a robust bone that lies posterior to the internal naris. The broad, distal end is lodged in connective tissue dorsal to the pars palatina of the maxillary and adjacent to the anterior maxillary process and pars facialis of the maxillary. The proximal end of the palatine lies ventral to the lateral, bony edge of the sphenethmoid and is separated from the sphenethmoid by a thin layer of dense connective tissue. The palatine bears a prominent ridge which terminates ventrally in a series of delicate odontoid spines.

The nasal is extremely large. Anteriorly, this bone articulates with the prenasal except where the former forms the posterior margins of the external naris. Laterally it articulates with the pars facialis of the maxillary and posterolaterally it forms the bony anterior margin of the orbit. The nasals converge anteromedially to the dermal sphenethmoid. The posterior margin of the nasal articulates with the frontoparietal dorsolaterally and the dermal sphenethmoid dorsomedially. The dorsal surface of this bone is completely involved in integumentary-cranial co-ossification. It bears a well developed canthal ridge extend-

ing from the posteromedial edge of the external naris to the anterodorsal corner of the orbit, where a series of small, deep pits appear in the ridge. A series of prominent ridges radiate out over the surface of the nasal from the posterior crest of the ridge. The ridges are best developed along the crest of the ridge and on the dorsal surface of the nasal.

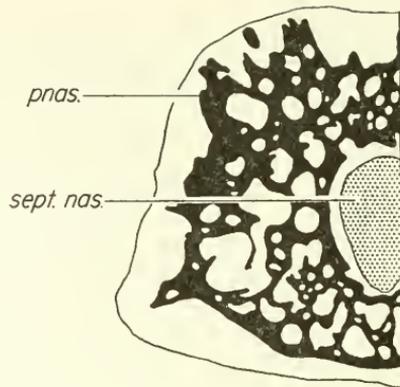
The maxillary is moderately robust and bears a relatively narrow flange which is most evident in ventral and lateral views. The flange is most extensive anterior to the premaxillaries. At this level and for a short distance posteriorly, the flange is horizontally oriented. At a level slightly anterior to the orbit, the maxillary flange diminishes in size and gradually assumes a more nearly vertical orientation lateral to the pars dentalis of the maxillary. The dorsal surface of the maxillary is involved in integumentary-cranial co-ossification; the ventral and lateral surfaces are not co-ossified. The pars facialis and pars palatina are well developed anteriorly; they diminish in size ventral to the orbit. The maxillary terminates posteriorly on the outer edge of the quadratojugal.

The anterior end of the nasal capsul lies far forward in the cranium, just posterior to the anterior end of the prenasal. The cartilaginous septum nasi projects anteriorly into a small medial cavity in the anterior tip of the prenasal (Fig. 72). The anterior corners of the tectum nasi exterior to the prenasal (Fig. 73), fusing with the septum a short distance posterior at the anterior margin of the external nares (Fig. 74). At a level just anterior to the fusion of the tectum and septum, the alary cartilage and superior prenasal cartilage appear ventral to the tectum, associated with the anterior tip of the alary process of the premaxillary. The lateral expansion of the solum separates the alary cartilage from the superior prenasal cartilage; the latter terminates at the level of the anterior end of the cavum medium. The inferior prenasal cartilage appears on the dorsomedial face of the alary process at the anterior ends of the recessus medialis and recessus lateralis of the cavum inferius; the inferior prenasal cartilage fuses with the solum posteriorly at a level just anterior to the formation of the planum terminale. A short crista subnasalis is present at the level of the palatine process of the premaxillary. The septum nasi is partly ossified at the anterior margin of the internal nares. At this level, cartilaginous lateral remnants of the solum are present in the olfactory eminence; the ventromedial part of the solum has been replaced by the prevomer. In posterior sections, at the mid-level of the internal nares, all cartilage is replaced by bone except the anterior maxillary process.

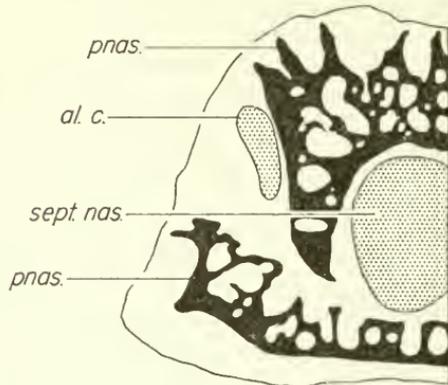
The anterior end of the septomaxillary is a horizontally oriented bar of bone, lying ventrolateral to the cavum principale at the mid-level of the external naris. The bone thickens laterally around the lateral edge of the cavum medium. As the cavum enlarges, it comes to lie within the septomaxillary. In cross-section, the latter resembles a "U" lying on its side with the open end facing ventromedially. In slightly posterior sections, the ventral side diverges from the main body of the U as the ventral ramus of the septomaxillary; the remaining dorsal part of the septomaxillary develops a vertically oriented dorsal ramus and then bifurcates into medial and lateral rami. The dorsal ramus is associated with the lateral septomaxillary ramus. Posterior to the lateral divergence of the nasolacrimal duct from the cavum medium, the ventral ramus of the septomaxillary fuses with the dorsolateral ramus.

The Sphenethmoid and Orbital Regions.—The frontoparietal articulates

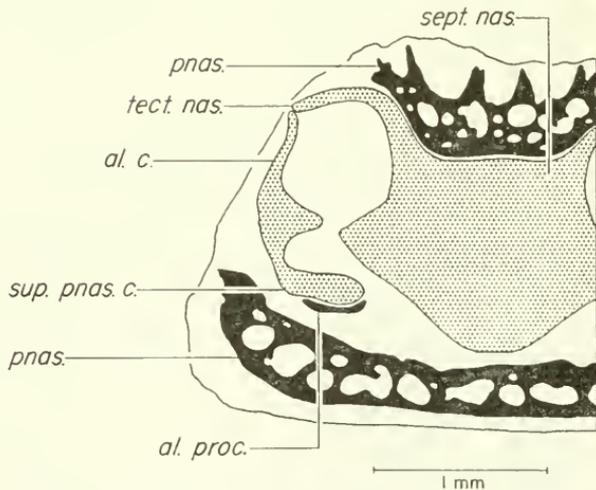
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FIGS. 72-74. Transverse sections through the anterior end of the skull of *Aparasphenodon brunoï* (KU 92214): (72) level of prenasal and anterior end of septum nasi; (73) anterior level of tectum nasi; (74) anterior level of alary cartilage and alary process of premaxillary. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *pnas.*, prenasal; *sept. nas.*, septum nasi; *sup. pnas. c.*, superior prenasal cartilage; *tect. nas.*, tectum nasi.

anterolaterally with the nasal and anteromedially with the dermal sphenethmoid (Pl. 9a). It forms a broad, bony supraorbital shelf and articulates posterolaterally with the squamosal. The frontoparietals converge medially throughout their entire lengths. The posterior margin of the frontoparietal overhangs the exoccipital medially, and laterally bridges the prootic to the squamosal. The dorsal surface of the frontoparietal is involved in integumentary-cranial co-ossification. The central part of the frontoparietal is pitted and rugose. From this area, ridges radiate out to all margins of the bone.

The dermal sphenethmoid is roughly triangular in shape, the base of the triangle being arcuate rather than flat. The bone lies posteromedial to the nasals and anteromedial to the frontoparietals. The dorsal surface of the dermal sphenethmoid is completely co-ossified and, like the frontoparietal, bears a central rugose area with a radiation of ridges peripherally. The dorsally exposed sphenethmoid is confluent with the underlying endochondral sphenethmoid as described in *Tripriion petasatus*, *Hyla septentrionalis*, and *Corythomantis greeningi*.

The endochondral sphenethmoid is in synosteotic continuity with the septum nasi anteriorly and is separated from overlying nasals and frontoparietals by a thin layer of dense connective tissue. Posterior to the planum antorbitale a small amount of cartilage remains in the dorsolateral corners of the sphenethmoid which lie ventral to the posterodorsal crests of the cantal ridges. This cartilage persists at the distal tip of the anterolateral wing of the sphenethmoid underlying the bony supraorbital shelf of the nasal and the anterior part of the frontoparietal. The margins of the orbitonasal foramen are bony (Fig. 75). Posterior to the terminus of the dermal sphenethmoid, the roof of the endochondral sphenethmoid splits to form the frontoparietal fontanelle ventral to the frontoparietals. Anteriorly, the margins of the fontanelle are bony; posteriorly, at about the mid-level of the orbit, the dorsolateral parts of the sphenethmoid are only partly ossified. From this level, posterior to the terminus of the sphenethmoid at the optic foramen, ossification decreases, and the margins of the frontoparietal fontanelle are formed by the cartilaginous taenia tectamarginalis.

The anterior end of the parasphenoid (Pl. 9b) lies at a level near the posterior end of the dermal sphenethmoid. Anterior to the otic capsule, the parasphenoid is extremely delicate and narrowly separated from the sphenethmoid and prootic dorsally. Posteriorly, at the anterior level of the otic capsule, the parasphenoid develops an unusual, conspicuously thickened, bony, ventral ridge which is transversely oriented. The ridge terminates laterally in thin, ventral projections which face anteroventral knob-like projections of the otic capsule. In sections posterior to this ridge, the parasphenoid becomes thinner and gradually narrows to a terminal point. The ventral surface of the parasphenoid does not bear any odontoid structures.

A bursa angularis oris is present in the posterior part of the orbit. The position and organization of the gland closely resembles that described for *Corythomantis greeningi*.

The Otic and Occipital Regions.—In dorsal view (Pl. 9a), the squamosal is a long, slim bone which extends from the posterior part of the orbit posteriorly to a level slightly beyond the posterior edge of the frontoparietal. The dorsal surface of the squamosal is co-ossified. The anterior arm of the squamosal is

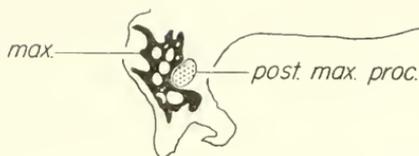
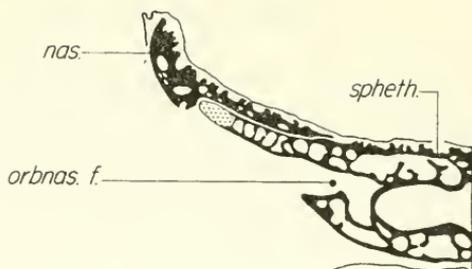
robust, laterally compressed, and extends slightly more than two-thirds the distance from the junction of the ventral and anterior arms of the squamosal to the maxillary. The posterior arm of the squamosal is equally as robust as the anterior arm but slightly shorter. The posterior arm lies adjacent to the posterolateral part of the frontoparietal but does not articulate with it. Ventral to the frontoparietal, the posterior arm of the squamosal bears a medial flange which articulates with the dorsolateral edge of the crista parotica. The ventral arm extends posteroventrally from approximately the midpoint of the arc formed by the anterior and posterior arms of the squamosal; posteroventrally, the terminus lies between the posterior ramus of the pterygoid and the quadratojugal.

The pterygoid is well developed (Pl. 9b). The anterior terminus of the anterior ramus of the pterygoid lies dorsal to the pars dentalis of the maxillary and medially adjacent to the posterior maxillary process in the anterior part of the orbit. The posterior ramus articulates with the ventral arm of the squamosal and the quadrate process posteriorly. The medial ramus is in contact with the prootic but does not bear a firm, bony articulation with it.

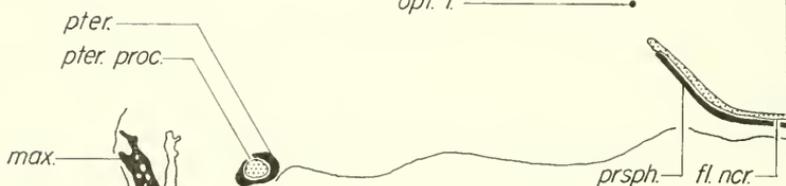
The quadratojugal lies along the medial surface of the posterior part of the maxillary. The anterior end lies at the posterior level of the optic foramen. The maxillary terminates posteriorly at the anterior level of the acoustic foramen. The quadratojugal terminates posteriorly on the quadrate process. The anterior border of the optic foramen (Fig. 76) is cartilaginous; the lamina perpendicularis of the frontoparietal forms the bony anterodorsal margin and the parasphenoid the anteroventral margin of the foramen. The prootic ossifies to provide the bony posterior margins of the optic foramen. A bridge of bone separates the optic foramen from the more posterior oculomotor foramen (Fig. 77). The margins of the latter are bony. The oculomotor foramen is very narrowly separated by bone from the large prootic foramen (Fig. 78) lying posterior. There is only one acoustic foramen (Fig. 79); it is entirely bordered by bone as is the posterior jugular foramen (Fig. 80).

The pseudobasal process (Fig. 78) first appears posterior to the level of the oculomotor foramen. The anterior tip of the crista parotica (Fig. 78) lies midway between the otic capsule and the squamosal at the mid-level of the prootic foramen. In posterior sections, the crista expands medially to establish a bony connection with the otic capsule and laterally in cartilage to the squamosal. The otic process then diverges ventrally from the crista parotica and fuses first with the pseudobasal process at the level of the posterior margin of the prootic foramen, and then the pterygoid process. At the level of the latter fusion, the ventral ledge of the otic capsule and pseudobasal process fuse. In slightly posterior sections, the otic process terminates, separating the pterygoid process and ventral ledge of the otic capsule from one another and the distal tip of the crista parotica dorsally. Ventrally, the cornu principalis diverges from the ventral, cartilaginous ledge of the otic capsule. The bony medial tip of the pars media plectri appears at the anterior levels of the acoustic foramen and is followed by the pars interna plectri. In posterior sections, the pars media plectri expands laterally toward the pars externa plectri. The latter is connected to the distal tip of the crista parotica by the pars ascendens plectri. The operculum, and the posterior and distal parts of the pars media plectri and pars externa plectri lie at the posterior levels of the acoustic foramen. The operculum terminates posteriorly just anterior to the jugular foramen.

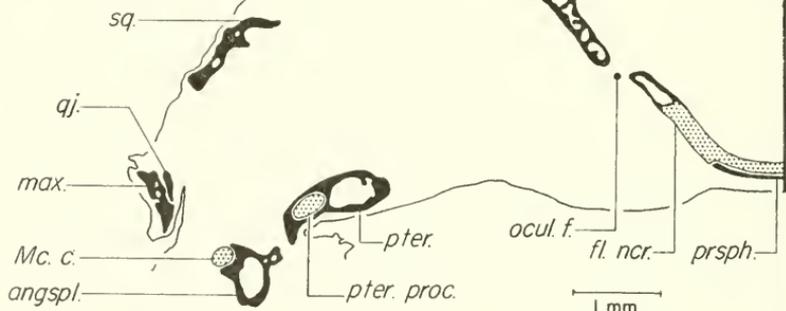
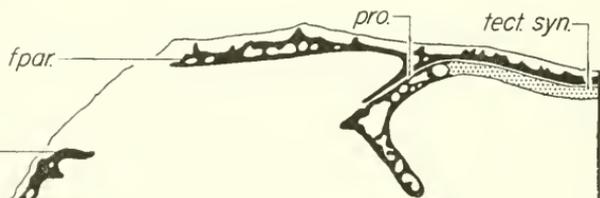
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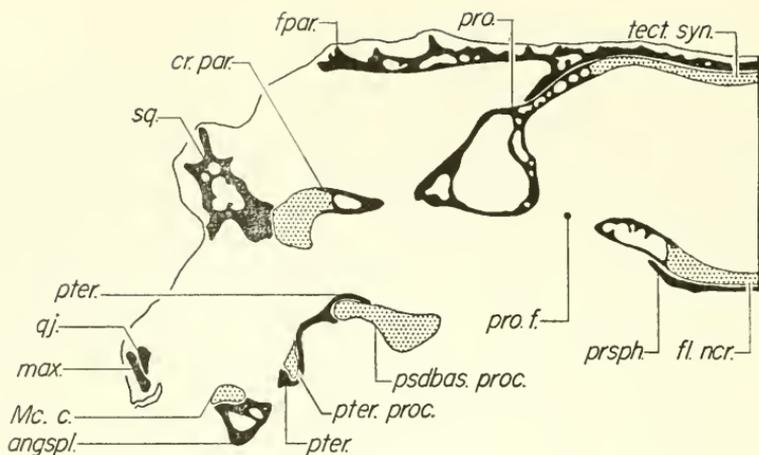
FIGS. 75-77. Transverse sections through the skull of *Aparasphenodon bruno* (KU 92214) at levels of cranial nerve foramina: (75) level of orbitonasal foramen; (76) level of optic foramen; (77) level of oculomotor foramen. Abbreviations: *angsp.*, angulosplenial; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *nas.*, nasal; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *orbnas. f.*, orbitonasal foramen; *post. max. proc.*, posterior maxillary process; *pro.*, prootic; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *spheth.*, sphenethmoid; *sq.*, squamosal; *t. t. mar.*, taenia tecti marginalis; *tect. syn.*, tectum synoticum.

At the posterior level of the optic foramen, the prootic is sparsely ossified around the margins of the foramen. The trochlear foramen lies dorsally adjacent to the lamina perpendicularis of the frontoparietal and within the bony margins of the optic foramen. The trochlear and optic nerves are separated by connective tissue. In more posterior sections, ossification gradually invades the cartilage of the tectum synoticum dorsally, and posterior to the oculomotor foramen, the floor of the neurocranium ventrally. The central part of the tectum, the floor of the neurocranium and the ventrolateral part of the otic capsule are cartilaginous at the anterior level of the acoustic foramen; whereas the dorsal parts of the otic capsule are bony at this level. In the vicinity of the posterior end of the acoustic foramen, the floor of the otic capsule and neurocranium is ossified except for a small ventromedial part of the neurocranial floor which remains cartilaginous. The dorsal part of the otic capsule and the neurocranial roof are almost exclusively cartilaginous at this level. Between the posterior end of the acoustic foramen and the jugular foramen, ossified tissue reappears dorsally; thus, at the level of the jugular foramen, the tectum is restricted to a small dorsomedial area of cartilage and the dorsal parts of the otic capsule are ossified medially but not laterally. The pars externa plectri, pars ascendens plectri, pars interna plectri, operculum, and distal tip of the crista parotica are cartilaginous. The pars media plectri is bony.

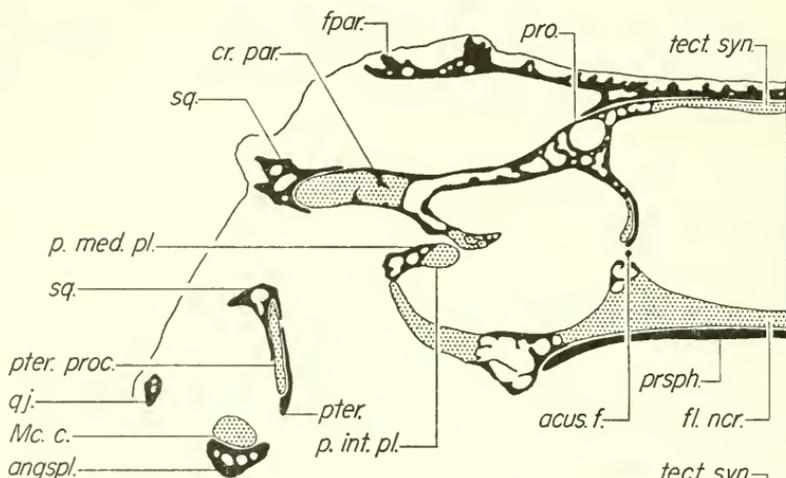
The Articular Region.—Anterior to the articular region, Meckel's cartilage lies dorsolateral to the angulosplenial bone. Posteriorly, the cartilage assumes a position dorsal to the angulosplenial bone and then enlarges and comes to lie in close association with the posterior ramus of the pterygoid, the ventral arm of the squamosal, and the quadrate process. At the posterior level of the acoustic foramen, the posterior ramus of the pterygoid fuses for a short distance with the ventral arm of the squamosal and the ossification of the quadratojugal invades the cartilage of the quadrate process. The pterygoid and squamosal persist posteriorly at the level of the jugular foramen, but the ossification of the quadratojugal has disappeared. Some perichondral ossification appears on the adjacent surfaces of the quadrate process and Meckel's cartilage. The quadrate process is the most posterior element of the articular region.

Remarks.—Variation noted among four specimens of *Aparasphenodon brunoi* is ontogenetic and involves the development of dermal bones, principally the prenasal, maxillary, frontoparietal, squamosal, and pterygoid. In a juvenile (head length 13.7 mm.), the external nares lie near the end of the snout, the cristae paroticae are visible in dorsal view, the maxillaries are widely separated anteriorly, the anterior and posterior arms of the squamosal have a poorly developed dorsal flange, and the parasphenoid lacks the transverse ridge characteristic of the adult. In a slightly larger individual (head length 18.6 mm.), the prenasal is better developed anteriorly, but the maxillaries are still widely separated anteroventrally; only the posterolateral corners of the cristae paroticae are visible dorsally because of the lateral growth of the frontoparietal. In this specimen, the parasphenoid bears two prominent lateral knobs; the transverse ridge is not developed. A specimen with a head length of 21.1 mm. has a prominent prenasal. The frontoparietal nearly reaches the squamosal laterally and the dorsal flange of the squamosal is even with the level of the frontoparietal in lateral view. Ventrally, the maxillaries are widely separated anteriorly, but the parasphenoid has developed a weak transverse ridge. The

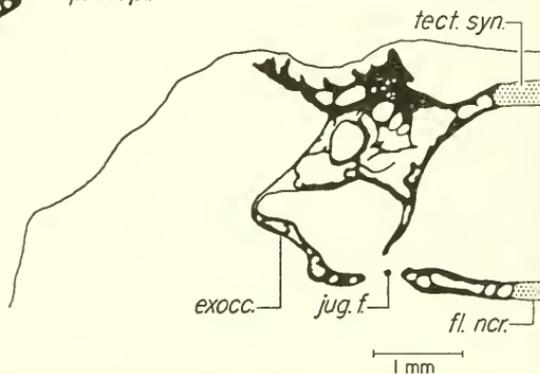
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FIGS. 78-80. Transverse sections through the skull of *Aparasphenodon bruni* (KU92214) at levels of cranial nerve foramina: (78) level of prootic foramen; (79) level of acoustic foramen; (80) level of jugular foramen. Abbreviations: *acus. f.*, acoustic foramen; *angspl.*, angulosplenic; *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *jug. f.*, jugular foramen; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

largest individual (head length 25.4 mm.) is a fully developed adult. In contrast to the smaller specimens, the prenasal extends farther anterior to the external nares making the snout seem highly acuminate by comparison. The extensive posterolateral development of the frontoparietals completely conceals the auditory region in dorsal view. Anteroventrally, the maxillaries are narrowly separated medially thus separating the prenasal anteriorly from the premaxillaries posteriorly. The parasphenoid bears prominent lateral knobs and a well developed transverse ridge.

Cranial Morphology of *Pternohyala*

The skull of *Pternohyala* is as wide as it is long (*P. dentata*) or slightly wider than long (*P. fodiens*) (Pl. 10a, b). Most of the dorsal surfaces of the skull are involved in integumentary-cranial co-ossification. Dorsally, all dermal bones are covered with small spines which are interconnected by a reticulate network of bony ridges (Pl. 10a). The distal margins of dermal roofing bones, and the squamosals and maxillaries terminate in delicate spinose protuberances. The skull of *Pternohyala* is characterized by a dorsally exposed sphenethmoid, the absence of a dermal sphenethmoid and prenasal, and massive maxillaries which lack extensive labial flanges. The vocal sac is bilobed and subgular. The following description is based on *Pternohyala dentata*, the least specialized member of the genus; differences noted in the cranial morphology of *P. fodiens* will be discussed in a separate section.

The Olfactory Region.—The premaxillaries (Fig. 81c, d) are moderately small, and lie slightly recessed to the anterior ends of the maxillaries (Fig. 82). The lateral corners of the premaxillaries are covered by the maxillaries; otherwise, the bones are externally exposed and not involved in integumentary-cranial co-ossification. The premaxillaries are separated medially from one another, and laterally from the maxillaries, by dense connective tissue. Ventromedially, each premaxillary is vertically oriented and about three times as long as the depth of the pars dentalis of the premaxillary. The process is convex anteriorly, and in contact with the alary cartilage and septum nasi dorsally.

In ventral view, the prevomer (Fig. 81d) lies lateral to the mid-line of the skull and ventral to the solum nasi and sphenethmoid. The anterior end of the prevomer is associated with the ventrolateral part of the lateral margin of the solum nasi (Fig. 84); the bone lies adjacent to the anteromedial edge of the maxillary. The prevomer does not articulate with the premaxillary. The prevomer bears delicate anterolateral and posterolateral processes which form the anterior and medial margins to the internal nares. The denticigerous processes of the prevomer are small and oriented at a slight angle (see Table 1) to the mid-line of the skull. Internally, the prevomer bears a delicate dorsal process which forms a bony support for the olfactory eminence. Posteriorly, the prevomer articulates with the sphenethmoid.

The palatine (Fig. 81d) is a robust bone which lies posterolateral to the internal naris. The distal base of the palatine is broad and flat and lies in connective tissue between the cartilaginous transition zone of the planum ant-orbitale and solum nasi and the pars palatina of the maxillary. Medially, the palatine articulates with the sphenethmoid posterior to the prevomer. The bone bears a conspicuous longitudinal ridge oriented posteroventrally; the ridge is smooth and the palatine edentate.

The nasal is moderately large (Fig. 81). Anteriorly, the bone terminates in a point at a level just posterior to the alary process of the premaxillary. The nasals converge medially, dorsal to the cartilaginous septum nasi (Fig. 84). At the anterior level of the internal nares the nasals diverge medially to expose dorsally the posterior, ossified part of the septum nasi; the latter is continuous with the sphenethmoid posteriorly. All margins of the nasal are free except the anteromedial edge and the posteroventral corner, which articulates with the

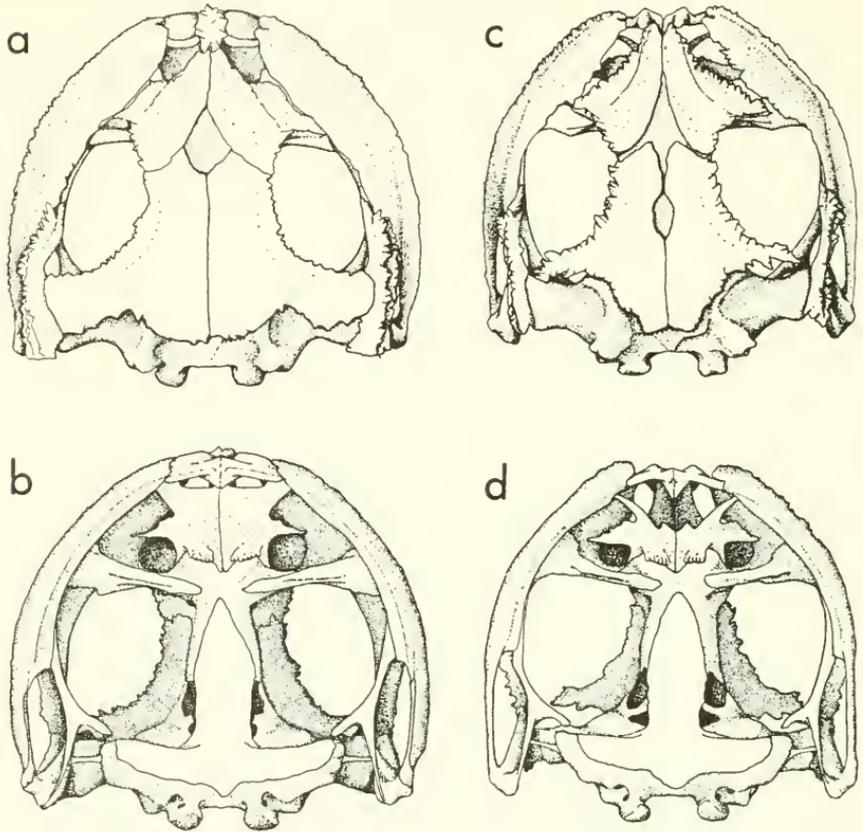


FIG. 81. Skulls of adult *Pternohyla*. (a and b) dorsal and ventral views of the skull of *Pternohyla fodiens*, ♂ (KU 86615); (c and d) dorsal and ventral views of the skull of *Pternohyla dentata*, ♀ (KU 106293). $\times 3.7$.

pars facialis of the maxillary. The canthal ridge is only moderately well developed; it extends from the anterior tip of the nasal to the anterodorsal corner of the orbit. The surfaces of the nasal lateral and medial to the canthal ridge are involved in integumentary-cranial co-ossification and are marked by a reticulate network of ridges and small spines. The posterior surface of the maxillary process of the nasal is smooth and is not co-ossified.

The maxillary is massive. The dorsal surface of the maxillary bears integumentary-cranial co-ossification marked by ridge and spines, but the outer edge

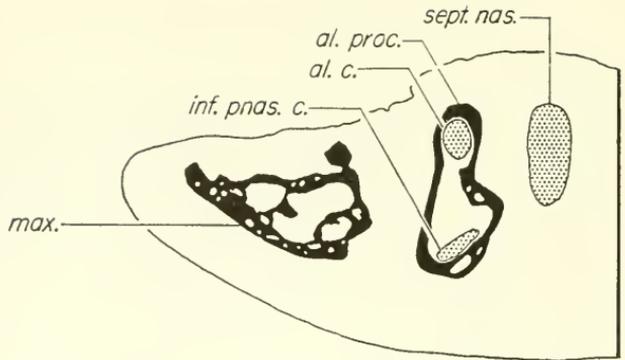
is smooth. Anteriorly (Fig. 84), the pars facialis and pars palatina are well developed. At the anterior margin of the orbit, at the point at which the maxillary articulates with the maxillary process of the nasal, the pars facialis is reduced to a small horizontally oriented shelf which overlies the posterior maxillary process (Fig. 85). Posterior to the pars dentalis and the divergence of the pterygoid and the pterygoid process from the maxillary, the pars palatina and pars facialis terminate (Fig. 86). The maxillary expands dorsally; in cross-section, the long axis of the bone is vertically oriented. The quadratojugal lies medially adjacent to the maxillary (Fig. 87). As the maxillary diminishes in size posteriorly, the quadratojugal increases in size and replaces the former at the level of the anterior acoustic foramen (Fig. 90).

The anterior end of the septum nasi appears between the alary processes of the premaxillaries. Slightly posterior, the superior prenasal cartilage appears on the posterodorsal face of the alary process and the inferior prenasal cartilage on the posteroventral face of the alary process (Fig. 82). The superior prenasal cartilage is closely associated with the alary cartilage posteriorly. The anterior end of the cavum principale is bifid and appears between the tectum nasi and alary cartilage at the anterior level of the overlying nasals. At the level of the anterior margin of the external naris and the cavum medium, the septum nasi expands horizontally and the tectum nasi diverges laterally from the septum nasi as the cartilago obliquus (Fig. 83). The anteromedial recess of the cavum inferius is absent. The anterolateral part of the cavum inferius appears at the level of the foramen of the ramus externus narius and ramus medius narius. In posterior sections, the cavum expands medially. The crista subnasalis is absent. Peripheral ossification appears dorsomedially in the septum nasi at the anterior levels of the olfactory eminence. In more posterior sections, peripheral ossification progresses ventrally and internal ossification centrally. At the anterior level of the internal nares, ossification of the septum nasi is complete, whereas the solum nasi is cartilaginous. The solum nasi is maximally ossified at the posterior margin of the internal nares at the level of the transition zone between the planum antorbitale and anterior maxillary process.

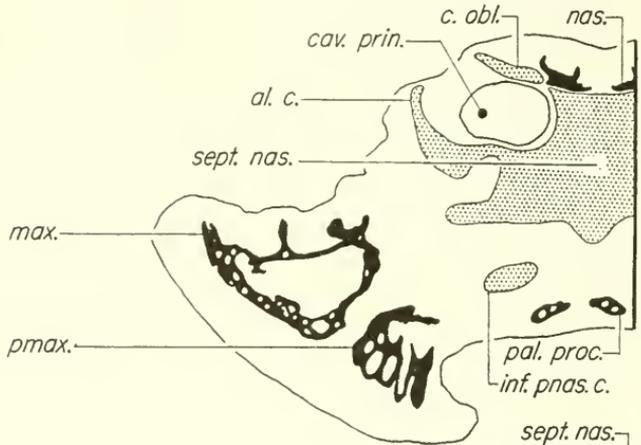
The anterior ramus of the septomaxillary is broad, thin, and slightly concave dorsally. In subsequent posterior sections, the anterior ramus thickens and the anterior end of the ventral spur appears beneath the cavum medium. The anterior ramus diverges into medial and lateral rami. The lateral ramus diminishes in size and persists as a delicate bone which lies adjacent to the margin of the lamina superior. The medial ramus increases in size in a ventromedial direction; it fuses with the dorsally expanding, ventral spur separating the anterior end of the nasolacrimal duct from the cavum medium (Fig. 84). The posterolateral ramus decreases in vertical thickness and in width in a medial direction; the lateral ramus terminates a short distance anterior to the medial ramus.

The Sphenethmoid and Orbital Region.—The frontoparietals converge medially throughout their lengths in some specimens; in other individuals (Fig. 81), they diverge in the orbital region to produce a small frontoparietal fontanelle anterior to the level of the optic foramen. All distal margins of the frontoparietal are free. The lateral edge extends over the orbit to form a narrow supraorbital flange and expands posterolaterally into a prominent lateral process which lies over the posterior part of the orbit anterodorsal to the prootic. The

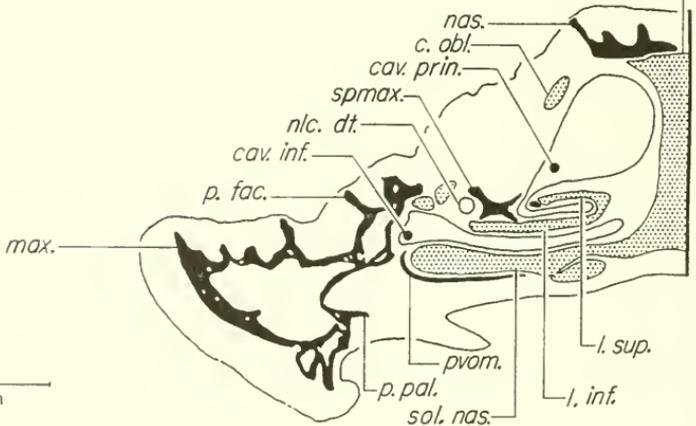
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FIGS. 82-84. Transverse sections through anterior end of skull of *Pternohyla dentata* (KU 111989): (82) level of alary process of premaxillary; (83) anterior level of cavum principale; (84) posterior level of septomaxillary. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *c. obl.*, cartilago obliqua; *cav. inf.*, cavum inferius; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *nas.*, nasal; *nlc. dt.*, nasolacrimal duct; *p. fac.*, pars facialis of maxillary; *p. pal.*, pars palatina of maxillary; *pal. proc.*, palatine process of premaxillary; *pmax.*, premaxillary; *pvom.*, prevomer; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spmax.*, septomaxillary.

dorsal surface of the frontoparietal is covered with a fine, reticulate network of ridges and spines. The lateral supraorbital margin of the frontoparietal terminates in a small, upturned flange of spines.

The dermal sphenethmoid is absent in *Pternohyala*. The dermal roofing bones do not converge medially and part of the sphenethmoid is visible (Pl. 10a; Fig. 81a, c). The dorsal surface of the sphenethmoid is smooth and is not involved in integumentary-cranial co-ossification (Fig. 85). The sphenethmoid is in synosteotic continuity with the septum nasi anteriorly. Internally, the sphenethmoid is separated from the overlying nasals and frontoparietals by a thin layer of dense connective tissue. The sphenethmoid is bony anterior to the orbitonasal foramen; at the level of the foramen (Fig. 85), a small amount of cartilage is located at the distal tip of the anterolateral wing of the sphenethmoid underlying the nasal. This cartilage persists for a short distance posterior to the orbitonasal foramen, and then disappears. Ventral to the frontoparietals in the mid-orbit region, the roof of the sphenethmoid splits to form the frontoparietal fontanelle (Fig. 86); the fontanelle extends posteriorly to the anterior level of the optic foramen. Dense connective tissue, which separates the sphenethmoid and frontoparietal, is continuous across the frontoparietal fontanelle ventral to the frontoparietals in all specimens. In some individuals, the frontoparietals diverge to expose the fontanelle dorsally. The sphenethmoid is completely bony at the anterior level of the frontoparietal fontanelle; a short distance posterior, the taenia tecti marginalis appear. At the anterior level of the optic foramen, the sphenethmoid is completely cartilaginous. The posterior border of the frontoparietal fontanelle is formed in cartilage by the tectum synoticum.

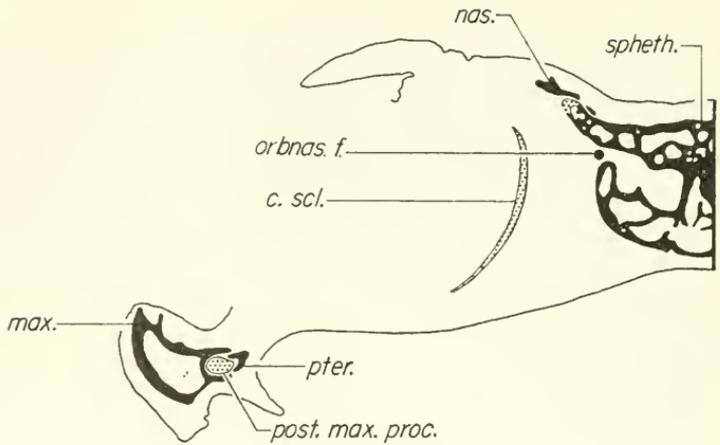
An isolated rod of cartilage lies ventromedial to the sphenethmoid at the level of the articulation of the palatines with the sphenethmoid. The cartilage is round in cross-section and about 0.32 mm. long. It lies in the dense connective tissue connecting the medial tips of the palatines across the venter of the sphenethmoid, but is otherwise unassociated with cranial elements.

The anterior end of the parasphenoid lies just posterior to the level of the orbitonasal foramen. The bone lies ventral to the sphenethmoid and prootic, and forms a bony bridge of support for the neurocranial floor at the synchondrotic union of the sphenethmoid and prootic. The parasphenoid is separated from adjacent bones by connective tissue. The bone is smooth and edentate.

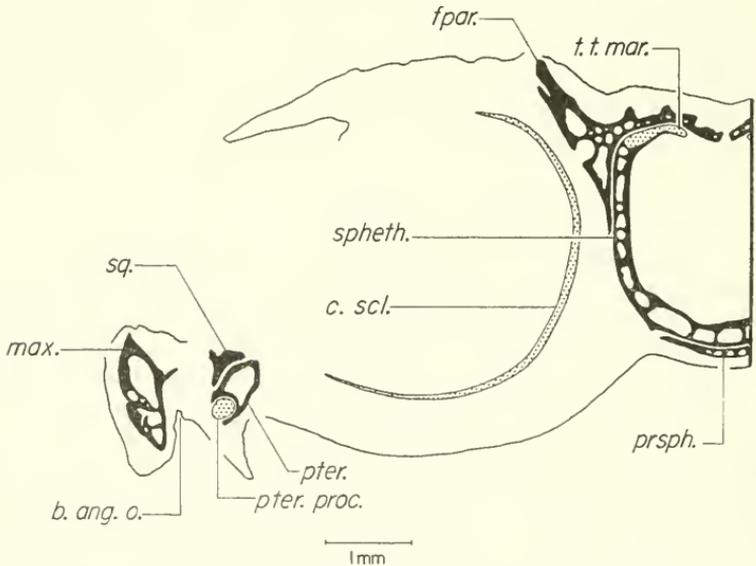
The bursa angularis oris (Fig. 86) is small and lies in the mid-orbital region at the anterior levels of the frontoparietal foramen. The bursa lies between the maxillary and the pterygoid process. It has no distinct central lumen as do the glands of *Tripriion spatulatus* and *Smilisca baudini*; the structure of the gland resembles that of *Tripriion petasatus* in being an unorganized mass of lymphoid tissue.

The Otic and Occipital Regions.—In dorsal view (Fig. 81c), the squamosal is a long, slim bone which extends from the mid-orbital region posterior to the posterior margin of the prootic. The dorsal and dorsolateral surfaces of the head of the squamosal are completely involved in integumentary-cranial co-ossification. The anterior arm of the squamosal is moderately robust and forms the bony posterior margin of the orbit; it terminates ventrally, on the dorsal surfaces of the pterygoid and maxillary at the level just posterior to the articulation of the maxillary and pterygoid (Fig. 86). A thin layer of dense

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FIGS. 85-86. Transverse sections through mid-region of skull of *Pternohyla dentata* (KU 111989): (85) level of orbitonasal foramen; (86) posterior region of orbit. Abbreviations: *b. ang. o.*, bursa anularis oris; *c. scl.*, cartilaginous sclera; *fpar.*, frontoparietal; *max.*, maxillary; *nas.*, nasal; *orbnas. f.*, orbitonasal foramen; *post. max. proc.*, posterior maxillary process; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *spheth.*, sphenethmoid; *sq.*, squamosal; *t. t. mar.*, taenia tecta marginalis.

connective tissue separates the anterior arm of the squamosal and the anterior ramus of the pterygoid. The posterior arm of the squamosal is equally as robust as the anterior arm, but unlike the latter, the posterior arm is straight and does not extend ventrally toward the maxillary. The ventral arm of the squamosal extends posteroventrally from the mid-point of the arc formed by the anterior and posterior arms of the squamosal; posteroventrally, the terminus lies between the quadratojugal and the posterior ramus of the pterygoid (Fig. 91).

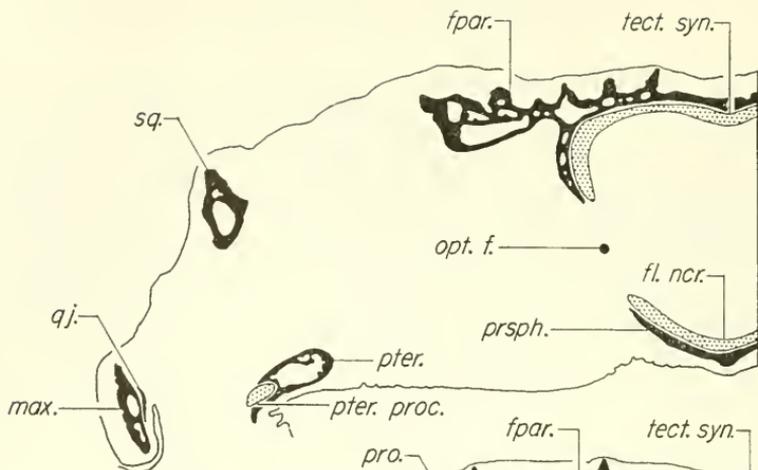
The pterygoid is moderately large (Fig. 81d). The anterior end of the anterior ramus lies in connective tissue adjacent to the posterior maxillary process and pars facialis of the maxillary at a level posterior to the palatines and anterior to the orbitonasal foramen (Fig. 85). In posterior sections, the anterior ramus increases in size and encases the medial surface of the posterior maxillary process. At the posterior terminus of the pars dentalis in the mid-orbital region, the anterior ramus of the pterygoid and the pterygoid process diverge medially from the maxillary (Fig. 86). The medial ramus is reduced and does not articulate with the prootic; it terminates at a level just anterior to the oculomotor foramen (Fig. 88). The posterior ramus articulates dorsally with the ventral arm of the squamosal, and posteriorly, lies medially adjacent to the quadrate process.

In cross-section, the quadratojugal is a long, narrow bone vertically oriented. It appears medial to the maxillary at the level of the optic foramen (Fig. 87). In successively posterior sections, the quadratojugal increases in size and the maxillary decreases in size; at a level just posterior to the prootic foramen, the maxillary terminates. Posteriorly, the quadratojugal decreases in size. At the posterior end of the quadratojugal, it lies ventrolateral to the ventral arm of the squamosal and is involved in ossification of the quadrate process.

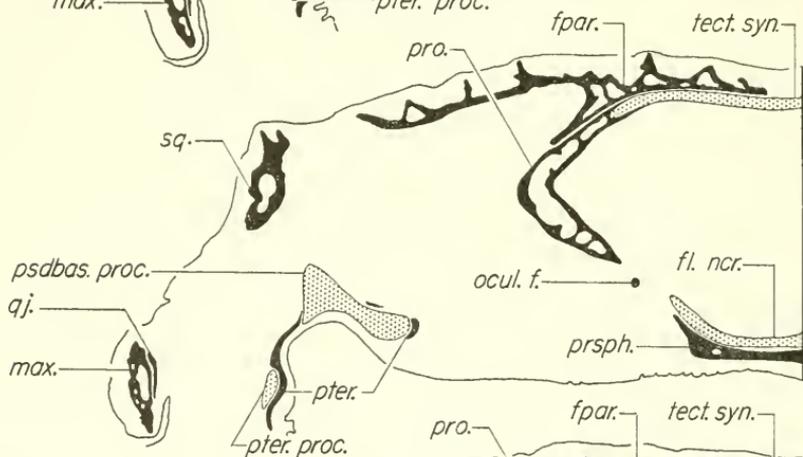
The anterior part of the optic foramen lies in the posterior, cartilaginous part of the sphenethmoid. The posterior and dorsal margins of the foramen are bony and formed by the prootic and lamina perpendicularis of the frontoparietal (Fig. 87). The trochlear foramen lies dorsal to the optic foramen in the lamina perpendicularis of the frontoparietal. The oculomotor foramen (Fig. 88) lies posteroventral to the optic foramen; dorsally, the foramen is bordered by bone and ventrally and posteriorly by cartilage. An extremely narrow bridge of bone separates the oculomotor foramen from the prootic foramen (Fig. 89); the latter lies immediately posterior and dorsal to the oculomotor foramen. The prootic foramen is bordered entirely by bone. The anterior acoustic foramen (Fig. 90) lies at the mid-level of the operculum posterior to the pars interna plectri and is bordered by bone. A bridge of bone and cartilage separates the anterior acoustic foramen from the posterior acoustic foramen (Fig. 91) at the posterior levels of the operculum. The posterior acoustic foramen is bordered by bone and lies just anterior to the level of the jugular foramen (Fig. 92).

The pseudobasal and otic processes appear just posterior to the optic foramen. The pseudobasal process (Fig. 88) lies lateral to the neurocranium; in posterior sections, the pseudobasal process expands dorsally into the otic process which lies medial to the dorsal part of the anterior arm of the squamosal. Posteriorly, the ventral part of this block of cartilage bifurcates vertically (in cross-section) to produce medial and lateral branches. The medial branch is continuous with the pseudobasal process. The lateral branch first diverges posteroventrally from the otic process and then fuses ventrally with the pterygoid process. At the level of the divergence of the dorsal and ventrolateral parts of the otic process, the medial branch splits, separating the otic process dorsally from the pseudobasal process ventrally. In subsequent sections, the otic process ossifies proximally and becomes horizontally oriented as the crista parotica (Fig. 89). The crista parotica joins the medial part of the otic capsule and the lateral part of the pseudobasal process diverges as the cornu principalis of the hyale at the posterior level of the oculomotor foramen.

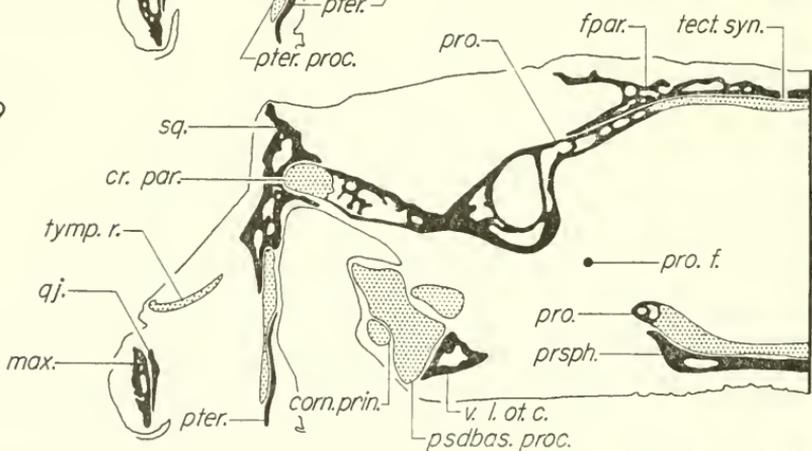
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FIGS. 87-89. Transverse sections through skull of *Pterohyla dentata* (KU 111989) at levels of cranial nerve foramina: (87) level of optic foramen; (88) level of oculomotor foramen; (89) level of prootic foramen. Abbreviations: *corn. prin.*, cornu principalis; *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadrate jugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring; *v. l. ot. c.*, ventral ledge otic capsule.

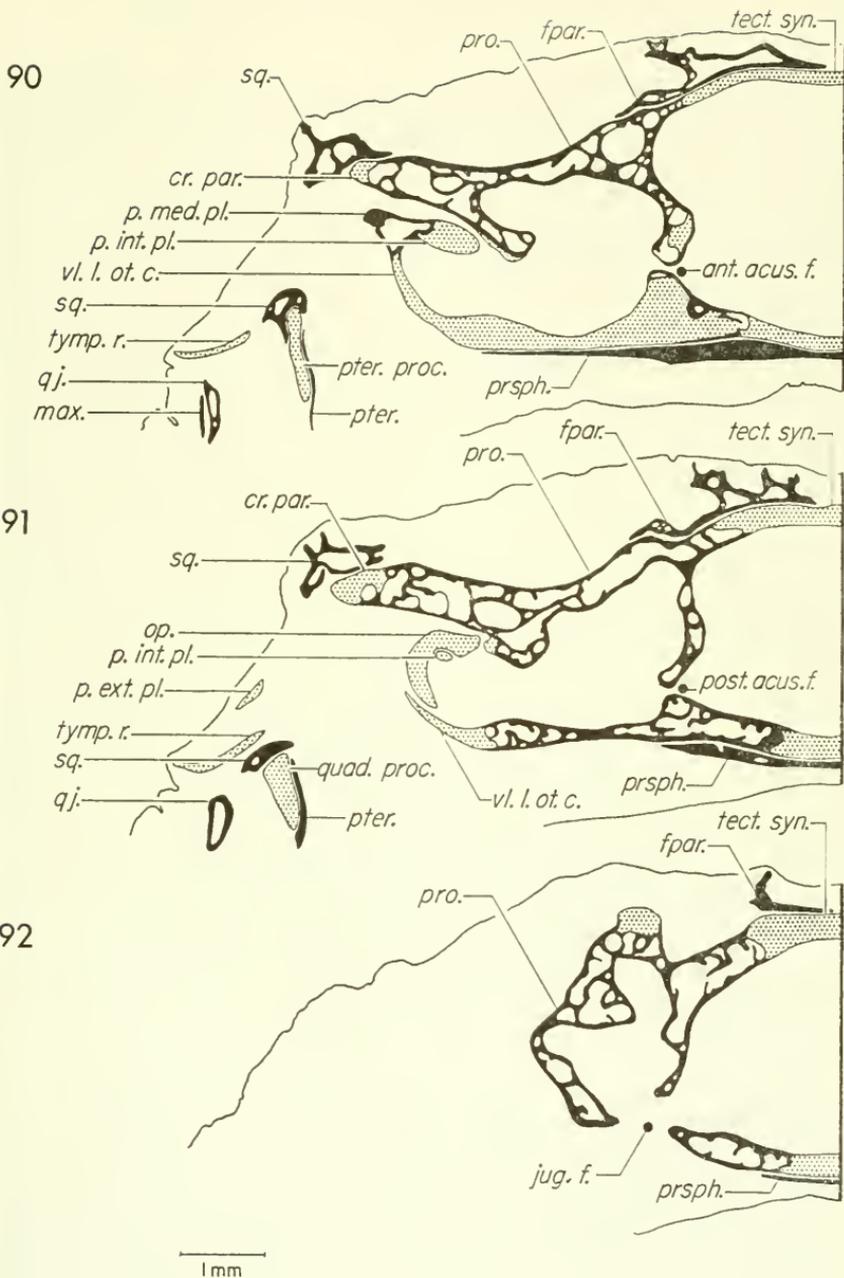


FIG. 90-92. Transverse sections through skull of *Pternohyla dentata* (KU 111989) at levels of cranial nerve foramina: (90) level of anterior acoustic foramen; (91) level of posterior acoustic foramen; (92) level of jugular foramen. Abbreviations: *ant. acus. f.*, anterior acoustic foramen; *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *jug. f.*, jugular foramen; *max.*, maxillary; *op.*, operculum; *p. ext. pl.*, pars externa plectri; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *post. acus. f.*, posterior acoustic foramen; *pro.*, prootic; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring; *v. l. ot. c.*, ventrolateral ledge of otic capsule.

The ventrolateral ledge of the otic capsule appears anteriorly at the anterior level of the prootic foramen. The pars interna plectri and pars externa plectri appear at the posterior level of the prootic foramen. In sections just posterior to the appearance of the latter structures, the pars ascendens plectri appears in association with the distal tip of the crista parotica. Posterior to the pars ascendens plectri and the prootic foramen, the pars media plectri appears. The anterior end of the operculum lies anterior to the level of the posterior acoustic foramen. The operculum terminates at the posterior level of the posterior acoustic foramen.

At the posterior level of the optic foramen, the prootic is ossified only ventrolaterally dorsal to the foramen; the floor of the neurocranium is cartilaginous. In posterior sections, ossification increases ventromedially in the neurocranium. At the level of the oculomotor foramen, the sides of the braincase are bony; whereas the roof and floor of the neurocranium are cartilaginous. Some ossification invades the floor of the otic capsule at the level of the anterior acoustic foramen, but the ventrolateral ledge of the otic capsule, the distal tip of the crista parotica, and the roof and dorsomedial part of the floor of the neurocranium remain cartilaginous. The pars media plectri is bony. The pars externa plectri, pars ascendens plectri, pars interna plectri, and operculum are cartilaginous. Posterior to the operculum, at the level of the jugular foramen, the otic capsule is bony except for a small dorsal tip; at this level and posterior, the dorsomedial and ventromedial parts of the neurocranium are cartilaginous.

The Articular Region.—Anterior to the articular region, Meckel's cartilage lies dorsal and slightly lateral to the angulosplenial bone. Posteriorly, the cartilage enlarges, moves dorsally, and comes to lie in close association with the ventral arm of the squamosal, the quadratojugal, posterior ramus of the pterygoid, and the quadrate process. At a level slightly anterior to the anterior acoustic foramen, the quadratojugal invades the cartilage of the quadrate process. The quadratojugal, squamosal, and pterygoid remain separated throughout their respective lengths. At the posterior level of the operculum and the posterior acoustic foramen, the quadrate process is cartilaginous and is bordered dorsolaterally by the posteroventral terminus of the squamosal and dorsomedially by the posterior ramus of the pterygoid. Both the squamosal and pterygoid terminate at the posterior margin of the posterior acoustic foramen.

Pternohyala fodiens.—The most obvious differences between the skulls of *Pternohyala fodiens* and *P. dentata* involve the dermal bones. The relative dimensions of the dermal roofing bones are greater in *P. fodiens* (Fig. 81a) and the maxillary has a shallow, but well developed labial flange. The presence of the labial flange accounts for the greater width of the skull as compared with *P. dentata*. The medial ramus of the pterygoid articulates with the prootic. Internally, the cranial structures of the two species are similar, although the skull of *P. fodiens* is more extensively ossified and some minor structural differences occur in the otic region. In the following discussion, only differences in the cranial structure of *P. fodiens* as compared with *P. dentata* are described. The description of *P. dentata* applies to all structures and regions which are not specifically mentioned below.

The most striking external difference in the olfactory region of *Pternohyala fodiens* is the presence of an anteromedial dermal bone, here termed the in-

ternasal (*intnas.*), because of its position medial to the external nares and the anterior tips of the nasals (Pl. 10a; Fig. 81a). The anterior end of the internasal lies anterior to the premaxillary. The dorsal surface is involved in integumentary-cranial co-ossification and bears bony ridges. In cross-section, the internasal is a wedge-shaped bone which extends posteriorly between the alary processes of the premaxillaries (Fig. 93). At the level of the pars dentalis of the premaxillary, the internasal lies dorsomedial to the alary processes of the premaxillary. Posteriorly, just anterior to the external nares (Fig. 94), the internasal lies dorsomedial to the septum nasi and is flanked ventrolaterally by well developed tecta nasi which support the medial margins of the nostrils. The internasal diminishes in size posteriorly, and near the posterior margin of the external nares is underlain by the anterior ends of the pared nasals (Fig. 95). A short distance posterior to the external nares, the internasal terminates.

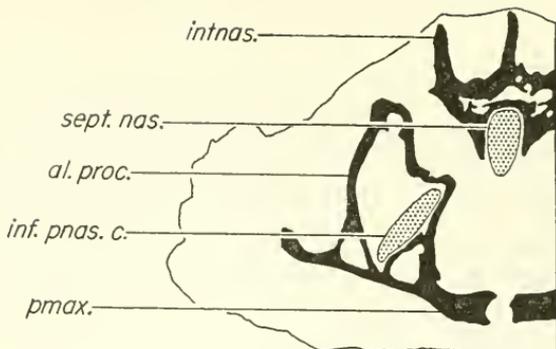
The premaxillary is much more robust in *Pternohyala fodiens* than in *P. dentata*. The alary process of the premaxillary is wide and thick; because of this, the anterior end of the premaxillary is even with the anterior ends of the maxillaries, rather than being recessed. The anterior surfaces of the alary processes are pitted and rugose and involved in integumentary-cranial co-ossification. Ventrally (Pl. 10b; Fig. 81b), the prevomer is much larger than in *P. dentata*. The anterolateral corner lies adjacent to the solum nasi, dorsal to the posterolateral corner of the pars dentalis of the premaxillary. In larger individuals, the prevomers converge medially, posterior to the palatine processes of the premaxillary. The nasal of *P. fodiens* is larger than that of *P. dentata*. The medial convergence of the nasals is greater and the anterolateral part of the bone is more extensive. The posterodorsal margin of the nasal articulates with the anterior margin of the frontoparietal. The canthal ridge is well developed and extends from the anteromedial tip of the nasal to the anterodorsal corner of the orbit.

The anterior end of the septum nasi appears between the alary processes of the premaxillaries ventral to the internasal (Fig. 93). The disposition of the inferior and superior prenasal cartilage is as described for *Pternohyala dentata*; *P. fodiens* also lack a crista subnasalis. The anterior end of the cavum principale is double and appears within the alary cartilage instead of lateral to it. The cavum medium appears just posterior to the anterior end of the cavum principale anterior to the level of the external nares. The anteromedial recess of the cavum inferius and the crista subnasalis are absent.

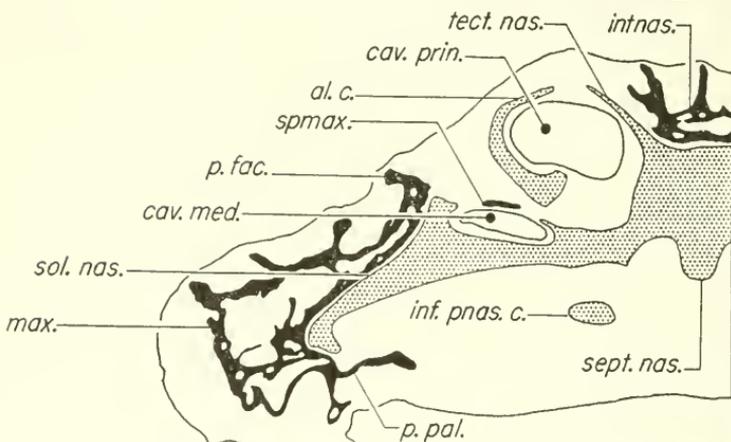
The frontoparietal articulates anteriorly with the nasal and posterolaterally with the squamosal. Anterolaterally, the frontoparietal extends over the orbit as a bony shelf. The frontoparietals converge medially throughout most of their lengths. The posterior margin of the frontoparietal terminates dorsal to the exoccipital and crista parotica. The frontoparietals and nasals do not converge medially in *Pternohyala fodiens*; thus a small part of the sphenethmoid is visible. Because the frontoparietals and nasals are larger in *P. fodiens*, less of the sphenethmoid is exposed dorsally than in *P. dentata*. Internally, ossification of the sphenethmoid is more extensive posteriorly in *P. fodiens* than in *P. dentata*. There is no isolated rod of cartilage ventromedial to the sphenethmoid.

The pseudobasal process does not appear until the anterior level of the prootic foramen. Slightly posterior, the anterior end of the otic process lies medially adjacent to the anterior arm of the squamosal. In posterior sections

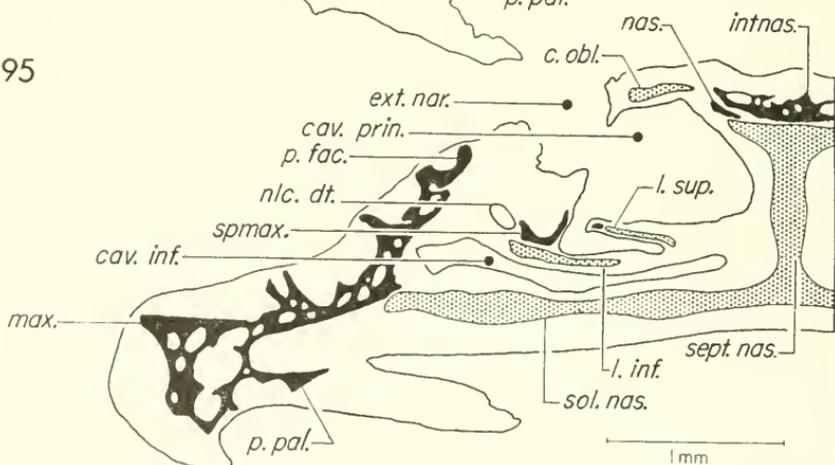
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FIGS. 93-95. Transverse sections through anterior end of skull of *Pterohyla fodiens* (KU 89925) in region of internasal: (93) level of alary process of premaxillary; (94) anterior levels of cavum medium and cavum principale; (95) posterior level of septomaxillary. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *c. obl.*, cartilago obliquus; *cav. inf.*, cavum inferius; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *ext. nar.*, external nares; *intrnas.*, internasal; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *nas.*, nasal; *nlc. dt.*, nasolacrimal duct; *p. fac.*, pars facialis of maxillary; *p. pal.*, pars palatina of maxillary; *pmax.*, premaxillary; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spmax.*, septomaxillary.

at the mid-level of the prootic foramen, the otic process expands medially to meet the otic capsule as the crista parotica; in subsequent sections, the pseudobasal and pterygoid processes diverge ventrally from the crista parotica. The ventrolateral ledge of the otic capsule appears posterior to the prootic foramen. The pars media plectri appears at the anterior level of the acoustic foramen. The appearance of the pars interna plectri in subsequent sections is followed by the pars externa plectri, pars ascendens plectri, and operculum, respectively. There is only one acoustic foramen.

Remarks.—Smith (1957) stated in his diagnosis of *Pternohyla dentata* that the species possesses parasphenoid “teeth.” None of the specimens that I have examined possess any type of parasphenoid odontoids. In his comparisons of *P. dentata* and *P. fodiens*, he pointed out that the palatine is ridge-like and with tooth-like irregularities in *P. dentata*, whereas the palatine is less elevated and lacks denticulations in *P. fodiens*. I agree that the palatine ridge is smoother in *P. fodiens*; however, I find no differences in the degrees of development of the ridges and hesitate to refer to the small irregularities of *P. fodiens* as “denticulations.”

The only variation noted among specimens of *Pternohyla* involves ossification of dermal roofing bones. In all individuals, the sphenethmoid is exposed dorsally. The size of the exposed part of the sphenethmoid, the presence of a dorsally exposed frontoparietal fontanelle, and the extensiveness of frontoparietal flanges depends on the development of the dermal roofing bones. Small specimens tend to have less well developed nasals and frontoparietals. Integumentary-cranial co-ossification is more extensive in larger specimens. Co-ossification is never complete; the nasal at the anterior margin of the orbit, the sphenethmoid, and the exposed, dorsal surface of the prootic are not co-ossified. In small individuals, the skin dorsal to the medial convergence of the frontoparietals is not co-ossified.

The basic structure of the skull of *Pternohyla* bears a striking resemblance to the cranial morphology of *Smilisca baudini* (see Duellman and Trueb, 1966, and Trueb, 1968). The shape of the skull and the relative sizes and shapes of the individual bones are similar. Comparison of the dorsal aspects of the skull of *S. baudini* and *P. dentata* (Fig. 96) shows that the latter can be derived from the former by the following changes: increase the size of the nasal to overlap the septum nasi and sphenethmoid dorsally, and extend the nasal toward the maxillary ventrolaterally; increase the size of the frontoparietal to overlap the sphenethmoid, and extend the supraorbital flanges of the frontoparietal posterolaterally over the rear of the orbit; increase the size of the maxillary, extending the pars facialis and creating a shallow labial flange along the outer margin of the maxillary; and increase the size of the squamosal. Ventrally, one need only extend the anterolateral wing of the prevomer, extend the anterior ramus of the pterygoid anteriorly, and eliminate the connection between the posterior ramus of the pterygoid and the prootic. Internally, only minor differences exist between the skulls of *Pternohyla* and *S. baudini*. Less cartilage exists in *P. dentata* than in *S. baudini*. *S. baudini* has a crista subnasalis and a medial recess of the cavum inferius; *Pternohyla* lacks these structures. The otic region is more extensive in an anterior-posterior direction in *P. dentata* than in *S. baudini*; however, the structure of the otic region in *P. fodiens* very closely resembles that of *S. baudini*. *P. fodiens* differs from the latter in having

one large acoustic foramen rather than two acoustic foramina. *Pterohyla fodiens* can be derived from *S. baudini* in the same manner as *P. dentata* by expansion of the dermal roofing bones and addition of the internasal bone anteriorly.

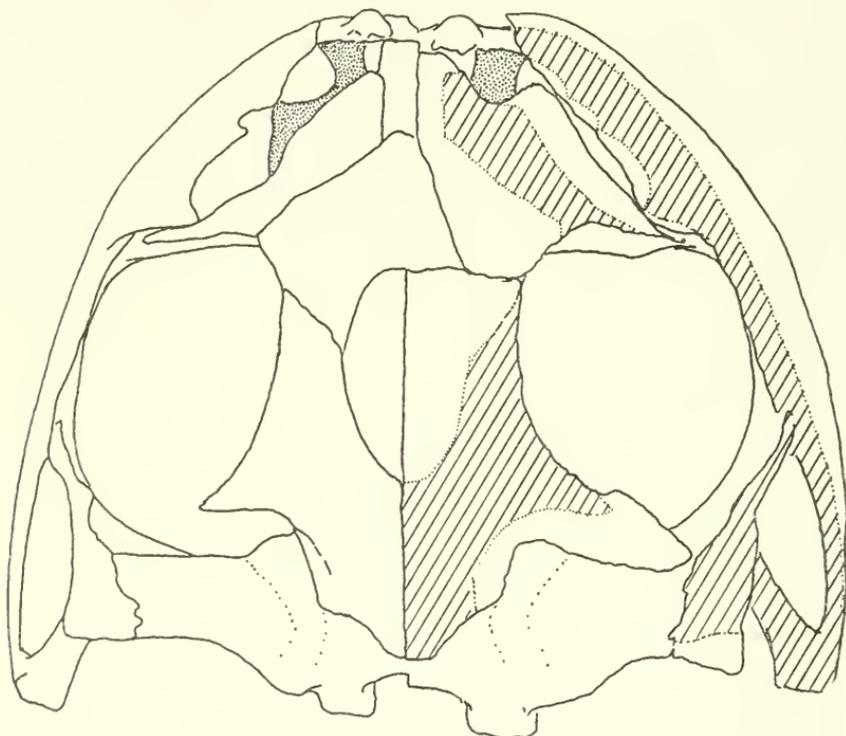


FIG. 96. Composite view of the skulls of *Pterohyla dentata* (KU 106293) and *Smilisca baudini* (KU 68184) approximately $\times 3$. Left half drawing represents *Smilisca baudini* and right half *Pterohyla dentata*. Structure of *S. baudini* is superimposed in cross-hatching on right side of figure.

Cranial Morphology of *Tripriion spatulatus*

The skull of *Tripriion spatulatus* is considerably longer than it is wide (Pl. 11a, b). All dorsal surfaces of the skull except the sphenethmoid are involved in integumentary-cranial co-ossification. Dorsally, all dermal bones are finely sculptured in a pattern of parallel or reticulate ridges. The distal margins of all dermal bones terminate in spinose protuberances; the latter are best developed on the outer edges of the maxillary and prenasal, the canthal ridge near the orbit, and the occipital crest. The skull of *Tripriion spatulatus* is characterized by having no part, or only a small part, of the sphenethmoid exposed dorsally, by the absence of a dermal sphenethmoid, the presence of a prenasal, and an extensive labial flange on the maxillary and prenasal anterior to the orbit. The vocal sac is single, median, and subgular.

The Olfactory Region.—The prenasal (Pl. 11a, b) lies anterior to the premaxillaries and nasals and between the anterior ends of the maxillaries. The

bone is flat ventrally; dorsally, it bears a prominent medial ridge and a flat, spinose labial flange. The dorsal surface of the bone is sculptured in longitudinal ridges medially and a reticulate pattern of ridges laterally. Posterolaterally, the prenasal articulates with the maxillary; posteromedially, it overlaps the anterior margin of the external nares. Ventromedially, the prenasal lies adjacent to the premaxillaries. Internally, the anterior part of the prenasal contains many small cavities (Fig. 97). A short distance posteriorly, the cavities coalesce to form a single, large, central cavity that is vertically oriented (Fig. 98). At about one-half the length of the prenasal, the vertical cavity is depressed ventrally and oriented horizontally; subsequently, it is divided into many smaller cavities. Two large, dorsal cavities, housing the anterior ends of the nasal capsules and alary processes of the premaxillaries, appear just anterior to the opening of the external nares (Fig. 99). There is an incomplete prenasal septum, which lies ventral to the septum nasi and separates the alary processes of the premaxillary throughout their lengths. The prenasals of the two subspecies of *Tripurion spatulatus* differ slightly in shape. The prenasal of *T. s. spatulatus* has a broad medial ridge and is triangular in cross-section, whereas that of *T. s. reticulatus* has a narrower medial ridge and is shaped like an inverted "T" in cross-section.

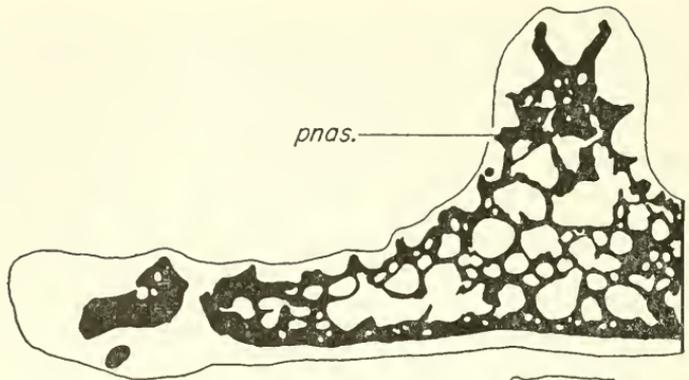
The premaxillaries are narrowly separated medially by connective tissue. Laterally, the premaxillary is separated from the pars palatina and the pars dentalis of the maxillary by an area of dense connective tissue. A small, inconspicuous palatine process is present posteromedially on the premaxillary. The alary processes of the premaxillary are inclined anteriorly at a 45-degree angle. The processes are straight and approximately five times as long as the depth of the pars dentalis of the premaxillary. The anterior two-thirds of the alary processes lie inside of the prenasal.

In ventral view (Pl. 11b), the prevomer lies lateral to the midline of the skull and ventral to the solum nasi and sphenethmoid. The anterior end of the prevomer lies dorsal to the articulation between the pars palatina of the maxillary and premaxillary. The posterior dentigerous part of the bone lies at a slight angle or perpendicular to the midline. The prevomer bears well developed, lateral wings that form the anterior, medial, and posteromedial margins of the internal naris. Internally, the prevomer bears a dorsal extension which supports the olfactory eminence.

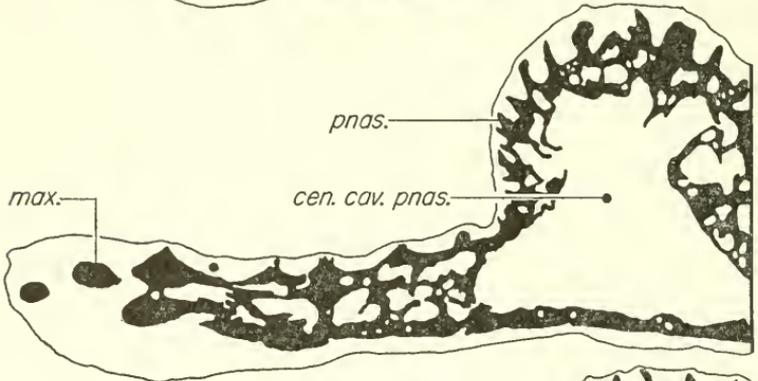
The palatine is a narrow, thin bone which lies posterolateral to the internal naris. The broad, distal end is lodged in connective tissue dorsal to the pars palatina of the maxillary and adjacent to the anterior maxillary process. The delicate, proximal end lies ventral to the lateral edge of the sphenethmoid and is separated from the sphenethmoid by a thin layer of loose connective tissue. The palatine bears a series of odontoids along the prominent ventral ridge.

The nasal is extremely large (Pl. 11a). Anteriorly, the nasal articulates with the prenasal, except where the former forms the posterior margins of the external nares. Laterally, the nasal articulates with the pars facialis of the maxillary, and posterolaterally, it forms the bony anterior margin of the orbit. The nasals converge anteromedially to the dorsally exposed part of the sphenethmoid. The posterior margin of the nasal articulates with the anterodorsal margin of the frontoparietal; a thin ventral flange of the frontoparietal underlies the posterior margin of the nasal. The dorsal surface of the nasal is completely involved in integumentary-cranial co-ossification. The nasal bears a well developed canthal ridge extending from the posteromedial margin of the external

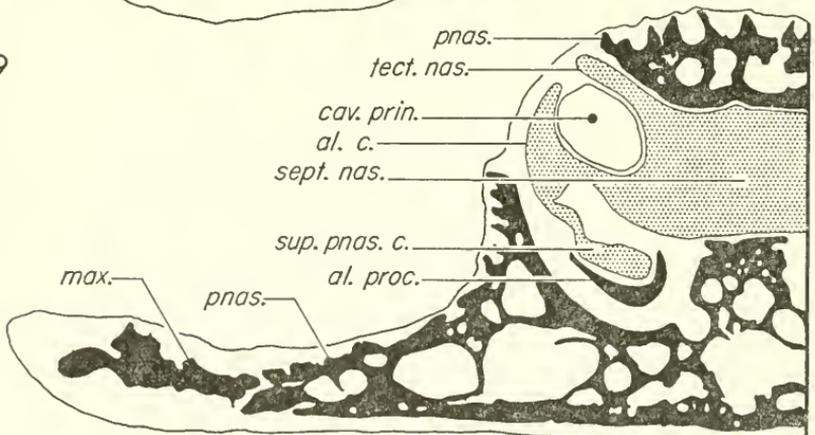
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— 1 mm —

FIGS. 97-99. Transverse sections through prenasal and anterior end of olfactory capsule of *Triprion spatulatus* (KU 86925): (97) anterior end of prenasal; (98) prenasal at level of central cavity; (99) anterior level of cavum principale. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *cav. prin.*, cavum principale; *cen. cav. pnas.*, central cavity of prenasal; *max.*, maxillary; *pnas.*, prenasal; *sept. nas.*, septum nasi; *sup. pnas. c.*, superior prenasal cartilage; *tect. nas.*, tectum nasi.

naris to the anterodorsal corner of the orbit, where a proliferation of small spines is present on the ridge. Lateral and medial to the canthal ridge, the surface of the nasal is marked by a fine reticulate network of ridges. The supraorbital margin of the nasal bears a series of small spines.

The maxillary is moderately robust. Anterior to the orbit, the maxillary bears a broad flange, which is deeply concave dorsally in front of the orbit and nearly flat anteriorly at its articulation with the prenasal. An inconspicuous flange, consisting of a row of small spines, is present along the lateral edge of the maxillary, ventral and posterior to the orbit. The dorsal and lateral surfaces of the maxillary are involved in integumentary-cranial co-ossification. The labial flange is sculptured into a series of fine ridges that terminate in long spines distally. The pars facialis of the maxillary is marked by a fine reticulate network of ridges. Medially, the maxillary bears a pars palatina (Fig. 100) extending the length of the bone dorsal to the pars dentalis. The pars palatina is best developed anterior to the orbit; posterior to the orbit, the pars palatina is barely evident. Dorsal to the pars palatina and anterior to the orbit, the maxillary bears a large pars facialis; the latter lies adjacent to the nasal anteriorly, and posteriorly forms the bony ventral margin to the orbit. Slightly posterior to the terminus of the pars dentalis, the quadratojugal lies ventromedial to the maxillary. A thin area of dense connective tissue separates the quadratojugal and maxillary.

The anterior end of the nasal capsule lies forward within the prenasal (Fig. 99). The cartilaginous septum nasi projects anteriorly into a medial cavity of the prenasal. This cavity is flanked laterally by two other cavities, each of which contains the anterior end of the alary process of the premaxillary and the associate superior prenasal cartilages. At the level of the anterior margin of the external nares the septum nasi expands horizontally, thereby separating the prenasal into a dorsal and ventral component. The anterior end of the cavum principale is bifurcate, and is encased by the alary cartilage, tectum nasi, and septum nasi, and lies at the same level. The tectum nasi is exceptionally short, extending only from the anterior end of the cavum principale to the anterior end of the cavum medium in *Tripriion spatulatus reticulatus*. In *T. s. spatulatus*, the tectum terminates anterior to the appearance of the cavum medium. The superior and inferior prenasal cartilages are well developed. The former lies anteroventral to the alary cartilage, extending from the cartilage to the posterior surface of the alary process of the premaxillary. The inferior prenasal cartilage appears on the posteromedial face of the alary process of the premaxillary, extends dorsally and fuses with the solum nasi at the posterior levels of the septomaxillary in *T. spatulatus reticulatus* and posterior to the septomaxillary in *T. s. spatulatus*. Both species have a crista subnasalis and anterior maxillary process. The nature of the nasal cavities and associated cartilages is the same as that described for *Tripriion petasatus*. Peripheral ossification of the septum nasi appears at the anterior levels of the olfactory eminence. Ossification spreads from central to peripheral parts of the septum in successively more posterior sections, and at the anterior level of the internal nares, both the septum and solum nasi are entirely ossified. Posteriorly, the septum nasi is continuous with the sphenethmoid. The septomaxillary of *T. spatulatus* resembles that of *T. petasatus*. The septomaxillary lacks the distinct dorsal ramus characteristic of the bone in *T. petasatus*; the lateral ramus is more robust, and medial branch is weaker by comparison.

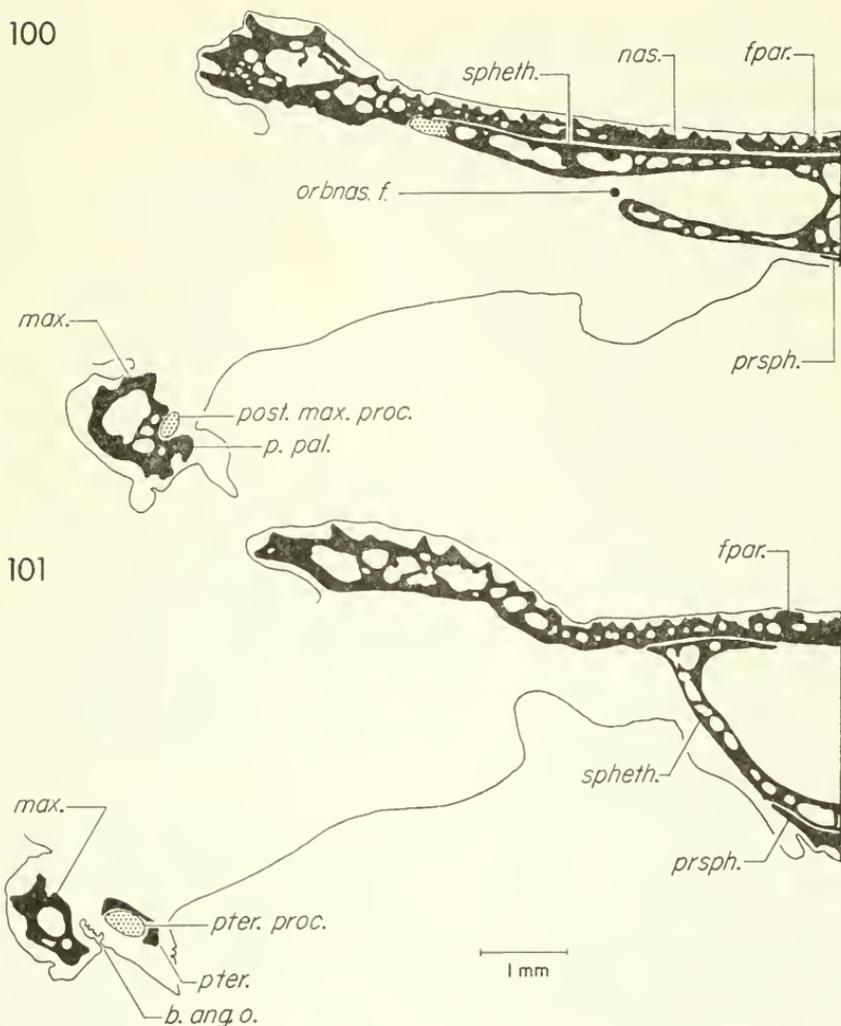
The Sphenethmoid and Orbital Region.—The frontoparietal (Pl. 11a) is a rectangular element which articulates anteriorly with the posterior margin of the nasal and posterolaterally with the squamosal. Anterolaterally, the frontoparietal extends over the orbit as a bony shelf. The frontoparietals articulate medially throughout their entire lengths. The posterior margin of the frontoparietal terminates in an upturned, spinose occipital crest. Ventral to the occipital crest, the frontoparietal is attached to the exoccipital; laterally, it bridges the prootic from the exoccipital to the squamosal. The dorsal surface of the frontoparietal is involved in integumentary–cranial co-ossification. The supraorbital part of the frontoparietal is marked by a pattern of parallel ridges which run from the center of the bone to the margin of the orbit where they terminate in small spines. The rest of the surface of the frontoparietal bears a reticulate network of ridges.

The dermal sphenethmoid is absent in *Tripriion spatulatus*. In most males and all but the large females the nasals do not meet one another posteromedially (Pl. 11a) and a small part of the sphenethmoid is visible. The dorsal surface of the sphenethmoid is smooth and is not involved in integumentary–cranial co-ossification. The sphenethmoid is in synchondrotic continuity with the septum nasi anteriorly. Internally, the sphenethmoid is separated from the overlying nasals and frontoparietals by a thin layer of dense connective tissue. At the level of, and anterior to, the orbitonasal foramen (Fig. 100), a small amount of cartilage is located at the distal tip of the anterolateral wing of the sphenethmoid underlying the nasal. The rest of the sphenethmoid is bony posterior to the anterior margin of the optic foramen; at this level, cartilage joins the sphenethmoid to the prootic. Ventral to the frontoparietals in the mid-orbital region, the roof of the sphenethmoid splits to form the frontoparietal fontanelle (Fig. 101); the fontanelle extends posteriorly to the level of the optic foramen. The dense connective tissue which separates the sphenethmoid and frontoparietals is continuous across the frontoparietal fontanelle ventral to the frontoparietals. The anterior half of the fontanelle has a bony margin; the posterior part has a cartilaginous margin formed by the taenia tecti marginalis posterolaterally, and the tectum synoticum posteromedially.

The anterior end of the parasphenoid lies at the level of the orbitonasal foramen. The bone lies ventral to the sphenethmoid and prootic and forms a bony bridge of support for the neurocranial floor at the synchondrotic union of the sphenethmoid and prootic. The parasphenoid is separated from adjacent bones by connective tissue. Ventromedially, the parasphenoid bears a well developed odontoid structure.

The bursa angularis oris lies in the posterior part of the orbit between the pterygoid and maxillary bones. The position and size of the gland are like that described for *Tripriion petasatus*; however, the bursa seems to be better developed in *T. spatulatus*. It is encased in dense connective tissue. The gland lies parallel to the maxillary. It has a central lumen lined with cuboidal, ciliated epithelium; the surface of the lumen is folded into plicae. A longitudinal slit-like aperture connects the central lumen of the bursa with the oral cavity.

The Otic and Occipital Regions.—In dorsal view (Pl. 11a), the squamosal is an arcuate bone which extends posteriorly from the posterior edge of the orbit to the level of the occipital crest. The dorsal and dorsolateral surfaces of



FIGS. 100-101. Transverse sections through mid-region of skull of *Triprion spatulatus* (KU 86925): (100) level of orbitonasal foramen; (101) posterior level of orbit. Abbreviations: *b. ang. o.*, bursa angularis oris; *fpar.*, frontoparietal; *max.*, maxillary; *nas.*, nasal; *orbnas. f.*, orbitonasal foramen; *p. pal.*, pars palatina of maxillary; *post. max. proc.*, posterior maxillary process; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *spheth.*, sphenethmoid.

the head of the squamosal are completely involved in integumentary-cranial co-ossification. The anterior arm of the squamosal is robust and forms the posterior margin of the orbit; it terminates ventrally, adjacent to the maxillary at a level just posterior to the articulation of the pterygoid and maxillary. Dense connective tissue separates the anterior arm of the squamosal from the maxillary. The posterior arm of the squamosal is equally as robust as the anterior arm and extends nearly half the distance to the maxillary; there is a

heavy tendinous connection between the posterior end of the quadratojugal and the posterior arm of the squamosal. The ventral arm of the squamosal extends posteroventrally from the mid-point of the arc formed by the anterior and posterior arms of the squamosal; posteroventrally, the terminus lies between the quadratojugal and posterior ramus of the pterygoid.

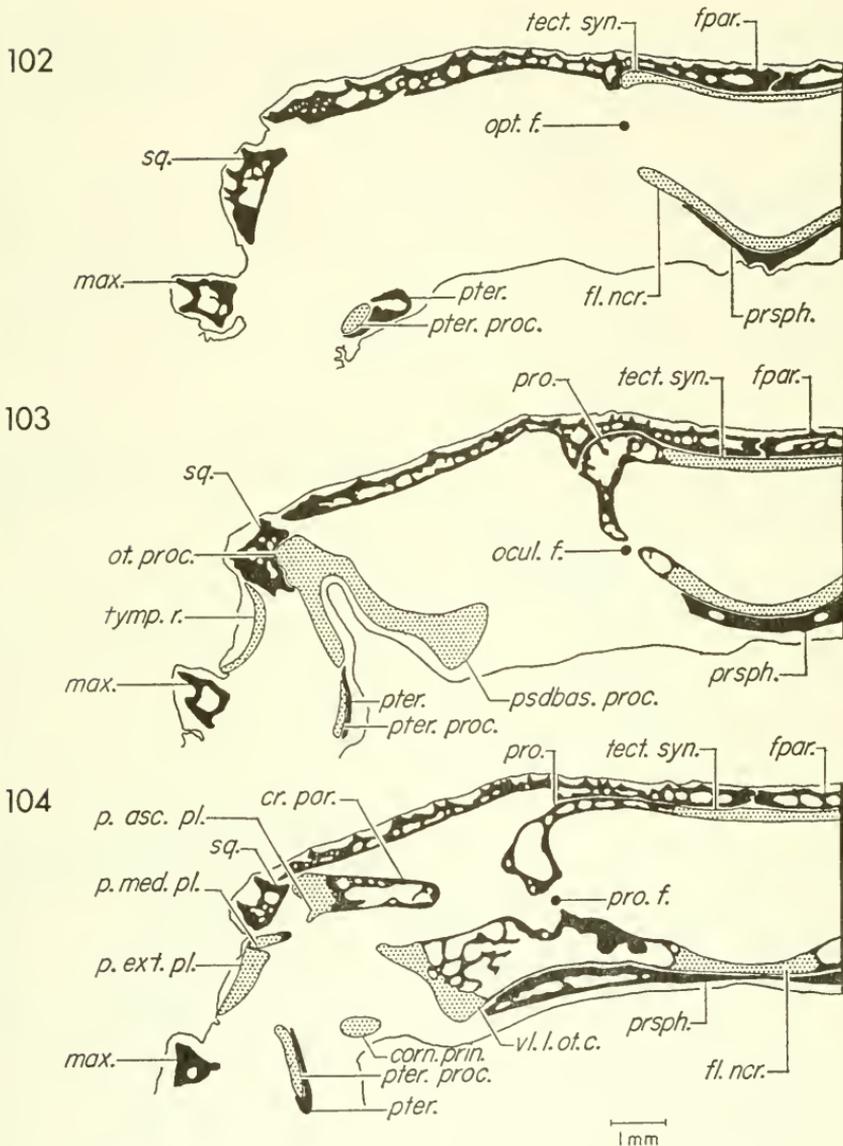
The pterygoid (Pl. 11b) is small. The anterior ramus attaches to the pars facialis of the maxillary, dorsal to the posterior end of the pars dentalis of the maxillary. The posterior ramus articulates with the ventral terminus of the squamosal. The medial ramus is reduced and does not articulate with the prootic.

The quadratojugal lies along the ventromedial surface of the maxillary. It terminates anteriorly, at the level of the articulation between the anterior arm of the squamosal and maxillary. Posteriorly, the quadratojugal extends beyond the end of the maxillary and lies adjacent to the ventral arm of the squamosal.

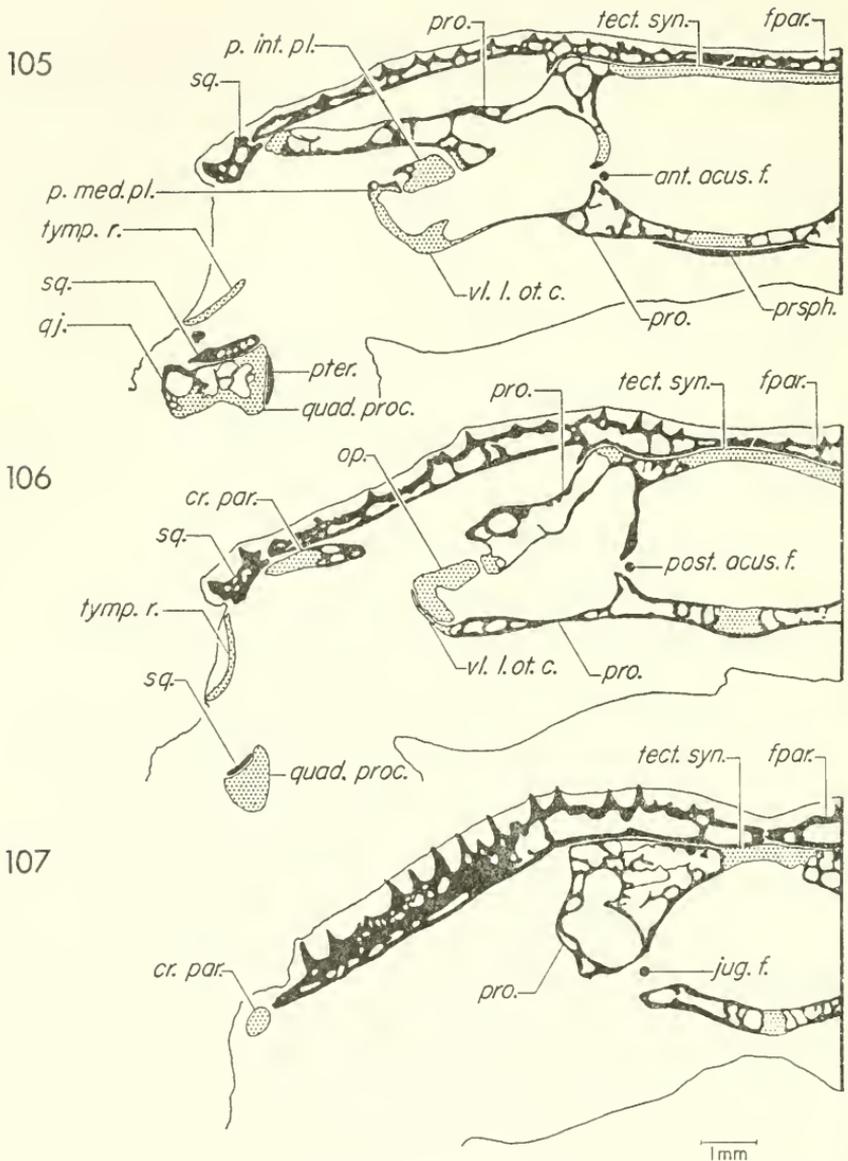
The anterior half of the optic foramen (Fig. 102) is cartilaginous; the posterior margins are bony and are formed by perichondral ossification of the prootic. The oculomotor foramen (Fig. 103) lies posteroventral to the optic foramen. The dorsal and posterior margins of the foramen are bony, whereas the anterior and anteroventral edges are cartilaginous. The trochlear foramen penetrates the lamina perpendicularis of the frontoparietal posterodorsal to the optic foramen. The large prootic foramen (Fig. 104) lies posterior to the oculomotor foramen and dorsal to the anteroventral edge of the otic capsule. The prootic foramen has a complete, bony margin. The anterior acoustic foramen (Fig. 105) is at the level of the pars interna plectri and has bony margins. The posterior acoustic foramen (Fig. 106), which lies at the level of the operculum, is separated from the anterior acoustic foramen by a narrow bridge of bone. The jugular foramen (Fig. 107) lies in bone posteroventral to the posterior acoustic foramen.

The anteriormost parts of the otic region are the pseudobasal and otic processes, which appear at the anterior level of the oculomotor foramen. The pseudobasal process lies ventrolateral to the neurocranium and expands medially in more posterior sections. The otic process appears initially as an oval cartilage lying medial to the anterior arm of the squamosal; it extends ventrally and fuses with the dorsolateral corner of the pseudobasal process at the posterior level of the oculomotor foramen. A short distance posterior to the latter fusion, the ventral part of the otic process divides; the medial part is fused to the pseudobasal process and the lateral part of the pterygoid process. Just anterior to the prootic foramen, the lateral part separates from the dorsal head of the otic process. The medial part of the otic process diverges from the pseudobasal process and becomes horizontally oriented as the crista parotica in posterior sections. At the same level as the separation of the otic and pseudobasal processes, the lateral part of the pseudobasal process diverges as the cornu principalis of the hyale.

At the posterior level of the ganglion prootic commune and the entry of the abducens nerve into the neurocranium, the pars ascendens plectri and pars externa plectri appear; both are cartilaginous. At the posterior margin of the prootic foramen, the pars ascendens plectri separates from the pars externa plectri and the pars media plectri appears; the latter is bony and attaches to the cartilaginous ventrolateral ledge of the otic capsule just anterior to the anterior acoustic foramen. The cartilaginous pars interna plectri appears at the



FIGS. 102-104. Transverse sections through skull of *Triprion spatulatus* (KU 86925) at levels of cranial nerve foramina: (102) level of optic foramen; (103) level of oculomotor foramen; (104) posterior level of prootic foramen. Abbreviations: *cr. par.*, crista parotica; *corn. prin.*, cornu principalis; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *ot. proc.*, otic process; *p. asc. pl.*, pars ascendens plectri; *p. ext. pl.*, pars externa plectri; *p. med. pl.*, pars media plectri; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring; *v. l. ot. c.*, ventrolateral ledge otic capsule.



FIGS. 105-107. Transverse sections through skull of *Tripirion spatulatus* (KU 86925) at levels of cranial nerve foramina: (105) level of anterior acoustic foramen; (106) level of posterior acoustic foramen; (107) level of jugular foramen. Abbreviations: *ant. acus. f.*, anterior acoustic foramen; *cr. par.*, crista parotica; *fpar.*, frontoparietal; *jug. f.*, jugular foramen; *max.*, maxillary; *op.*, operculum; *p. int. pl.*, pars interna plectri; *post. acus. f.*, posterior acoustic foramen; *pro.*, prootic; *prsph.*, parasphenoid; *pter.*, pterygoid; *qj.*, quadratojugal; *quad. proc.*, quadrate process; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring; *v. l. ot. c.*, ventrolateral ledge otic capsule.

level of the anterior acoustic foramen; the cartilaginous operculum is well developed at the posterior margin of the foramen. The pars interna plectri terminates at the level of the posterior acoustic foramen and the operculum closes the fenestra ovalis at the posterior margin of the posterior acoustic foramen.

At the posterior level of the optic foramen, the prootic is ossified only peripherally around the margin of the foramen. In subsequent sections, ossification increases in dorsomedial and ventromedial directions. At the posterior level of the prootic foramen, the medial part of the tectum synoticum and ventromedial part of the neurocranium, the distal edge of the crista parotica, and the ventrolateral ledge of the otic capsule are cartilaginous. Posteriorly, ossification increases in the floor of the neurocranium and decreases in the sides and roof. At the posterior level of the otic capsule, narrow dorsomedial and ventromedial strips of cartilage remain. The rest of the exoccipital region is bony.

The Articular Region.—Anterior to the articular region, Meckel's cartilage lies dorsolateral to the angulosplenic bone. Posteriorly, the cartilage enlarges and comes to lie in a dorsal position with respect to the angulosplenic; the latter assumes an arcuate shape in cross-section. The quadratojugal first appears in sections posterior to the union of the anterior pterygoid ramus with the maxillary. From an initial position ventromedial to the maxillary, the quadratojugal enlarges posteriorly and moves to a position medial to the maxillary as the latter decreases in size. Slightly anterior to the anterior acoustic foramen, the ossification of the quadratojugal invades the cartilage of the quadrate process. The quadratojugal remains separated from the pterygoid and squamosal throughout its length. At the level of the posterior acoustic foramen, the quadrate process is overlain by the posteroventral terminus of the ventral arm of the squamosal. The posterior end of Meckel's cartilage is attached ventrally to the quadrate process by connective tissue.

Remarks.—Little variation was noted in the skulls examined. The cranial differences noted between the subspecies of *Tripurion spatulatus* are minor and probably are indicative of individual variation, rather than subspecific differences. The skulls of mature females are much larger than those of mature males. In most males and in some small females, the sphenethmoid is exposed dorsally; in large females, the frontoparietals and nasals converge medially and completely cover the sphenethmoid.

Peters (1955:5) reported that "In this genus [*Tripurion spatulatus*] the labial shelf is made up of bony spines, . . . the group [of spines] on the tip of the snout is formed by the fusion of units from the two premaxillary bones." With reference to *Tripurion petasatus*, Peters stated in the same paper that "The fusion of the premaxillaries at the tip of the snout is complete . . ." Peters was unaware of the existence of the prenasal in *Tripurion* and thus misinterpreted the nature of the premaxillary.

VARIATION IN CRANIAL ELEMENTS IN CASQUE-HEADED, CO-OSSIFIED HYLIDS

The preceding morphological descriptions have shown that some areas and/or structures of the skull vary little from one genus to

another, whereas other cranial elements differ noticeably between closely related species. The purpose of the following account is to summarize and assay the kind and amount of morphological variation in individual cranial elements found in the genera of casque-headed, co-ossified hylids considered. Genera and species examined are: *Aparasphenodon brunoi*, *Corythomantis greeningi*, *Osteocephalus taurinus*, *Pternohyla dentata*, *Pternohyla fodiens*, *Trachycephalus jordani*, *Trachycephalus nigromaculatus*, *Tripriion petasatus*, *Tripriion spatulatus*, *Hyla septentrionalis*, *Hyla brunnea*, and *Hyla dominicensis*. Serial cross-sections of the heads were not available for *Hyla brunnea* and *H. dominicensis*; therefore these two species are not included in discussions of internal cranial elements. The accounts which follow are organized in the same order as each morphological description. The cranium has been divided into general areas which are treated in an anterior to posterior sequence. External bones associated with a particular area are discussed first and are followed by discussion of the appropriate internal bones and cartilages.

The Olfactory Region (Including the Upper Jaw)

External Dermal Bones

Prenasal.—The prenasal is present in only two of the genera, *Aparasphenodon* and *Tripriion*. In both, the prenasal is dermal in origin, lies anterior to the premaxillary and nasal bones, and is co-ossified dorsally and smooth ventrally. Internally, the bone is hollow and contains the anterior parts of the alary processes of the premaxillaries and the anterior parts of the olfactory capsule. The prenasals of *Tripriion petasatus* and *T. spatulatus* differ from each other internally only slightly in the relationships of the prenasal septa and septa nasi. Externally, the prenasals of *T. petasatus* and *T. spatulatus* differ in patterns of co-ossification. Moreover, the prenasal of *T. spatulatus* bears a distinct dorsomedial ridge and a labial flange which turns down in lateral view, whereas the prenasal of *T. petasatus* lacks a distinct dorsomedial ridge and bears a labal flange which is dorsally concave in lateral view. The prenasal of *Aparasphenodon* differs from that of *Tripriion*; it lies between the anterior ends of the maxillaries, does not articulate with the premaxillaries posteriorly, and lacks a labial flange. Internally, the prenasal of *Aparasphenodon* lacks a prenasal septum.

Internasal.—The internasal is present only in *Pternohyla fodiens*. The relationship of this bone to the prenasal is unclear. The internasal is dermal and lies dorsal to the septum nasi between the external nares. In cross-section it resembles the posterodorsal part of the prenasal which extends between the external nares dorsal to the septum nasi. However, the two bones develop from different centers of ossification, and obviously differ functionally. The prenasal forms a bony anterior extension of the skull which encases and protects the anterior part of the nasal capsule, whereas the internasal seems

to act as a single anterior extension of the posterior nasal roofing bones. In *Corythomantis greeningi* the nasal extend anteriorly and anteroventrally and form a bony outgrowth similar in function and appearance to the prenasal. The modifications of the skulls of *Pternohyla*, *Triprion*, *Aparasphenodon*, and *Corythomantis* suggest a parallel trend among the casque-headed, co-ossified hylids to reinforce, protect and extend the anterior part of the skull. The minimal modification is that of *Pternohyla* with the addition of one, small, inconspicuous bone. *Aparasphenodon* and *Triprion* have amplified this trend with the addition of more elaborate bone, whereas *Corythomantis* has structured the same type of skull by modification of the nasal roofing bones.

Premaxillary.—Certain aspects of the premaxillary seem not to be subject to modification. The bone is always paired; the pair usually is separated medially by dense connective tissue and the bones are separated laterally from the maxillaries by dense connective tissue. Premaxillary dentition is invariably present. Some kind of alary process is present and acts as a bony abutment for the anterior end of the nasal capsule; the pars palatina and palatine process are present in greater or lesser degrees of development. The premaxillaries lie at the anterior end of the skull between the anterior ends of the maxillaries. In *Pternohyla* and *Aparasphenodon* the premaxillaries lie slightly recessed to the anterior ends of the maxillaries because of the anterior extension of the maxillaries.

The striking variation in the structure of the premaxillary almost exclusively involves various modifications of the alary process. The alary process is inclined anteriorly or posteriorly, or is nearly vertical in orientation. Alary processes vary in proportionate height and shape, and they are co-ossified or not. The alary processes are inclined anteriorly at approximately a 45-degree angle in *Triprion*, *Corythomantis*, and *Aparasphenodon*; these are the three genera characterized by anterior growth of dermal bone as a prenasal or an extension of the nasals. The alary processes of these frogs lie internal to the dermal bone at the anterior end of the skull. Consequently, the processes are not co-ossified; they are usually long, slender extensions of the pars dentalis of the premaxillary. In the remaining genera of frogs the alary processes are either vertically oriented or inclined slightly posteriorly. The degree of posterior inclination seems to be a function of the position of the anterior margin of the nasals or other dermal roofing bones. Thus, if the nasal projects forward between the external nares, dorsal to the level of the pars dentalis of the premaxillary, as it does in *Trachycephalus jordani* and *Osteocephalus taurinus*, the alary processes extend vertically from the pars dentalis to the level of the dorsal roofing bone. If the nasal terminates posterior to the level of the pars dentalis, as it does in *Hyla septentrionalis*, the alary processes are inclined posteriorly from the pars dentalis to the anterodorsal level of the dermal roofing bone.

The height of the alary processes varies principally in accordance with the projection and orientation of dermal roofing bones. Thus, the anteroventral projection of the nasals in *Trachycephalus jordani* results in proportionally shorter alary processes than those characteristic of *Hyla septentrionalis*. Lateral expansion of the alary processes is correlated with the occurrence of co-ossification of the alary processes in *Pternohyla fodiens*, *Trachycephalus jordani*, and *T. nigromaculatus*. This trend is least pronounced in *Pternohyla* in which the alary processes are laterally expended and slightly thickened by the develop-

ment of bony rugosities on the anterior surfaces of the processes. In *Trachycephalus nigromaculatus* the alary processes are completely co-ossified and expanded to articulate with one another medially and with the pars facialis of the maxillary laterally. The structure of the alary processes of *Trachycephalus nigromaculatus* is modified in *T. jordani* to include an anterior extension of bone into a small labial flange and a proliferation of bony spines dorsal to the flange.

Prevomer.—The prevomer of the casque-headed hylids is fully ossified. The anterior end lies dorsal to the pars palatina of either the premaxillary or the maxillary, or the articulation between the two bones. The prevomers are large, usually convergent medially, and all bear lateral wings which form the anterior, medial, and posteromedial margins of the internal nares. There is notable variation in the posterior dentigerous processes of the prevomer. Three genera are characterized by prevomers bearing small dentigerous processes. Those of *Tripriion* and *Corythomantis* are small and anteromedially inclined, whereas those of *Pternohyla* are small and posteromedially inclined. The prevomerine dentigerous processes of the other casque-headed hylids are larger, and either angular or curved. Those of *Hyla septentrionalis* and *Trachycephalus nigromaculatus* are slightly curved (see Table 1), whereas the dentigerous processes of *T. jordani* and *Hyla dominicensis* are more noticeably curved (see Table 1); the dentigerous processes of *Hyla brunnea* are very strongly curved (see Table 1); the dentigerous processes of *Osteocephalus taurinus* has large, angular processes (see Table 1); those of *Aparasphenodon* are angular but smaller.

Palatine.—There is variation in the occurrence, the development, and the addition of ventral ridges and odontoid structures of the palatines of casque-headed hylids. The palatine is absent in *Corythomantis*, and reduced to an inconspicuous bone lying adjacent to the maxillary in *Tripriion petasatus*. In the other frogs, the palatines extend from the maxillaries to the sphenethmoid and vary from moderately robust to robust structures. There is a great deal of variation in the nature of ventral bony projections from the palatine. Some kind of bony ridge is present on all fully developed palatines. In its simplest state, the palatine ridge is low and smooth (*Hyla brunnea*). In other frogs (*Hyla dominicensis*, *Pternohyla dentata*, and *P. fodiens*), the ventral edge of the palatine ridge is slightly irregular. The palatine ridges of *Tripriion spatulatus*, *Osteocephalus*, *Trachycephalus nigromaculatus*, *T. jordani*, *Aparasphenodon*, and *Hyla septentrionalis* bear series of fine denticulate serrations and have therefore been classified as bearing odontoid structures. The palatines of *Hyla septentrionalis* are unique among the casque-headed hylids; each bone bears a row of tooth-like structures which protrude from the venter of the palatine posterior to the serrate palatine ridge.

Nasal.—There is little noteworthy variation among the nasals of the casque-headed hylids. The nasals converge medially and provide maximal dorsal coverage for the olfactory region. The culmination of this trend is the anterior development of the nasals in *Corythomantis*. The nasals provide a bony anterior margin for the orbit and articulate with the pars facialis of the maxillary at the anteroventral corner of the orbit. There is a complete articulation between the ventrolateral part of the nasal and the pars facialis of the maxillary in all the casque-headed hylids except *Trachycephalus nigromaculatus*, *Osteocephalus taurinus*, and *Pternohyla*. The dorsal configuration of the nasal surface is highly

variable. This is a function of the development of co-ossification; thus, frogs having the skin of the skull completely fused to the underlying cranial bones have heavier depositions of dermal bone. The pattern of bone deposition or sculpturing varies from irregular rugosities in partly casque-headed frogs, to reticulate or radial patterns of low bony ridges, and finally to reticulate or radial patterns of bony ridges which bear small spines in wholly casque-headed hylids.

Maxillary.—Variation in the maxillary is superficial, involving development of flanges along the outer surface, dermal surface configurations, extended anterior and posterior growth and the height of the pars facialis of the maxillary. The maxillaries of all the casque-headed hylids are alike in being robust and articulating anteriorly with the premaxillary and posteriorly with the quadratojugal; all have well developed partes faciale and partes palatinae. The partes faciale of all species, except *Pternohyla dentata*, *Osteocephalus taurinus*, and *Trachycephalus nigromaculatus* articulate along their dorsal margins with the nasals. In the latter species, the partes faciale articulate posterodorsally with the nasal to form a bony and complete anterior margin to the orbit. The pattern of co-ossification varies as described previously for the nasal. The nature of the development of labial flanges is a highly specific character and varies from a complete absence in *Hyla septentrionalis*, *Trachycephalus nigromaculatus*, and *Osteocephalus taurinus* to moderate development in *Corythomantis*, *Pternohyla*, *Aparasphenodon*, and *Trachycephalus jordani*, and finally, very extensive development in *Tripurion*. *Aparasphenodon* is distinguished by an anterior extension of the labial flange in front of the premaxillary; the pars dentalis terminates, as usual, adjacent to the pars dentalis of the premaxillary. Posteriorly, the maxillaries of all the casque-headed hylids are somewhat extended, forming a stronger articulation with the quadratojugal. This tendency is especially marked in *Corythomantis* in which the quadratojugal is reduced and the maxillary extended posteriorly to articulate with the quadrate process.

Internal Bones and Cartilages and Associated Structures

Superior Prenasal Cartilage.—The superior prenasal cartilage is present in all casque-headed frogs for which sections were available. The cartilage lies adjacent to the posterodorsal surface of the alary process of the premaxillary and fuses posteriorly with the alary cartilage. The superior prenasal cartilage is more closely associated with the alary cartilage in those frogs having nearly vertical or posteriorly inclined alary processes of the premaxillaries. In *Pternohyla* the superior prenasal cartilage is a short rod of moderate diameter which extends from the alary process to the anteroventral part of the alary cartilage posteriorly (Pl. 12a). *Hyla septentrionalis* is similar except that the superior prenasal cartilage is longer and extends posterolaterally from the alary process to terminate at the anterior end of the alary process. The superior prenasal cartilage of *Osteocephalus taurinus* resembles that of *H. septentrionalis*, except that it is more massive. *Trachycephalus nigromaculatus* has the largest prenasal cartilage of the casque-headed hylids. The anterior end of the cartilage covers the dorsal half of the posterior surface of the alary process. The prenasal cartilage extends posterolaterally and dorsally and terminates at the anterior end of the alary process, which lies posteriorly adjacent to the lateral half of the superior prenasal cartilage.

In those frogs with anteriorly inclined alary processes of the premaxillaries, the superior prenasal cartilages are less well developed and not closely associated with the alary cartilage. The superior prenasal cartilages of *Aparasphenodon* and *Corythomantis greeningi* are depressed (Pl. 12b); they extend posterolaterally along the posterodorsal surface of the alary process. The anterior end of the alary cartilage is vertically oriented and fused to the lateral end of the prenasal cartilage. At the level of the posterior fusion of the alary cartilage with the solum nasi, the superior prenasal cartilage diverges posteroventrally from the alary cartilage and terminates. The superior prenasal cartilage of *Tripriion* is a compressed, laterally inclined rod (Pl. 12c), which extends posterolaterally from the posteromedial surface of the alary process. The dorsal part of the process thickens posteriorly and expands dorsally as the alary process.

Alary Cartilage.—There is only minor variation in the alary cartilages of the casque-headed hylids, since all the cartilages serve a similar function of laterally encasing the anterior end of the cavum principale. There is variation in the nature of the fusion of the superior prenasal cartilage and the alary cartilage as discussed previously. In all casque-headed, co-ossified hylids except *Pternohyala fodiensis*, the alary cartilage is fused with the septum nasi (or solum nasi) anterior to the level of the cavum medium. In those frogs with nearly vertical alary processes and closely associated superior prenasal and alary cartilages (*Pternohyala dentata*, *Hyla septentrionalis*, *Trachycephalus nigromaculatus*, and *Osteocephalus taurinus*), the alary cartilage joins the septum nasi anterior to the development of the solum nasi. The latter is brought about either by the fusion of the dorsomedial or the ventromedial corner of the alary cartilage with the septum nasi. In frogs having anteriorly inclined alary processes (*Aparasphenodon*, *Corythomantis*, and *Tripriion*), the ventromedial corner of the alary cartilage fuses with the solum nasi. Posterior to the appearance of the cavum medium, the alary cartilage is typically arcuate in cross-section. It reaches its maximum size anterior to the anterior margin of the external nares. Posterior to the latter level, the alary cartilage gradually diminishes in size and terminates.

Inferior Prenasal Cartilage.—The anterior end of the inferior prenasal cartilage lies adjacent to the posteroventral surface of the alary process of the premaxillary. From the alary process, the inferior prenasal cartilage curves posterodorsally and then extends posteromedially to fuse with the ventral surface of the solum nasi. The anterior end of the inferior prenasal cartilage lies at approximately the same level in all the casque-headed hylids examined. However, there is some variation in the level at which the inferior prenasal cartilage fuses with the solum. The cartilage is shortest in *Hyla septentrionalis* and *Trachycephalus nigromaculatus*; it fuses with the solum nasi at a level just anterior to the formation of the nasolacrimal duct and the opening of the cavum principale into the cavum medium. In *Corythomantis*, fusion of the inferior prenasal cartilage occurs at the level of the nasolacrimal duct formation and the opening of the cavum principale into the cavum medium. In *Pternohyala* and *Osteocephalus taurinus*, fusion occurs slightly posterior to the latter level. *Tripriion* and *Aparasphenodon* differ from all other casque-headed hylids in having inferior prenasal cartilages which fuse with the solum nasi posteriorly at the level of the planum terminale and the confluence between the cavum principale and cavum inferius.

Nasal Cavities.—There are always three nasal cavities (the cava principale, medium, and inferius) in the olfactory capsules of the casque-headed hylids. The cavities show some minor variations in the positions and occurrence of recesses but on the whole are remarkably similar in structure. *Hyla septentrionalis* is exceptional in having the anterior ends of the nasal cavities aligned in a reverse sequence as compared with the other frogs, in which, in an anterior to posterior direction, the appearance of the cavum principale is followed by the cavum medium and finally by the cavum inferius, whereas the reverse is true in *H. septentrionalis*. *Pternohyla* and *Tripriion* differ from the other frogs by having a bifurcate cavum principale; the anterior end of the cavum in these genera is divided into medial and lateral recesses by a thin septum. In the majority of the casque-headed species, the cavum inferius bears only an antero-lateral recess. The cava inferius of *Aparasphenodon* and *Tripriion* bear an anteromedial recess of equal size to the anterolateral recess.

Tectum Nasi, Septum Nasi, and Solum Nasi.—A detailed report of the variation in these and associated structures such as the lamina inferior and superior, crista intermedia, planum antorbitale, planum terminale, crista subnasalis, cartilago obliqua, and the anterior and posterior maxillary processes would yield a variety of small differences. The significance of such variation is doubtful and of questionable value in a study like this one. It is important to note that with the exception of the crista subnasalis, all of these structures are present in the casque-headed hylids and show no major variation in form or relative positions. Endochondral ossification occurs only in the septum nasi and solum nasi. The anterior limits of ossification in the septum nasi lie at approximately the anterior level of the olfactory eminence. The solum nasi ossifies slightly posterior, at the anterior level of the internal nares. Both elements are completely ossified at the posterior level of the internal nares. The septum nasi is synosteoically united with the sphenethmoid posteriorly.

Septomaxillary.—The septomaxillaries of the casque-headed hylids have certain structural characteristics in common. All are basically "U"-shaped bones, which are oriented in a horizontal plane with the closed end lying anterior. There is a dorsal ramus arising from the lateral branch of the U-shaped structure, and a ventral ramus attaching in some fashion to the same branch. The anterior end of the septomaxillary always lies dorsal to the cavum medium. The posterior separation of the medial and lateral branches of the septomaxillary accommodates the confluence of the cava principale and medium; the dorsal ramus provides lateral support, and the medial branch forms medial support for the canal joining the two cava. The ventral ramus lies beneath the cavum medium; it fuses with the dorsal and lateral rami just posterior to the lateral divergence of the nasolacrimal duct from the cavum medium.

There are two basic variations, both involving the ventral ramus, on the structural plan described above. In *Pternohyla* and *Tripriion*, the ventral ramus attaches only to the posteroventral part of the lateral branch of the septomaxillary (Type I septomaxillary, Fig. 108a). In all other genera, the ventral ramus is laterally joined to the anterior end of the septomaxillary (Type II septomaxillary, Fig. 108b); posteriorly, the ventral ramus fuses with the lateral branch of the septomaxillary in the same way that it does in *Pternohyla* and *Tripriion*.

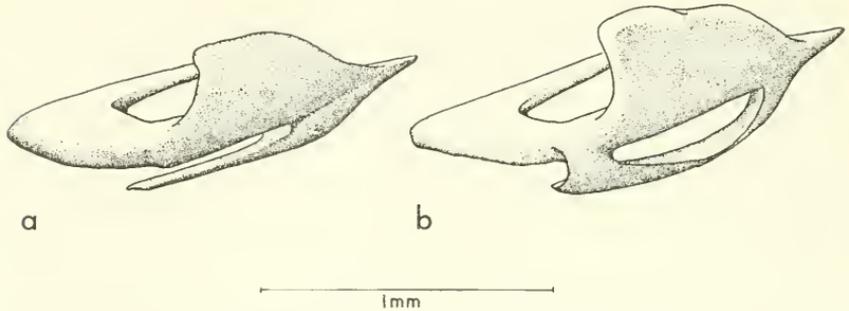


FIG. 108. Septomaxillaries of casque-headed, co-ossified hylids. Anterolateral views: (a) Type I septomaxillary, (b) Type II septomaxillary.

Relationship of Internal to External Structure

Superficial examination of the external aspects of the skull show that there is a great amount of morphological variation in the dermal bones of the olfactory region. This striking variation, unfortunately, does little to reveal the kind of associated internal changes that have occurred concomitant to external modification. Some of the minor variations in the superior and inferior prenasal cartilages and the associated types of premaxillaries have been discussed previously. The rest of the olfactory structures have been shown to be surprisingly uniform.

The entire olfactory region can be conveniently divided into two regions. The first and most anterior of these includes the septomaxillaries, the external nares, the cavum medium, the anterior end of the cavum principale, and the cavum inferius posterior to the posterolateral recess of the cavum at the level of the planum terminale. The superior and inferior prenasal cartilages lie anterior to the anterior unit and brace it against the alary process of the premaxillary. The planum terminale marks the posterior border of this part of the olfactory region. The second part of the olfactory capsule consists of the posterior parts of the cavum principale, the lateral recess of the cavum inferius, the olfactory eminence, and the internal nares. This region is bordered posteriorly by the palatine bones and the transition zone of the planum antorbitale, which marks the anterior end of the sphenethmoid and orbital region.

Whereas only minor variation was noted in the separate elements of the anterior part of the olfactory region, there is considerable variation in the position of the anterior unit with relation to the external bones. Among those frogs lacking labial flanges and having vertical or posteriorly inclined alary processes of the premaxillaries, the position of the anterior unit of the olfactory region is determined anteriorly by the position of the alary processes. In *Osteocephalus taurinus* the alary processes are inclined slightly anteriorly; the anterior end of the cavum principale lies near the base of the alary process anterior to the level of the pars dentalis of the premaxillary. The alary processes are inclined only slightly posteriorly in *Trachycephalus*, and the anterior end of the cavum principale lies dorsal to the posterior part of the pars dentalis of the premaxillary. The posterior inclination of the alary processes is especially marked in *Pterohyla fodiens*; in this species the anterior end of the cavum

principale lies dorsal to the terminal level of the palatine process of the premaxillary.

In *Tripriion*, *Aparasphenodon*, and *Corythomantis* an entirely different situation prevails with respect to the positions of the anterior and posterior units of the olfactory capsule. The planum terminale, or the posterior border of the anterior unit, lies dorsal to the level of the pars dentalis of the premaxillary. The posterior unit terminates as usual at the planum antorbitale just anterior to the orbit. In the account of the development of the skull of *Tripriion petasatus*, it was shown that the young frog has a blunt snout. Further development results in the anterior growth of the nasals and consequently an anterior shift of the external nares, which are bordered posteriorly by the anterior ends of the nasals. An anterior rotation of the premaxillaries occurs concurrent with the latter change. Since the external nares are closely allied morphologically with the anterior ends of the cava principale, it seems reasonable to conclude that anterior migration of the external nares causes the forward shift of the anterior unit of the olfactory region. The posterior unit of these frogs is proportionately much longer than the same area of the remaining casque-headed species. Thus, it is apparent that anterior growth of the posterior region, coordinated with the anterior extension of the overlying nasals, forces the anterior part of the nasal capsule forward. The pressure of the anterior growth and movement of the olfactory capsule is probably responsible for the anterior rotation of the alary processes of the premaxillaries in these three genera.

The Sphenethmoid and Associated Bones

Frontoparietal.—The frontoparietal is extremely well developed in all of the casque-headed species. The bone articulates anteriorly with the nasal and the dermal sphenethmoid, if the latter is present. The frontoparietals articulate medially throughout their lengths, thereby eliminating the occurrence of a dorsally exposed frontoparietal fontanelle. Variation in the frontoparietal primarily consists of lateral, posterolateral, and posterior extension of the bone. The frontoparietal is the least developed in *Osteocephalus taurinus*, which has only a narrow supraorbital flange extending along the outer edge of the bone. *Pternohyla dentata* has added a posterolateral process to the frontoparietal; this process is an extension of the supraorbital flange around the posterior end of the orbit. In the rest of the casque-headed hylids, the frontoparietal forms a broad supraorbital flange and terminates laterally at the level of the squamosal, and posteriorly near the posterior margin of the crista parotica of the prootic. The frontoparietal articulates laterally with the anterior and/or posterior arms of the squamosal in *Hyla septentrionalis*, *H. dominicensis*, *Pternohyla fodiens*, *Tripriion petasatus*, and *T. spatulatus*. In *Hyla brunnea*, *Corythomantis*, *Aparasphenodon*, *Trachycephalus nigromaculatus*, and *T. jordani*, the frontoparietal lacks a lateral articulation. The frontoparietal bears a prominent transverse occipital crest in *Tripriion*. The crest is moderately developed in *Trachycephalus jordani*, *Corythomantis*, and *Aparasphenodon*, but absent in the remaining species and genera. The most obvious single source of variation in the frontoparietal is in the configuration of the dorsal surface. The latter is a highly specific character and varies in the manner described for the nasal.

Dermal Sphenethmoid.—A dermal sphenethmoid occurs in all the casque-headed hylids examined except *Pternohyla* and *Tripriion spatulatus*. The bone is approximately diamond-shaped, or triangular with an anterior apex. The dermal sphenethmoid lies in the centrally depressed region of the skull between the paired nasals anteriorly and the frontoparietals posteriorly. It is always confluent with the underlying endochondral sphenethmoid as described for *Hyla septentrionalis* (Trueb, 1966).

The dermal sphenethmoid is laid down at the same time that the other dermal roofing bones are co-ossifying and represents the co-ossification of the dorsally exposed part of a cartilage replacement bone. The development and co-ossification of the dermal sphenethmoid allows the dorsal surface of the skull to be configured into a uniform and complete pattern. The presence of the dermal sphenethmoid provides bony margins with which the nasals and frontoparietals articulate anteriorly and posteriorly, thereby strengthening the skull.

Sphenethmoid.—The endochondral sphenethmoid of all species of casque-headed hylids are overlapped dorsally by the nasals and frontoparietals. In most species, dorsal coverage is completed by the addition of the dermal sphenethmoid centrally or the convergence of the posteromedial corners of the nasals and anteromedial corners of the frontoparietals. *Pternohyla* is distinctive in having a dorsally exposed sphenethmoid which is smooth and not co-ossified. Ventrally, there is little variation in the sphenethmoid; all are ossified dorsal to the prevomers, and heavily ossified posteriorly. The sphenethmoid of *Tripriion petasatus* differs from those of the remaining genera and species in its bony, ventrolateral articulation with the nasal. The latter is probably a structural compensation for the reduced palatines, which do not articulate with the sphenethmoid.

Internally, there is very little variation in the structure of the sphenethmoid. Anteriorly, the bone is ossified, except for the anterolateral wings ventral to the nasals. The margins of the orbitonasal foramen are bony. The roof of the sphenethmoid splits ventral to the frontoparietals, forming a frontoparietal fontanelle in all species. The anterior end of the fontanelle corresponds approximately with the anterior margins of the frontoparietals. The anterior margins of the fontanelle are bony, whereas the posterior margins are formed in cartilage by the taenia tecti marginali laterally and the tectum synoticum posteriorly at the level of the optic foramen. The frontoparietal fontanelle is completely roofed by the overlying frontoparietals in all species.

Parasphenoid.—The parasphenoid lies ventral to the sphenethmoid and prootic, and forms a bony bridge of support for the floor of the neurocranium between the levels of the ossified parts of the two bones. The anterior end of the parasphenoid is usually acuminate and lies slightly posterior to the level of the palatines; posteriorly, the parasphenoid terminates at the exoccipital. The parasphenoid is smooth and edentate in most of the species of casque-headed hylids (*Hyla dominicensis*, *H. brunnea*, *H. septentrionalis*, *Pternohyla*, *Aparasphenodon*, and *Corythomantis*). *Trachycephalus nigromaculatus* has a single, smooth longitudinal ridge, and *Osteocephalus taurinus* has a small proliferation of two or three odontoids located ventromedially just anterior to the base of the parasphenoid. *Trachycephalus jordani* and *Tripriion petasatus* have long,

serrate, medial ridges, and *Tripriion spatulatus* a wide, longitudinally oriented, proliferation of small denticules.

There is some variation in the basolateral wings of the parasphenoid, which probably conforms to, and reflects variation in, the configuration of the underlying prootic. The wings slope posterolaterally in *Hyla dominicensis*, *H. brunnea*, *H. septentrionalis*, and *Osteocephalus taurinus*; in the remaining species the wings are perpendicularly oriented to the longitudinal axis of the parasphenoid. The wings are moderately slender in all species, except *Tripriion spatulatus*, in which they are wide. The basal part of the parasphenoid is smooth in all species, except *Aparasphenodon* and *Corythomantis*, in which the parasphenoids bear prominent anteroventral-projecting, transverse ridges at the level of the anterior margins of the basolateral wings of the parasphenoid.

The Orbital, Otic, and Occipital Regions

External Dermal Bones

Squamosal.—The squamosal is robust in all species of casque-headed hylids. The head of the squamosal (the anterior and posterior arms) articulates with the ossified crista parotica medially. In *Hyla dominicensis*, *H. septentrionalis*, and *Tripriion*, the head of the squamosal also articulates with the posterolateral margin of the frontoparietal. The anterior arm of the squamosal articulates with the maxillary in *Tripriion* and usually in *Hyla septentrionalis*. The anterior arm of the squamosal in *Pternohyla* articulates with the pterygoid and maxillary. The arm lies dorsally adjacent to, but does not articulate with, the maxillary in *Hyla dominicensis*, *Trachycephalus nigromaculatus*, *T. jordani*, and *Corythomantis*. In the remaining species (*Osteocephalus taurinus*, *Aparasphenodon*, and *Hyla brunnea*) the anterior arm is narrowly to widely separated from the maxillary. The anterior and posterior arms of the squamosal are involved in integumentary-cranial co-ossification in all but two species, *Hyla brunnea* and *Osteocephalus taurinus*; these species are characterized by the poorest development of co-ossification and the shortest anterior squamosal arms among the casque-headed hylids.

Pterygoid.—Variation in the pterygoid involves the length of the anterior ramus and the presence or absence of a bony articulation between the medial ramus of the pterygoid and the ventrolateral ledge of the otic capsule. The anterior ramus is the longest in *Pternohyla* in which it terminates between the levels of the palatine and the orbitonasal foramen. In *Trachycephalus nigromaculatus*, *T. jordani*, *Aparasphenodon*, and *Corythomantis*, the end of the anterior ramus lies slightly posterior to the level of the orbitonasal foramen. The remaining species (*Hyla septentrionalis*, *H. brunnea*, *H. dominicensis*, *Osteocephalus taurinus*, and *Tripriion*) have short anterior rami which terminate at approximately the mid-level of the orbit. The medial ramus of the pterygoid bears a strong articulation with the prootic in *Corythomantis*, *Trachycephalus jordani*, *Osteocephalus taurinus*, *Pternohyla fodiens*, *Hyla septentrionalis*, and *H. brunnea*. The articulation is absent in the other species.

Cursory inspection of the architecture of an anuran skull suggests that three primary elements (the palatine, pterygoid, and squamosal) share the important function of securing and bracing the maxillary against the neurocranium. The palatine constitutes a brace between the anterior part of the maxillary and

sphenethmoid. Similarly, the pterygoid braces the mid- and posterior parts of the upper jaw against the prootic. The squamosal acts to secure the position of the maxillary by articulating with the prootic dorsally (the crista parotica) and the maxillary ventrally. *Pternohyla fodiens* is unique among the casque-headed hylids in having the maximal and fully articulated states of development of all three of these bones. Thus, the palatine is robust and articulates with the maxillary and sphenethmoid; the pterygoid bears a long anterior ramus which articulates with the maxillary from a level slightly posterior to the palatine, posterior to the level of divergence of the pterygoid from the maxillary. The medial ramus of the pterygoid articulates with the prootic, and the anterior arm of the squamosal articulates with the pterygoid and pars facialis of the maxillary.

In the other casque-headed hylids, the relative development of the anterior arm of the squamosal, the anterior and medial rami of the pterygoid, and the palatine seems to be compensatory or interdependent in nature. For example, in a group of moderately-ossified hylids composed of *Osteocephalus taurinus*, *Hyla brunnea*, and *H. dominicensis*, the palatines are moderately well developed, and the anterior rami of the pterygoids terminate at the mid-level of the orbit. The anterior arm of the squamosal is widely separated from the maxillary in *Osteocephalus taurinus* and *Hyla brunnea*, but the medial ramus of the pterygoid bears a strong articulation with the prootic. A converse arrangement occurs in *Hyla dominicensis*, in which the anterior arm of the squamosal lies dorsally adjacent to the maxillary and articulates with the latter by means of dense connective tissue, but the medial ramus of the pterygoid does not articulate with the prootic. Both *Aparasphenodon* and *Corythomantis* lack firm articulations between the squamosals and maxillaries and have lengthy articulating surfaces between the anterior rami of the pterygoids and the maxillaries. *Aparasphenodon* has a robust palatine but lacks an articulation between the pterygoid and prootic, whereas *Corythomantis* lacks a palatine but bears a pterygoid-prootic articulation. A parallel situation exists in *Triprion*, which is characterized by the absence of an articulation between the pterygoid and prootic. In *Triprion petasatus*, the palatine is reduced to a seemingly non-functional sliver of bone adjacent to the maxillary, whereas the articulation between the anterior arm of the squamosal and maxillary is strong. In *Triprion spatulatus*, the latter articulation is much weaker, but the palatine is better developed.

Quadratojugal.—The quadratojugal varies little in its occurrence in the casque-headed hylids. The bone lies posteromedial to the maxillary and articulates throughout its length with the maxillary. Posteriorly the ossification of the quadratojugal invades the cartilage of the quadrate process. *Corythomantis* is distinctive among the casque-headed hylids by having a greatly reduced quadratojugal.

Exoccipital-Prootic-Frontoparietal.—There is little or no variation in the relationship of these three elements. The frontoparietal lies dorsally adjacent to the exoccipital and prootic and is always separated from the latter bones by a thin layer of dense connective tissue. The prootic and exoccipital are fused; the juncture of the two bones is indistinguishable.

Internal Bones and Cartilages

Cranial Nerve Foramina.—Variation in the cranial nerve foramina is minor and involves the positions of the trochlear foramen, the oculomotor foramen with respect to the optic and prootic foramina, and the number of acoustic foramina. The trochlear foramen is usually located in the dorsomedial part of the optic foramen; the trochlear and optic nerves are separated by connective tissue. In *Corythomantis* the foramen lies in the posterodorsal part of the optic foramen, and in *Pternohyla* and *Tripriion* it is located dorsomedial to the optic foramen in the lamina perpendicularis of the frontoparietal. In all species examined, except *Hyla septentrionalis* and *Tripriion*, the oculomotor foramen lies slightly anterior to the prootic foramen. In *Hyla septentrionalis*, the oculomotor foramen lies just posterior to the optic foramen and is widely separated from the posterior prootic foramen, whereas in *Tripriion* the oculomotor foramen lies approximately equidistant between the levels of the optic and prootic foramina. *Aparasphenodon* and *Pternohyla fodiens* are unique among the casque-headed hylids in having only one large acoustic foramen instead of two smaller foramina (the anterior acoustic and posterior acoustic foramina).

Otic Region.—The basic pattern of the otic region seems to vary only in two major respects. The first concerns the relative positions of the otic and pseudobasal processes, and the second, the orientation of the columella. In *Tripriion* and *Pternohyla*, the anterior ends of the otic and pseudobasal processes lie at approximately the same level; the elements fuse a short distance posterior to their appearance. The anterior end of the otic process lies far anterior to the pseudobasal process in *Osteocephalus taurinus*. In the remaining species, the anterior end of the pseudobasal process lies anterior to the otic process; the elements are separated by a relatively short distance in *Corythomantis*, *Aparasphenodon*, and *Hyla septentrionalis*, and by a great distance in *Trachycephalus nigromaculatus*.

Three types of columellae occur in the casque-headed hylids. The columellae are oriented anterolaterally or posterolaterally. Among those directed anterolaterally, the columellae of *Trachycephalus nigromaculatus*, *Osteocephalus taurinus*, and *Pternohyla* are curved, whereas those of *Tripriion spatulatus*, *Hyla septentrionalis*, and *Corythomantis* are straight. The columellae of *Tripriion petasatus* and *Aparasphenodon* are oriented posteriolaterally and are straight.

There is considerable variation in the relative positions of the structures of the otic capsule and the cranial nerve foramina. This is most striking anteriorly. Thus, among those frogs in which the oculomotor foramen lies only slightly anterior to the prootic foramen, the anterior end of the pseudobasal process lies at the level of the optic foramen in *Trachycephalus nigromaculatus*, at the posterior edge of the optic foramen in *Pternohyla*, and between the levels of the oculomotor and prootic foramen in *Aparasphenodon* and *Corythomantis*. The anterior end of the otic process of *Osteocephalus taurinus* lies at approximately the same level as the pseudobasal process of *Aparasphenodon* and *Corythomantis*. The oculomotor foramen of *Hyla septentrionalis* occupies a position just posterior to the optic foramen; the anterior end of the otic capsule lies slightly posterior to the oculomotor foramen. In *Tripriion petasatus* and *T. spatulatus* the oculomotor foramen lies equidistant between the optic and prootic foramina and the anterior ends of the otic capsules lie at the level of the optic foramen

and just posterior to the optic foramen, respectively. As a rule, the posterior edge of the operculum lies between the levels of the posterior acoustic and jugular foramina, or in the case of *Aparasphenodon*, anterior to the jugular foramen. *Osteocephalus taurinus* is exceptional; the operculum terminates posterior to the jugular foramen.

At this time, it is impossible to evaluate the data presented above. Obvious difference in sizes and proportions of the otic capsule occur. Specifically, the otic region appears to occupy a much greater area in *Tripriion* and *Trachycephalus* than in *Corythomantis* and *Aparasphenodon*, for example. But such conclusions are tenuous without a definite frame of reference.

The degree of ossification of the otic region is remarkably consistent in the casque-headed hylids. The tectum synoticum is cartilaginous; posteriorly some ossification invades the roof of the neurocranium, but ossification is never complete. Similarly, the floor of the neurocranium retains a ventromedial strip of cartilage varying in width depending on the species. The sides of the neurocranium are bony, and with rare exceptions the cranial nerve foramina are bordered by bone. The otic capsules are well ossified. Cartilage usually forms the ventrolateral ledge and to varying degrees the posterodorsal part of the otic capsule. Ossification of the columellae and cristae paroticae is consistent. The distal tip of the crista parotica, which is encased in the head of the squamosal, is cartilaginous. Medial to the squamosal, the crista parotica is ossified. The pars externa plectri, pars ascendens plectri, pars interna plectri and operculum are cartilaginous, whereas the pars media plectri is ossified.

Bursa Angularis Oris

The bursa angularis oris is present in varying states of development in all casque-headed hylids. It is the most highly organized in *Osteocephalus taurinus*, *Corythomantis*, and *Aparasphenodon*. In these species, the bursa is a long, tubular structure, encased in connective tissue, and having a central lumen and distinct aperture into the oral cavity. *Hyla septentrionalis*, *Trachycephalus nigromaculatus*, and *Tripriion spatulatus* have bursae that are somewhat less well developed. The gland is long and encased in connective tissue, but does not bear a central lumen anterior to the aperture into the oral cavity. The bursa is very poorly developed in *Tripriion petasatus* and *Pternohyla*. The gland is loosely encapsulated in connective tissue. It bears no central lumen and is situated along the surface of the oral cavity adjacent to the maxillary.

The Articular Region

With the single exception of *Corythomantis*, the articular regions of the casque-headed genera are the same and composed of six elements, the quadrate process, the ventral arm of the squamosal, the posterior ramus of the pterygoid, the quadratojugal, Meckel's cartilage, and the angulosplenial. The pterygoid process fuses posteriorly with the quadrate process. The posterior ramus of the pterygoid lies medially adjacent to the quadrate process; the ventral arm of the squamosal is dorsally adjacent to it, and the quadratojugal lies laterally adjacent. The three bony elements surrounding the quadrate process remain separate. The ossification of the quadratojugal invades the cartilage of the quadrate process posteriorly; the posterior terminus of this ossification marks the end of the quadratojugal. Posterior to the quadratojugal, the remaining

bony elements terminate, leaving the quadrate process and Meckel's cartilage as the most posterior elements of the articular region. *Corythomantis* departs from this pattern; the maxillary invests the quadratojugal laterally, and lies adjacent to the quadrate process posterior to the terminus of the quadratojugal.

EVOLUTIONARY RELATIONSHIPS OF THE CASQUE-HEADED, CO-OSSIFIED HYLIDS

Hylid frogs are represented by approximately 30 genera and some 450 species (see Goin, 1961, for the most recent synopsis of the Hylidae). All the genera are represented in the New World except *Nyctimantis* of the Papuan region. By far the greatest diversity of hylids occurs in the New World tropics. The distribution of the casque-headed, co-ossified hylids is restricted to the New World tropics with the single exception of the northern part of the range of *Pternohyla fodiens*. The geographical distribution of the casque-headed, co-ossified hylids is summarized as follows: *Pternohyla*—low and moderate elevations from southwestern United States (Arizona) to Michoacán, México; *Triprion*—the Pacific lowlands from Sinaloa to Oaxaca, México, the Yucatan Peninsula of México, and northern Guatemala; *Hyla septentrionalis* group—the West Indies and southern Florida of the United States; *Trachycephalus*—the Pacific slopes of Colombia and Ecuador, and the lowlands of eastern Brazil southward to Argentina; *Osteocephalus*—the upper Amazon Basin in Brazil, Peru, and Ecuador; *Corythomantis*—the xeric region of northeastern Brazil; *Aparasphenodon*—the coastal region of southeastern Brazil and the upper Orinoco Basin of Venezuela.

Savage (1966) pointed out that the Middle American and South American herpetological assemblages are distinct, having been separated throughout much of the Cenozoic by seaways. It is obvious, from the numbers of kinds of frogs and their diversities, that the primary differentiation of the hylids occurred within the South American or Neotropical assemblage, whereas the Mesoamerican or Central American assemblage was a secondary center of diversification. *Triprion* and *Pternohyla* are members of the latter fauna. *Aparasphenodon*, *Corythomantis*, *Trachycephalus*, and *Osteocephalus* belong to the first, or Neotropical, group. The history of the West Indian hylids is somewhat problematic. The most recent work on the relationships of the Antillean faunas relates them to South American forms and therefore makes the Antillean faunas a northeastern extension of the Neotropical assemblage. My own observations suggest that the West Indian *Hyla septentrionalis* group is more closely allied with South American forms than any other known group.

The *Hyla septentrionalis* Group

In attempting to ferret out the relationships of a specialized group of frogs, one seeks a less specialized animal sharing basic morphological features and, ideally, a distributional pattern which links it geographically and/or chronologically with the more specialized members. The *Hyla septentrionalis* group presents problems from the outset because there are no frogs currently inhabiting the Antilles which could have given rise to this group, or clearly descend from an ancestral type.

The osteology of the *Hyla septentrionalis* group is very similar to that of another specialized genus, *Osteocephalus*; but these two groups of tree frogs differ in one essential morphological character (Table 1). *Osteocephalus* is characterized by paired, lateral vocal sacs which lie behind the angles of the jaws, whereas frogs of the *Hyla septentrionalis* group have single, median, subgular vocal sacs. The same character divergence differentiates this group from *Trachycephalus*. It is obvious, on the basis of general appearance alone, that the *Hyla septentrionalis* group is not related to *Aparasphenodon*, *Corythomantis*, *Pternohyla*, or *Triprion*.

There is a group of large, generalized tree frogs in South America which have single, median, subgular vocal sacs, and show osteological affinities with the *Hyla septentrionalis* group. These are the frogs of the *Hyla boans* group (*faber*, *boans*, and *rosenbergi*). Although principally restricted to the Amazonian lowlands or the Pacific slopes of South America, the ranges of two members of this group extend northward into Central America. *Hyla rosenbergi* is found along the Pacific slopes of Central America as far north as southern Costa Rica, and *Hyla boans* inhabits the Caribbean lowlands of eastern Panamá. The skulls of this group are large and broader than long. The maxillaries and premaxillaries are robust. The pars facialis of the maxillary is extensive but poorly ossified anteriorly; posteriorly, the pars facialis articulates with the maxillary process of the nasal, forming a bony anterior orbital margin. The dermal roofing bones are not greatly expanded, consequently the olfactory region is poorly covered laterally, and a frontoparietal fontanelle is exposed posteromedially. The ossification of the sphenethmoid is greatly expanded. In *Hyla boans* the sphenethmoid, at its widest level (at the level of the palatines), comprises more than one-third the width of the skull. The bone diminishes rapidly in width posteriorly. The quadratojugal is robust and articulates firmly with the maxillary. The squamosal arch is incomplete, but in all species the squamosal bears a broad articulation with the crista parotica. The palatines are moderately developed and edentate, although they do bear well defined ventral ridges. The prevomers are large and characterized by massive dentigerous processes which are angular and curved (see Table 1). The parasphenoids are well developed and edentate. The pterygoids are robust and fully articulated.

The evidence for an alliance between the *Hyla boans* group and the *Hyla septentrionalis* group is inconclusive. Although this conclusion is based partly on negative evidence and largely on speculation, I think it is at least reasonable to assume tentatively that the West Indian hylids evolved from a generalized, mainland South American stock. With respect to the former, there are no tree frogs currently known in Central America which seem to be related to the *Hyla septentrionalis* group. This fact limits the choice to a South American group. The current interpretation of the colonization of the Greater Antilles

favors over-water dispersal from the mainland of South America and lower Central America (Simpson, 1956; Darlington, 1957; King, 1962). If the latter is in fact the case, then distributionally the *Hyla boans* group or its progenitors is a plausible candidate for waif dispersal to the Greater Antilles.

On the basis of osteology, two evolutionary lines are evident within the *Hyla septentrionalis* group. *Hyla vasta* is found on Hispaniola, and has been observed to deposit eggs on the ground as well as in bromeliads (Noble, 1923). *Hyla dominicensis* and *H. septentrionalis* are obviously closely related and constitute one phyletic line. Both species have developed greatly expanded dermal roofing bones and co-ossification. *Hyla septentrionalis* is probably the more advanced of the two species; the dermal ossification of *H. septentrionalis* is more extensive, the nasals overlap the sphenethmoid farther posteriorly, and the squamosal arch is complete. The breeding habits of both species are generalized. *Hyla dominicensis* breeds in streams and ponds in the forest and has been noted to utilize cisterns (Mertens, 1939). Similar observations to the latter were made for *Hyla septentrionalis* by Duellman and Schwartz (1958). *Hyla dominicensis* is found on Hispaniola, whereas *H. septentrionalis* ranges throughout Cuba, the Isle of Pines, the Bahamas, and north to southern Florida. The distributional and morphological evidence suggest that *Hyla septentrionalis* and *H. dominicensis* could have evolved from a *vasta*-like ancestor which first colonized Hispaniola. Subsequent adaptive radiation probably produced a casque-headed frog on Hispaniola ancestral to *Hyla septentrionalis* and *H. dominicensis*. Later dispersal of this form to Cuba could reasonably have resulted in the evolution of *Hyla septentrionalis* which has subsequently dispersed throughout islands nearby Cuba and the adjacent North American mainland.

Hyla brunnea and *H. lichenata* represent the second phyletic line. Both have developed extensive dermal ossification and have similarly diverged from the *H. septentrionalis*-*H. dominicensis* line by a modification of the nasals. The nasals project farther forward and bear more distinct canthal ridges. By comparison with *Hyla septentrionalis* and *H. dominicensis*, the breeding habits of these frogs are specialized; they are only known to deposit their eggs in bromeliads (Myers, 1950). Both *Hyla brunnea* and *H. lichenata* are endemic to Jamaica. This would seem to suggest that an ancestral form, probably casque-headed, migrated from Hispaniola to Jamaica and subsequently produced these two species.

Aparasphenodon and *Corythomantis*

Although it is generally agreed that *Aparasphenodon* and *Corythomantis* are closely related, there is no consensus of opinion concerning their relationships with the other casque-headed, co-ossified hylids. Rivero (1961) was under the erroneous impression that *Aparasphenodon* possessed paired, lateral vocal sacs; thus, he related *Aparasphenodon* to *Trachycephalus*. Miranda-Ribeiro (1920) proposed that *Aparasphenodon* represented a subsection of *Diaglana* (*Tripriion spatulatus*); later, Myers (1942) suggested that *Aparasphenodon* and *Corythomantis* were members of a natural group also including *Tetrapriion* (*Trachycephalus jordani*), *Tripriion*, and *Diaglana* (*Tripriion spatulatus*). Miranda-Ribeiro (1920) noted the similarity between *Aparasphenodon* and *Tripriion spatulatus*, but excluded *Tripriion petasatus* because it possessed verti-

cal pupils. Myers (1942) did not regard the latter character to be important, and based his conclusions on zoogeographic evidence and the similarity of cranial-casque patterns.

Aparasphenodon and *Corythomantis* share a number of characteristics which evidence a close relationship between them and clearly separate the two genera from the other casque-headed hylids (Table I). The skulls are narrow anteriorly and long. The labial flanges are absent or poorly developed; therefore the snouts are acuminate by comparison with the other casque-headed hylids. The parasphenoids are poorly developed and edentate. *Aparasphenodon* and *Corythomantis* are obviously distinct from the Antillean casque-headed hylids on the bases of size and general appearance. Furthermore, the skulls of *Aparasphenodon* and *Corythomantis* are characterized by labial flanges, prominent patterns of co-ossification, the presence of a prenasal or anterior extension of the nasals, anteriorly concave canthal ridges, and poorly developed parasphenoids. The single, median, subgular vocal sacs of these two genera distinguish them from the South American *Trachycephalus* and *Osteocephalus*. Superficial examination seems to suggest that *Aparasphenodon* and *Corythomantis* are closely related to the geographically distant *Tripriion*. However, there are several important differences between the South American genera and the Middle American *Tripriion*. The parasphenoid of *Tripriion* is robust and bears odontoid structures. The labial flanges of *Tripriion* are very well developed. The surface configuration of the dermal bones of *Tripriion* is delicate and in low relief, whereas that of *Aparasphenodon* and *Corythomantis* is coarse by comparison. The quadratojugal tends to be reduced in *Aparasphenodon* and *Corythomantis*; the bone is robust in *Tripriion*. The otic region is anteriorly expanded in *Tripriion* and not expanded in *Aparasphenodon* and *Corythomantis*. The cavum principale is anteriorly bifurcate in *Tripriion* and single in *Aparasphenodon* and *Corythomantis*. The latter genera have Type II septomaxillaries, whereas *Tripriion* has a Type I septomaxillary.

In the descriptive account of *Corythomantis greeningi*, attention was drawn to the striking resemblance of this species to a member of the *Hyla rubra* group. This is a group of small to moderate-sized hylids, containing about 24 species (León, in press). These frogs are widespread from lowland México to Argentina and are most diverse in southeastern Brazil (Cochran, 1955). Members of this group have a single, median, subgular vocal sac. According to León, the members of this group are characterized by the following osteological features: prevomerine teeth on transverse ridges; skull generally longer than wide; nasals large (length more than 40 per cent total length of skull); quadratojugal slender, always joined to maxillary by bony suture; crista parotica slender and short; columella delicate and spatulate; squamosal arch incomplete; and prevomer, premaxillary, and maxillary teeth present. The cranial characters in the *Hyla rubra* group are highly variable and show a trend towards reduction of ossification. Unlike other small hylids, the reduction principally involves the prootic region, prevomers, palatines, pterygoids, and parasphenoid. The members of the *Hyla rubra* group retain a well-ossified sphenethmoid and dermal roofing bones.

Hyla boulengeri (Fig. 109a) is one of the more completely ossified members of the *Hyla rubra* group. The skull is depressed and the snout attenuate. The nasals are extremely large, the sphenethmoid well ossified, and the frontoparietals convergent medially. The palatines, parasphenoid, prootic, and prevomers are

well developed, and the latter articulate with the premaxillaries anteriorly. The medial ramus of the pterygoid articulates with the prootic. By comparison, the cranial elements of another member of the *H. rubra* group, *Hyla staufferi* (Fig. 109b), are greatly reduced in ossification. Like *Hyla boulengeri*, the skull is depressed, the nasal large, and the sphenethmoid well ossified. The frontoparietals are not completely convergent medially; thus, a small frontoparietal

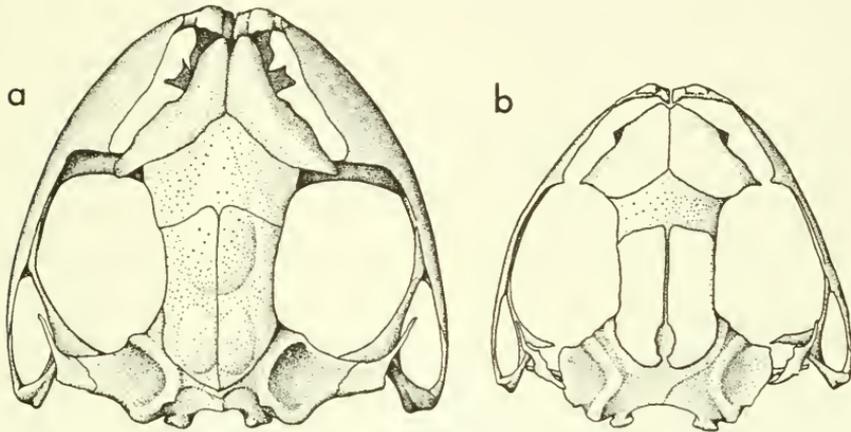


FIG. 109. Dorsal views of the skulls of (a) *Hyla boulengeri* (KU 104352), and (b) *Hyla staufferi* (KU 60614). $\times 3.3$.

fontanelle is exposed. The prevomers are small and do not articulate with the maxillaries or premaxillaries. The parasphenoid and prootic are only moderately developed. The medial ramus of the pterygoid does not articulate with the prootic, and the palatines are absent. The "*Hyla rubra*" (Fig. 71a) from Jacareacanga, Pará, Brazil, has a skull somewhat intermediate between those of *Hyla boulengeri* and *H. staufferi*. The pterygoid articulates with the prootic, but the parasphenoid and palatines are very poorly developed.

The similarity between the "*Hyla rubra*" from Jacareacanga and *Corythomantis greeningi* suggests that the latter represents a phyletic line derived from the *Hyla rubra* group. Although *Corythomantis* has increased ossification of dermal roofing bones, other elements are markedly reduced or absent. Among the most important are the absence of the palatine and the reduced parasphenoid and quadratojugal. *Aparasphenodon* shows slightly different evolutionary trends, and it has a greater amount of dermal ossification than *Corythomantis*. The former has a prenasal, whereas in *Corythomantis* the anterior extension of the nasals fulfills the same functional requirement. The dentigerous processes of the prevomers are massive and angled in *Aparasphenodon*, whereas they are small and transverse in *Corythomantis*. The palatines are reduced but not absent in *Aparasphenodon*, and the medial ramus of the pterygoid does not articulate with the prootic as it does in *Corythomantis*. These differences in cranial characters, together with the larger size of *Aparasphenodon*, are the features by which the genera are separated. The similarity of cranial structure suggests a common ancestor for the two genera, but the differences preclude the evolution of *Aparasphenodon* from *Corythomantis*.

The widespread geographical and ecological distribution of the *Hyla rubra* group in South America, the range of osteological characters possessed by the group, and the similarity of the general cranial structure and vocal sacs to those of *Aparasphenodon* and *Corythomantis* suggests that they were derived from the *Hyla rubra* group. *Corythomantis* and *Aparasphenodon brunoi* are restricted to the subhumid environments of the *caatinga* of northeastern Brazil and the *restinga*, the coastal lowlands from Espirito Santo to Guaynabara, of southeastern Brazil, respectively. The single specimen of *Aparasphenodon venezolana* is from the savanna-scrub region of Venezuela. At least as recently as the late Pliocene, subhumid environments (open woodland and savanna) were more widespread in eastern South America than they are today; possibly these environments were continuous from the cerrado of southern Brazil to the Caribbean (Ducke and Black, 1953; Savage, 1955). Probably *Corythomantis* and *Aparasphenodon* had a common ancestor, which was at least partly casque-headed and inhabited these subhumid areas. This ancestral stock differentiated into a stock of small frogs restricted to the xeric *caatinga* and another stock of larger frogs that was widespread in subhumid savannas and/or open woodlands. The development of the present-day distribution of rainforest in the Amazon Basin in the Pleistocene separated the latter stock, *Aparasphenodon*, into Venezuelan and Brazilian populations; the former developed into *A. venezolana* and the latter into *A. brunoi*. The development of the forests further isolated the *Corythomantis* stock in the *caatinga*, where it developed into *C. greeningi*.

Osteocephalus and *Trachycephalus*

Osteocephalus and *Trachycephalus* are moderately large South American tree frogs which are distinguished by two characters from all other New World hylids. The crania of these genera are casqued and co-ossified, and the vocal sacs are paired, lateral, and located behind the angles of the jaws. The latter character separates *Osteocephalus* and *Trachycephalus* from the other casque-headed, co-ossified hylids (Table I), and the former character differentiates these two genera from *Phrynohyas*, the only other hylid with paired, lateral vocal sacs. Relatively little is known about *Osteocephalus*. Goin (1961) assigned eight or ten species to this genus. I have examined only *O. taurinus* and *O. leprieuri* (*O. leprieuri* is virtually indistinguishable from *O. taurinus* osteologically) and hesitate to include any other species in the genus. *Osteocephalus* is purported to range from the Guyanas and northern Brazil to Colombia (Lutz and Kloss, 1952). Bokermann (1964) reported on some field observations of *O. taurinus* made in Rondonia Territory, near Marmelo, Brazil. There is considerably more information available on *Trachycephalus*, an inhabitant of disjunct, sub-humid environments. At least four species are assigned to this genus; these are *T. jordani* from the Pacific lowlands of Ecuador and southern Colombia, *T. atlas* from the eastern coast and probably the *caatinga* of Brazil (Bokermann, 1966), *T. nigromaculatus* from southeastern Brazil (Lutz, 1954; Cochran, 1955), and *T. siemersi* from Uruguay and northeastern Argentina.

Lutz and Kloss (1952:655) alluded to a relationship between *Osteocephalus* and *Trachycephalus* in their statement that *O. taurinus* “. . . seems intermediate between *Hyla* and *Trachycephalus*.” A strong case can be postulated for a close relationship between *Osteocephalus* and *Trachycephalus* on the bases of the similar structure of the vocal sacs and their osteological character-

istics. The skulls of both genera are longer than broad and the snouts rounded. The dermal roofing bones are expanded and co-ossification is partial or entire. The canthal ridges are distinct and not anteriorly concave. Prenasal and inter-nasal bones are absent. The prevomers are large and fully ossified. The dentigerous processes of the prevomers are massive and curved. The palatines are well developed and bear odontoids. Both genera have Type II septomaxillaries (Fig. 108b). The parasphenoids are well developed and bear some type of odontoid structure. The cranial nerve foramina are arranged in the same spatial sequence.

There are obvious differences between the skulls of *Osteocephalus* and *Trachycephalus*, but these are principally the result of a marked evolutionary trend toward increased dermal ossification from *Osteocephalus* to *Trachycephalus*. The snout of *Osteocephalus* is less rounded (tending toward a truncate shape; compare plates 5a and 6a) than that of *Trachycephalus*. The alary processes of the premaxillaries of *Trachycephalus* are expanded and co-ossified; the addition of bone anteriorly imparts a more rounded shape to the snout. The nasal and pars facialis of the maxillary have increased in size and tend to articulate with one another, forming a complete or nearly complete lateral cover to the olfactory region in *Trachycephalus*. Proliferation of frontoparietal ossification results in a wider supraorbital shelf (and consequently a greater interorbital width), extension of the frontoparietal over the crista parotica to the medial margin of the squamosal, and the development of a posterior, transverse occipital crest in *Trachycephalus*. The surface configuration of the dermal roofing bones is prominently developed in *Trachycephalus*, whereas in *Osteocephalus* it is inconspicuous. The pattern of co-ossification in *Osteocephalus* is a reticulate network formed of low, bony ridges which is reminiscent of the pattern established during the early development of co-ossification in *Triprion petasatus*. This seems to suggest that *Osteocephalus* represents a rather primitive state in the phyletic development of co-ossification. By comparison with *Trachycephalus*, the squamosal of *Osteocephalus* is poorly developed. It is not involved in co-ossification and the anterior arm extends only about half the distance to the maxillary. The squamosal arch is essentially complete in *Trachycephalus*. The anterior arm of the squamosal does not articulate firmly with the maxillary, but it lies dorsally adjacent to the maxillary. Correlative with the strengthened squamosal arch, the pterygoid of *Trachycephalus* has undergone modification. The medial ramus of the pterygoid does not articulate with the prootic as it does in *Osteocephalus*, but the articulation of the anterior ramus is stronger. The anterior end of the anterior ramus of the pterygoid extends forward to a level just posterior to the trochlear foramen in *Trachycephalus*, whereas the anterior ramus terminates at the mid-level of the orbit in *Osteocephalus*.

The parasphenoid of *Osteocephalus* is characterized by slender basal wings which slope posterolaterally. The basal wings of the parasphenoid in *Trachycephalus* are wider by comparison and transversely oriented. The shapes of the basal parts of the parasphenoids conform to differences in the prootic bones and otic capsules overlying them. In view of this, it is interesting to note that the otic capsule of *Osteocephalus* lies between the levels of the oculomotor and jugular foramina. In *Trachycephalus*, the otic capsule occupies the area between the optic and jugular foramina (*T. nigromaculatus*) or the area from the anterior level of the oculomotor foramen to the jugular foramen (*T. jordani*);

thus, the otic capsule of *Trachycephalus* is somewhat expanded anteriorly in comparison with *Osteocephalus*.

The structural variation of the bursa angularis oris in *Osteocephalus* as compared with *Trachycephalus* is probably indicative of the reduction of this gland in more advanced forms. The bursa is very well developed in *Osteocephalus*, in which it is long, tubular, encased in a connective tissue capsule, and characterized by a distinct aperture into the oral cavity. In *Trachycephalus* the bursa is similarly developed but distinguished by a relatively poorly developed central lumen and connective tissue capsule.

The trend towards increased ossification is evident within *Trachycephalus*. *Trachycephalus nigromaculatus* (Pl. 6a) is the least specialized member of the genus. I have examined photographs (Bokermann, 1966: Figs. 3-4, p. 123) of the skull of *T. atlas* from Bahia, Brazil; this species is obviously closely related to the more southern *T. nigromaculatus*. In the description of the species, Bokermann (1966) reported the following osteological differences between *T. nigromaculatus* and *T. atlas*: (1) the interorbital space of *T. atlas* is wider; (2) the loreal region is more vertical; and (3) the frontoparietals project farther posteriorly and are more heavily sculptured in *T. atlas*. In terms of increased ossification these differences may be accounted for by (1) lateral extension of the frontoparietal into a wider supraorbital shelf; (2) proliferation of the nasal and pars facialis of the maxillary, extending the length of the articulation of the two bones; and (3) posterior expansion of the frontoparietals and a general proliferation of surface rugosities characteristic of increased co-ossification. The same three evolutionary trends have been further exploited in *T. jordani* (Pl. 7a) on the west coast of South America. *Trachycephalus jordani* is further distinguished from the eastern members of the genus by a development of shallow maxillary and premaxillary flanges. An anteromedial notch between the alary processes of the premaxillaries is characteristic of *T. atlas* and *T. nigromaculatus*. A similar notch is present in *T. jordani* but is reduced because of the proliferation of dermal bone on the alary processes. Examination of the internal structure of the anterior end of the skull of *T. jordani* shows that the bony posterior surface of the alary processes have been secondarily resorbed, forming cavities within the projecting anterior ossification of the premaxillaries. The nasal capsule has moved forward to occupy this shallow cavity, foreshadowing slightly the condition characteristic of *Triprion*, *Aparasphenodon*, and *Corythomantis*.

Earlier in this discussion, attention was drawn to a third genus of hylid frogs, *Phrynohyas*, which possesses paired, lateral vocal sacs like those of *Trachycephalus* and *Osteocephalus*. *Phrynohyas* consists of at least six species (*hebes*, *imitatrix*, *ingens*, *quadrangularum*, *mesophea*, and *venulosa*); the genus is widespread in the lowlands of South America along the Caribbean coast, in the Orinoco basin, the Guianas, the Amazon Basin west to Bolivia and Ecuador and south to Paraguay and northern Argentina. The genus is also known from the islands of Trinidad and Tobago, and the west coast of Ecuador. One species, *Phrynohyas venulosa*, ranges north from South America along the Pacific coast of Panamá and Costa Rica, and thence northward along both the Pacific and Caribbean coasts to Tamaulipas and Sinaloa, México (Duellman, 1956). *Phrynohyas venulosa* is the best known and most widely distributed member of the genus and like the others is morphologically generalized.

The skull of *Phrynohyas venulosa* closely resembles that of *Osteocephalus*; this was discussed at the end of the descriptive account of the latter. Some of the more important features are worth recounting here. The anterior dermal roofing bones are expanded. The maxillaries and premaxillaries are robust. The squamosal arch is incomplete. The prevomers are large, and their dentigerous processes are massive and curved. The palatines are well developed. The pterygoid is fully articulated. The terminus of the anterior arm of the pterygoid lies at the mid-level of the orbit. The basal wings of the parasphenoid are slender and slope posterolaterally. Fundamentally, the skulls of *Phrynohyas venulosa* and *Osteocephalus taurinus* are the same. All but one of the osteological characters which distinguish *Osteocephalus* from *Phrynohyas* can be evolved by proliferation of dermal bone in the same way that *Trachycephalus* was derived from *Osteocephalus*. The single character which separates *Phrynohyas* and *Osteocephalus* is the condition of the septomaxillary. *Phrynohyas* has a Type I septomaxillary, which, at the present stage of investigation, is known to occur only in this genus, *Smilisca*, *Pternohyla*, and *Triprion*. *Osteocephalus*, *Trachycephalus*, *Hyla rubra* and *H. lanciformis* of South America, *Pseudacris* of North America, and the other genera of casque-headed, co-ossified hylids are characterized by a Type II septomaxillary. The consequences of this single character divergence of the septomaxillary are difficult to evaluate in view of the other outstanding similarities among *Phrynohyas*, *Osteocephalus*, and *Trachycephalus*. The widespread distribution, and the generalized habits and morphology of *Phrynohyas* would seem to indicate that its members represent a logical choice for modern descendants of a progenitor which gave rise to a single phyletic line of casque-headed frogs beginning with *Osteocephalus* and terminating with *Trachycephalus jordani*.

It is possible that the condition of the septomaxillary in *Phrynohyas* represents an evolutionary link with another generalized stock of hylids, *Smilisca*. This genus is widespread in Central America; two members are present in northwestern South America. *Smilisca* is postulated to be an autochthonous Middle American group (Duellman and Trueb, 1966). Like *Phrynohyas venulosa*, the skull of *Smilisca baudini*, the most widespread and generalized member of the genus, is unspecialized. The species inhabits lowlands and shows few specializations of habits. The vocal sacs are bilobed and subgular, a condition thought by Duellman (1966) to be less advanced than the paired, lateral vocal sacs of *Phrynohyas*.

It can be hypothesized that *Phrynohyas* and *Smilisca* arose from a single ancestral stock, which probably inhabited the lowlands and had a weakly bilobed vocal sac and a Type I septomaxillary. This stock was separated into Central American and South American components by the Panamanian Portal throughout much of the Cenozoic; these components evolved into *Smilisca* and *Phrynohyas*, respectively.

It has been hypothesized that the extensive tropical rain forest in the Amazon Basin probably did not reach its present distribution until late Pleistocene (Duellman, 1958). Earlier in the Cenozoic, much of the basin was an epeiric sea in which there was a deposition of sediments from the erosion of the Andes (Oliveira, 1956). The savanna and open woodlands that now exists in south-central Brazil were probably continuous with those in northern South America in the Pliocene and probably into the Pleistocene, as evidenced by isolated patches of this habitat throughout the eastern part of the Amazon Basin (Ducke

and Black, 1953, and Veloso, 1947). If this was the case, the prototype of *Phrynohyas* must have adapted to subhumid conditions. The habits of *Phrynohyas venulosa* were summarized by Duellman (1956), and indicate adaptation to existence in subhumid environments. The activity of the frog is controlled by seasonal rainfall. The frogs take day-time and dry-season refuge in bromeliads, banana plants, and occasionally palms. *Phrynohyas* is an inhabitant of gallery forests, savannas, and rain forests in areas where rainfall is strongly seasonal. If the ancestral *Phrynohyas* stock was similarly adapted to subhumid environments, it could have dispersed southward along the north-western coast of South America, eastward through the northern scrub forest, savanna, and open woodlands, and thence southward toward eastern Bolivia and northern Paraguay. Temporally and geographically, this distributional pattern is compatible with that suggested for the *Leptodeira annulata* stock by Duellman (1958).

It seems feasible to postulate that during this extended period of subhumid conditions, an evolutionary trend toward increased ossification within the widespread *Phrynohyas* stock resulted in the development of the casque-headed genera *Osteocephalus* and *Trachycephalus*. Like *Phrynohyas*, *Osteocephalus* is a forest inhabitant, principally in areas of seasonal rainfall. *Trachycephalus*, on the other hand, is an inhabitant of more arid areas, usually characterized by low forest and scrub vegetation and marked by prolonged dry seasons. It is possible that prior to the uplift of the Andes and the development of rain forests in the Amazon Basin, a subhumid habitat was distributed across the South American continent and occupied by a casque-headed hylid intermediate between *Osteocephalus* and *Trachycephalus*. After the uplift of the Andes and the development of tropical rain forests in the Amazon Basin, a *Trachycephalus* stock was divided into two isolated units in the eastern and western coastal regions of South America. The western component gave rise to *T. jordani*, and the eastern component to a frog like *T. nigromaculatus*. The latter was probably distributed along the coastal region of South America from northeastern Brazil to northeastern Argentina and later differentiated into a southern species (*T. siemersi*), a central species (*T. nigromaculatus*), and a northern species (*T. atlas*).

Triprion and *Pternohyla*

Considerable attention has been devoted to the two Middle American genera of casque-headed hylids, *Triprion* and *Pternohyla*. *Triprion* has been associated most often with *Trachycephalus jordani* (Rivero, 1961; Smith, 1957; Myers, 1942; and Peters, 1955), on the bases of the shapes of the skulls and the nature of odontoids present. Smith (1957) included *Pternohyla* in this group. Although they are not similar in superficial appearance, several characters relate *Pternohyla* and *Triprion*. Both genera have bilobed, or median, subgular vocal sacs, Type I septomaxillaries, and cava principalae which are bifurcate anteriorly (Table 1). These characters separate *Pternohyla* and *Triprion* from the Antillean casque-headed hylids (single, median, subgular vocal sac, Type II septomaxillary, non-bifurcate cavum principale), *Aparasphenodon* and *Corythomantis* (single, median, subgular vocal sac, Type II septomaxillary, non-bifurcate cavum principale), and *Osteocephalus* and *Trachycephalus* (paired, lateral vocal sacs, Type II septomaxillary, non-bifurcate cavum principale).

Pternohyla and *Tripriion* share the same three characters with *Smilisca baudini*, a moderate-sized, generalized hylid which ranges throughout the Pacific and Atlantic lowlands of México from southern Sonora and the Río Grande embayment of Texas southward to Costa Rica. Duellman and Trueb (1966) have hypothesized an evolutionary history of the genus *Smilisca*. According to their account, the prototype of *Smilisca* lived in the mesic tropical environment of the eastern part of the Central American Peninsula. Earlier this stock diverged from the stock which gave rise to *Phrynohyas*, *Osteocephalus*, and *Trachycephalus* in South America. In the late Miocene the ancestral stock of the *Smilisca baudini* group dispersed northwestward into upper Central America and then into southern México. The subsequent elevation of mountains in late Miocene or Pliocene resulted in the development of subhumid lowland areas. The *Smilisca* stock inhabiting the Pacific lowland areas during this period is postulated to have given rise to *Smilisca baudini*. It is reasonable to assume that this stock also produced a casque-headed phyletic line which was adapted to the more xeric environments along the Pacific lowlands. Subsequently, this group, the prototype of *Tripriion*, dispersed across the Isthmus of Tehuantepec and into the Yucatan Peninsula. This dispersal probably took place during a glacial period of the Pleistocene when, due to fluctuations in the water table, semi-arid environments were continuous at times from the Pacific lowlands across the isthmus to the Gulf lowlands. During interglacial periods of higher water tables, the lowlands . . . were more restricted (Duellman, 1960). The restriction of suitable subhumid environments through the subsequent development of wet forests on the Atlantic side of the isthmus resulted in the isolation of populations of the *Tripriion* stock on the Pacific lowlands of México and in the Yucatan Peninsula. The former gave rise to *Tripriion spatulatus*, a somewhat less specialized species than *Tripriion petasatus*, which inhabits the arid portions of the Yucatan Peninsula and also exists as relict populations in the savannas in El Petén, Guatemala. *Tripriion petasatus* differs from *T. spatulatus* in having a dermal sphenethmoid, a reduced palatine, a very poorly developed bursa angularis oris, and a bilobed vocal sac. The vocal sac of *T. spatulatus* is single and median. Although *T. spatulatus* lacks a dermal sphenethmoid, the nasals and frontoparietals converge medially, dorsal to the sphenethmoid; this condition is probably functionally equivalent to the development of the dermal sphenethmoid. However, *T. spatulatus* has only a moderately developed palatine and bursa angularis oris, characters which are further reduced in *T. petasatus*.

In the descriptive account of *Pternohyla*, it was shown that structurally *Smilisca baudini* is very similar to both species of *Pternohyla*. Moreover, it was demonstrated that one form could be derived from another by increased dermal ossification in the following sequence: *Smilisca baudini*—*Pternohyla dentata*—*Pternohyla fodiens*. The structure of the skull of *Pternohyla*, unlike that of the other casque-headed hylids, shows adaptations reflecting the fossorial habits of the genus. In both species, the crania are depressed. Although solidly roofed, the skulls lack distinct labial flanges. The palatines are robust, the squamosal arches complete, and the pterygoids fully articulated. Further specialization is evident in *Pternohyla fodiens* which has developed an internasal and more extensive dermal roofing bones, and has incorporated the two acoustic foramina into one large acoustic foramen.

The resemblances between *Triprion* and *Smilisca baudini* involve the septomaxillaries, the olfactory capsule, the prevomerine dentigerous processes, and the structure of the vocal sac. *Pternohyla* shares the same characters with *Smilisca baudini* as does *Triprion*. Additionally it has been demonstrated that the shape of the skulls of *Pternohyla* and *Smilisca* are similar and that *Pternohyla* differs principally from *S. baudini* in the presence of co-ossification, further expansion of dermal roofing bones, and addition of the internasal in *P. fodiens*. The dermal roofing bones are much less expanded in *Pternohyla* than in *Triprion*. *Pternohyla* lacks a dermal sphenethmoid and the nasals and frontoparietals are not completely convergent dorsal to the sphenethmoid. Co-ossification of the skull of *Pternohyla* is not complete, and the pattern of co-ossification forms a poorly organized reticulate network reminiscent of the pattern formed in the early development of co-ossification in *Triprion*. These morphological data suggest that *Pternohyla* may have been more recently derived from the *Smilisca* stock than *Triprion*. Furthermore, the structure of the skull of *Pternohyla* seems to reflect adaptations of the frogs to fossorial habits. A *Smilisca baudini*-like ancestor probably gave rise to a fossorial stock in response to the increased aridity during the Pleistocene. The fossorial ancestor was probably widespread over the Pacific lowlands of México and very similar in appearance to *Pternohyla dentata*. Further evolution in this stock resulted in the appearance of the more advanced *Pternohyla fodiens*. *Pternohyla dentata* is known only from the upper Río Santiago Basin on the Mexican Plateau, and probably represents a relict population of the ancestral stock of *P. fodiens*.

CONCLUSIONS

Geographical and morphological evidence indicates that the casque-headed, co-ossified condition has arisen at least six times within the Hylidae. Thus, five phyletic lines gave rise separately to *Triprion*, *Pternohyla*, *Trachycephalus* and *Osteocephalus*, *Aparasphenodon* and *Corythomantis*, the *Hyla septentrionalis* group, and the gastrothecine hylids. The first five groups are treated in this study. The last group, consisting of *Gastrotheca*, *Flectonotus*, *Anotheca*, *Nyctimantis*, and *Amphignathodon*, is discussed only briefly. The gastrothecine hylids seem to bear little evolutionary relevance to the other groups. Moreover, they are represented by so few specimens that it is impossible to complete a satisfactory morphological study of them at the present time.

An hypothesized phyletic arrangement of the other five groups of casque-headed, co-ossified hylids is shown in Figure 110. The vertical scale represents geological time. The horizontal scale is divided into the three geographical areas in which the evolution of the casque-headed forms occurred. The heavy horizontal bars intersecting phyletic lines in the Pliocene and Pleistocene represent the development of casques and co-ossification. These morpho-

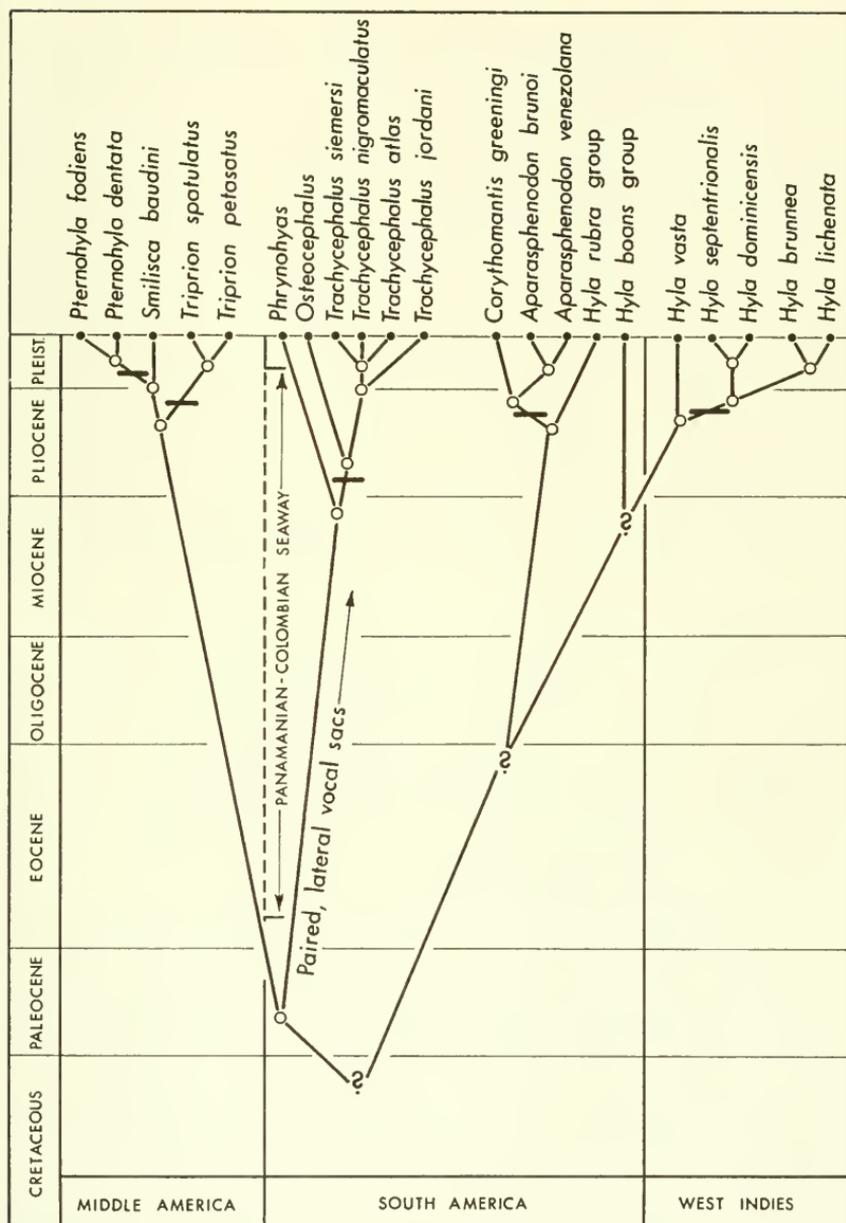


FIG. 110. Proposed phylogenetic relationships of the casque-headed, co-ossified hylids. Vertical scale represents geological periods. Vertical exaggeration of the Pleistocene is $\times 2$. The horizontal scale shows the geographical areas in which evolution of the casque-headed hylids took place. Open circles represent frogs which no longer exist, whereas closed circles are frogs presently known and named at the top of the figure. Heavy horizontal bars intersecting phyletic lines indicate the development of casques and co-ossification.

logical specializations are apparently associated with the widespread occurrence of subhumid environments in the latter part of the Pliocene and the Pleistocene.

Three principal problems have confused the previous systematic interpretations of the casque-headed, co-ossified hylids. Several of the species are poorly represented in collections, and until now, no one person has had the advantage of studying examples of each genus. Previous workers have attributed too much reliability to the taxonomic value of the presence or absence of odontoids on the palatines and parasphenoid. This has been shown to be a highly labile character which is closely associated with sexual and ontogenetic variation. And finally, the striking parallelism which has been involved in the evolution of these frogs has been overlooked.

The single most obvious quality shared by the casque-headed, co-ossified hylids is the similarity of their environments. Thus, those genera which utilize the most similar habitats look the most alike externally. Taking all of these points into consideration, the following arrangement is possible.

1. *Tripriion*, *Aparasphenodon*, *Corythomantis*, and *Trachycephalus*.—These four genera are characterized by long skulls, labial flanges, sculpturing of dermal roofing bones, and the addition of dermal bone at the anterior end of the skull. All inhabit xeric environments where terrestrial bromeliads and three holes often afford the only suitable moist shelters. *Trachycephalus*, the least specialized of the group, is also found in less xeric environments where it utilizes trees for shelter.

2. *Osteocephalus*, *Hyla septentrionalis*, *Hyla brumnea*, and *Hyla dominicensis*.—These species are very similar in general appearance. They are large, and the skulls are only slightly broader than long. They lack labial flanges, prominent sculpturing, and addition of dermal bone at the anterior end of the skull. All are characterized by inconspicuous dermal sculpturing and the presence of a dermal sphenethmoid. These frogs are inhabitants of forests, which although wet, are characterized by highly seasonal rainfall.

3. *Pternohyla*.—The frogs in this genus are unique in possessing a depressed skull in which few, if any, signs of internal reduction are evident. One species has an internasal bone. The genus is an inhabitant of xeric areas, where it utilizes terrestrial burrows for shelter.

Unfortunately the above arrangement does not take into account widely disjunct geographical ranges, or less obvious anatomical

differences. For example, bone added to the anterior end of the snout of members of the first group is formed by the nasals in *Corythomantis*, the premaxillaries in *Trachycephalus*, and the addition of a prenasal in *Aparasphenodon* and *Triprion*. Furthermore, *Corythomantis* and *Aparasphenodon* have single, median, subgular vocal sacs, *Triprion* a bilobed or single median vocal sac, and *Trachycephalus*, paired lateral vocal sacs. In the second group, *Osteocephalus* has paired, lateral vocal sacs, whereas the others have median, subgular vocal sacs.

It is obvious from the preceding arrangement that the evolution of the casque-headed, so-ossified hylids has resulted in a striking amount of parallelism. Apparently the evolution of species has been largely a process of adaptation to similar environments. However, the wide geographical isolation of seemingly similar genera and the variety of internal and external anatomical characters which separate them in each case cannot be disregarded. Therefore, the casque-headed, co-ossified condition must have arisen at least twice in Middle America (*Triprion* and *Pternohyla*), once in the West Indies (*Hyla septentrionalis* group), and twice in South America (one line composed of *Osteocephalus* and *Trachycephalus* and the other of *Aparasphenodon* and *Corythomantis*).

The development of the casque-headed, co-ossified condition is closely associated with a behavioral trait known as "phragmosis." Barbour (1926) first associated this behavior with frogs which utilize their heads to fill cavities or block holes. Phragmotic behavior has been reported in *Pternohyla*, *Triprion*, *Aparasphenodon*, and *Trachycephalus*. *Pternohyla* is fossorial and thus uses its head to block entries to burrows. *Triprion* blocks tree holes with its head (Stuart, 1935). *Aparasphenodon* plugs entrances to terrestrial bromeliads with its head (Carvalho, 1939), and *Trachycephalus* uses its head to block entrances to both terrestrial bromeliads and tree holes (Lutz, 1950). Phragmotic behavior has not been reported in *Corythomantis greeningi*. The structure of the head in *Corythomantis* and its occurrence in xeric areas where terrestrial bromeliads provide the most likely shelter, suggest that it probably uses its head in the same way that *Aparasphenodon* does. Phragmosis is unknown in *Osteocephalus* and the *Hyla septentrionalis* group. These frogs are inhabitants of more humid, forested areas where suitably moist hiding places are more common.

The development of co-ossification is brought about by the increase of dermal ossification. This structural modification probably

reduces the danger of desiccation in arid environments. The dermal and epidermal layers of skin which overlie membrane bone are poorly organized and characterized by reduced numbers of glands and poor vascularization. Because of the extensive development of bone, the importance of the skin as a sensory and protective organ is diminished. Although it is almost certain that the skin overlying the dorsum of the skull suffers desiccation, the process probably has few, if any, detrimental effects on the physiology of the organism as a whole.

Probably the two most important structural modifications of the skulls with respect to the phragmotic habits of the frogs are the development of labial flanges and extensive dermal roofing bones. In each of the genera exhibiting phragmosis, the roofing bones are fully expanded, or nearly so; thus, there are partial or full articulations between the nasals and partes faciale of the maxillaries, and the paired frontoparietals and nasals are medially convergent. The dermal sphenethmoid has developed from the sphenethmoid; the nasals and frontoparietals articulate with the former in all species except *Pternohyla* and *Tripriion spatulatus*. In these the postero-medial corners of the nasals and the anteromedial corners of the frontoparietals are convergent. The presence of a wide supraorbital shelf, composed of the nasals anteriorly and the frontoparietals posteriorly provides a bony orbital roof under which the frogs can partially or wholly retract their eyes. The auditory region is completely covered by the frontoparietals. This provides protection for the muscles which attach to the anterodorsal surface of the crista parotica and in some cases provides an additional attachment for the *m. rhomboideus anterior* (*occipitosuprascapularis*) which originates on the dorsal parts of the median side of the suprascapula and inserts on the back of the skull. In most of these frogs this muscle is moderately or greatly enlarged, which enables the frogs to flex the head up to nearly a 90-degree angle to the body. Once a frog finds an appropriate shelter, it is capable of fitting its body into a hole or crevice, flexing the head, if necessary, in order to insert its head into the opening, and withdrawing its eyes beneath the bony supra-orbital shelves. A frog thus oriented exposes only its casque head externally, a distinct advantage to the animal in avoiding predators and desiccation.

The development of heavy external ossification in these frogs has been countered with the reduction of bone internally. This is principally a mechanism to reduce the weight of the skull and sec-

ondarily, to reduce the calcium requirements of the frog. The trend towards elimination of bone is especially evident in the cancellous construction of the cranial bones. The palatine is either reduced or absent in the presence of the reinforcement of the maxillary arches anteriorly by the nasals or prenasal, and the medial ramus of the pterygoid is reduced in the presence of a palatine and well developed squamosal.

The development of labial flanges and the associated anterior growth of the maxillaries has resulted in an over-all increase in the length of the skulls of *Aparasphenodon*, *Corythomantis*, and *Tripurion*. The extension of the nasals anterior to the premaxillaries in *Corythomantis* and the addition of the prenasal bone in *Aparasphenodon* and *Tripurion* developed in response to the need of a structural brace at the anterior end of the skull. These bones act as architectural keystones bracing the maxillary arches laterally. The nasals are lengthened anteriorly and provide adequate dorsal coverage for the olfactory region. This anterior extension of bone necessitated the relocation of the external naris anteriorly. The external naris opens directly into the anterolateral part of the cavum principale; thus, once the naris has moved forward, the structure of the olfactory capsule must be reorganized. The posterior part of the olfactory capsule is lengthened and the anterior part moves forward and occupies cavities in the prenasals of *Aparasphenodon* and *Tripurion*, and in the nasals of *Corythomantis*.

Contrary to the other casque-headed, co-ossified hylids, *Pternohyla* is adapted to a fossorial existence. The head is not long; it is depressed and well ossified. *Pternohyla fodiens* has an additional dermal roofing bone on the anterior part of the olfactory capsule. The internasal lies dorsal to the anterior end of the septum nasi between the alary processes. Thus, it does not brace the maxillary arches but probably reinforces the anterior end of the snout. The internal reduction characteristic of the other casque-headed, co-ossified hylids is not evident in *Pternohyla*. The squamosal arch is complete; the palatine robust; and the pterygoid well developed and fully articulated.

SPECIMENS EXAMINED

The following is an alphabetical list of specimens examined in this study. Only those species which are specifically mentioned in text are included. Unless otherwise designated, the specimens are dry skeletons; "CS" indicates cleared and stained specimens, x-sec., serial cross-sections of the cranium, and x-ray, radiographs of the cranium. Abbreviations for museum specimens are listed below:

AMNH	American Museum of Natural History
CAS	California Academy of Sciences
FMNH	Field Museum of Natural History
KU	University of Kansas Museum of Natural History
LBSC	Long Beach State College
SNM	Senckenbergische Natur-Museum
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum

- Anotheca spinosa*.—KU 59881, 71758, 84899-900.
Amphignathodon guntheri.—USNM 163380 (x-ray).
Aparasphenodon brunoi.—KU 51326, 92216-18, 92214 (x-sec.).
Aparasphenodon venezolana.—SNM 22168 (x-ray).
Corythomantis greeningi.—KU 74253, 92222 (x-sec.), 92223-4.
Gastrotheca ceratophrys.—KU 104361.
Gastrotheca marsupiatum.—KU 99124-7 (CS), 99128-9.
Gastrotheca nicefori.—KU 111911 (x-ray).
Hemiphractus panamensis.—KU 93504-8.
Hyla bistrincta.—KU 69093.
Hyla boans.—KU 104402-9.
Hyla boulengeri.—KU 41069, 64328 (CS), 84983-4, 87774 (CS), 99191-6, 104350-3, 104846-7.
Hyla brunnea.—KU 84693.
Hyla chaneque.—KU 58563, 84907-8.
Hyla dominicensis.—KU 84701.
Hyla elaeochroa.—KU 25207-8, 25221, 41073-84, 68281-91 (CS), 84985-6, 93938 (CS), 104354-6.
Hyla eximia.—KU 59902-3 (CS), 92309-10.
Hyla lancasteri.—KU 31763, 41087-9, 68298-9, 104325, 104344.
Hyla lanciformis.—KU 92507, 99299-301 (CS), 104398-401, 104911 (x-sec.).
Hyla legleri.—KU 84987, 87767-8 (CS).
Hyla microcephala.—KU 59907-11 (CS), 68293-7 (CS), 68616-22 (CS).
Hyla miliaria.—KU 98451.
Hyla phlebodes.—KU 41095-8, 68300-07 (CS).
Hyla rosenbergi.—KU 41107-08, 68164, 84990-91, 96046-70, 96172-3.
Hyla rubra.—KU 74280 (CS), 92151, 104411-2, 111810 (x-sec.).
Hyla rufoculis.—KU 41109-112, 68611-12 (CS), 84992, 87765-6 (CS).
Hyla septentrionalis.—KU 69098, 72889-98, 84660-1 (CS), 89929-30 (x-sec.), 94151-3; UMMZ S-1309-17, S-1480 (3, CS), S-2452, 106101 (3 of a lot of tadpoles, CS), 108264 (2 of a lot of tadpoles, CS), 108268 (1 of a lot of metamorphosing young, CS).
Hyla staufferi.—KU 41113, 59924-7 (CS), 68614-5 (CS).
Hyla taeniopus.—KU 55602-3, 59826.
Hyla uranochroa.—KU 68165, 68623 (CS), 84993, 87769 (CS).
Hyla valancifer.—KU 95416.
Hyla vasta.—KU 84711.

SPECIMENS EXAMINED—*Continued*

- Nyctimantis rugiceps*.—KU 109559 (x-ray).
Osteocephalus lepreiuri.—KU 99424.
Osteocephalus taurinus.—KU 84725, 92243 (x-sec.), 92247-8.
Phrynohyas imitatrix.—KU 92249.
Phrynohyas mesophea.—KU 92257.
Phrynohyas venulosa.—KU 59880, 68173-7, 111990 (x-sec.); UMMZ S-1184, S-1216.
Plectrohyla avia.—KU 106295.
Plectrohyla glandulosa.—KU 59827-30, 59943-7.
Plectrohyla guatemalensis.—KU 59831-2, 68664.
Plectrohyla ixil.—KU 59833-6.
Plectrohyla matudai.—KU 59948; UMMZ S-1043.
Plectrohyla quecchi.—KU 68172.
Plectrohyla sagorum.—UMMZ S-836.
Pseudacris triseriata.—KU 111988 (x-sec.).
Pterohyla dentata.—KU 106291-4, 111989 (x-sec.).
Pterohyla fodiens.—FMNH 98261-8; KU 69145-6 (CS), 86611-15, 89925 (x-sec.).
Ptychohyla euthysanota.—KU 59937-8 (CS).
Ptychohyla ignicolor.—KU 71343 (CS).
Ptychohyla leonhardschultzei.—KU 68630 (CS), 103035 (CS).
Ptychohyla schmidtorum.—KU 59936 (CS), 59940 (CS).
Ptychohyla spinipollex.—KU 59939 (CS), 68631-2 (CS).
Smilisca baudini.—KU 26326-8 (CS), 26332 (CS), 55614 (CS), 55615 (CS), 55616-21, 59801-12, 60024 (1 of a lot of metamorphosing young, CS), 60026 (2 of a lot of metamorphosing young, CS), 60027 (1 of a lot of tadpoles, CS), 62138-9, 68178-84, 69101-3, 84944-9, 89924 (x-sec.).
Trachycephalus jordani.—KU 111994 (x-sec.); LBSC 575 (x-sec.), 577.
Trachycephalus nigromaculatus.—CAS 12659; KU 100353 (x-sec.).
Trachycephalus siemersi.—AMNH 19918 (preserved specimen).
Triprion petasatus.—KU 71473 (x-sec.), 71734 (CS), 71736 (4 of a lot of tadpoles, CS), 71744 (CS), 71759-60, 71778-80, 89926-8 (x-sec.), 92720 (CS); UMMZ S-167.
Triprion spatulatus.—KU 69092, 73845-7, 84901-6, 86925 (x-sec.), 89923 (x-sec.); LBSC 1146; UMMZ S-1769-70, S-1938-9, S-2149, S-2154.

GLOSSARY

The following is an alphabetical list of technical terms used in the text. Each designation is provided with the abbreviation which has been used for it. The derivations are those given in Webster's Third New International Dictionary. The following abbreviations are used with respect to the derivations: E., English; F., French; Gk., Greek; L., Latin; MF., Middle French; ML., Medieval Latin; NL., New Latin; OF., Old French; S., Spanish.

- Acoustic foramen.—*acus. f.*, [Gk. *akoustikos*, of hearing, from *akouein* to hear.] Nerve foramen of the prootic bone in region of the otic capsule. One or two (anterior and posterior) foramina are present, allowing passage of the acoustic nerve (eighth cranial nerve; somatic sensory) from the floor of the medulla to the cristae and maculae of the internal ear.
- Alary cartilage.—*al. c.*, [L. *alarius* from *ala*, wing + *-arius*, -ary.] A principal cartilage of the olfactory capsule. The cartilage surrounds the anterolateral aspect of the *cavum principale* anterior to the external naris; it is fused with the superior prenasal cartilage anteriorly, and usually with the *solum nasi* posteromedially.
- Alary process.—*al. proc.*, [L. *alarius* from *ala*, wing + *-arius*, -ary.] Dorsomedial bony process of the premaxillary bone of the upper jaw. Process serves as an anterior abutment for the superior and inferior prenasal cartilages of the olfactory capsule.
- Angulosplenic.—*angsp.*, [L. *angulo* from *angulus*, angle + *splenic* from *splenium*, patch.] Dermal bone of the lower jaw. The bone lies medial and posteriorly, ventrally adjacent to Meckel's cartilage.
- Anterior acoustic foramen.—*ant. acus. f.*, see acoustic foramen.
- Anterior arm of the squamosal.—That part of the squamosal which extends anteroventrally from the crista parotica towards the maxillary, thereby forming a partial or complete posterior margin to the orbit.
- Anterior maxillary process.—*ant. max. proc.* Small rod of cartilage which lies medially adjacent to the maxillary anterior to the *planum antorbitale*. The process terminates at the *planum antorbitale*.
- Anterior ramus of the pterygoid.—That branch of the pterygoid which lies medially adjacent to the maxillary and posterior maxillary process. The anterior end of the ramus usually lies between the levels of the orbitonasal foramen, anteriorly, and the mid-orbital region, posteriorly.
- Bursa angularis oris.—*b. ang. o.*, [ML. *bursa*, bag; L. *angulus*, angle; L. *ora*, border or edge.] Tubular lymphoid gland which lies between the maxillary laterally, and the pterygoid process and pterygoid, medially, in the posterior part of the orbit. Function of the gland is unknown.
- Canthal ridge.—[Gk. *kanthos*, angle.] Dorsal angle of the nasal. Ridge may be sharp or indistinct and usually extends from the orbit, posteriorly, to the tip of the snout, anteriorly.
- Cartilage.—*c.*, [L. *cartilago*, akin to L. *cratis*, wickerwork.] A specialized, fibrous connective tissue which forms the chondrocranium of adult and larval anurans and gives rise to endochondral bones of the osteocranium of the adult.
- Cartilaginous sclera.—*c. scl.*, [NL. from Gk. *skleros*, hard.] The internal, cartilaginous tunic of the eyeball.
- Cartilago obliquo.—*c. obl.*, [L. *obliquus*, slanting.] Nasal capsule cartilage which diverges posterolaterally from the dorsal tectum nasi to join the lamina inferior laterally and thereby form the *planum terminale*.
- Casque.—[influenced by F. *casque* from S. *casco*, potsherd, skull, helmet, cask.] The expansion and thickening of dermal roofing bones and jaw bones.
- Cavum.—*cav.*, [L. *cava* from *cavus*, hollow.] A cavity.

- Cavum inferius.—*cav. inf.* The most ventral of the three nasal cavities contained in the nasal capsule.
- Cavum medium.—*cav. med.* The smallest of the three nasal cavities. This cavity lies between the cavum inferius and principale. Posteriorly the nasolacrimal duct diverges laterally from the cavum medium.
- Cavum principale.—*cav. prin.* The largest and most dorsal of the three nasal cavities contained in the nasal capsule. The external naris opens into the anterolateral part of the cavum principale.
- Columella.—*col.*, [NL. from L., small column, diminutive of *columna*, column.] The cartilaginous and bony rod which connects the tympanum with the inner ear in amphibians; the stapes.
- Co-ossification.—[*co-*, from L. *com-* with + ossification, probably from NL. *ossificatus* (past participle of *ossificare*, to ossify) + L. *-ion*, *-io*, *-ion*.] The formation of bone, continuous with the underlying dermal bone, in the dense connective tissue dermis of the skin.
- Cornu principalis.—*corn. prin.*, [L. *cornu*, horn.] The terminal portion of the posterolateral process of the hyale, which joins the hyoid apparatus to the pseudobasal process of the osteocranium.
- Crista.—*cr.*, [L. *crista*, crest.]
- Crista intermedia.—*cr. int.* A bridge of cartilage uniting the lamina inferior and lamina superior, laterally, with the septum nasi, medially, in the anterior part of the olfactory capsule.
- Crista parotica.—*cr. par.*, [NL. *paroticus* from L. *para-*, *para-* + NL. *oticus*, otic, from Gk. *otikos*, relating to the ear.] The dorsal part of the prootic which overlies the columella and extends from the braincase, medially, to the squamosal, laterally.
- Crista subnasalis.—*cr. sub.*, [NL. from *sub-*, under + *nasalis*, nasal.] A small rod of cartilage which diverges posterolaterally from the solum nasi ventral to the anterior end of the nasal capsule, and lies adjacent to the maxillary.
- Dentary.—*den.*, [L. *dentalis*, from *dent-*, *dens*, tooth + E. *-ary*.] Dermal bone of the lower jaw of anurans. Bone is located anterolateral to Meckel's cartilage and articulates anteriorly with the mentomeckelian.
- Dermal sphenethmoid.—*derm. spheneth.*, [NL. from Gk. *derm-*, dermo-, from *derein*, to skin; NL. from Gk. *sphen-*, wedge + *ethmoeides*, like a strainer.] The dorsal, dermal component of the endochondral sphenethmoid. The bone is co-ossified with the overlying skin, completely fused with the underlying bone, and usually articulates with the nasals anteriorly and frontoparietals posteriorly.
- Duct.—*dt.*, [L. *ductus*, act of leading, shape.]
- Eminence.—*em.*, [L. *eminentia*, prominence.]
- Endochondral sphenethmoid.—*spheneth.*, [Gk. *endon*, within + *chondros*, cartilage; NL. from Gk. *sphen-*, wedge + *ethmoeides*, like a strainer.] The large, endochondral bone forming the anterior end of the braincase. The sphenethmoid lies between the olfactory capsules anteriorly and the prootic posteriorly.
- Epiotic eminence.—*epi. em.*, [Gk. *epi-*, on, upon, to + *-otic*, of the ear.] Dorsal part of otic capsule which lies medial to crista parotica.
- Eustachian tube.—*E. t.* [Eustacian, in reference to Bartolommeo Eustachio, an Italian anatomist, 1520-1574.] Tube connecting tympanic cavity with pharynx.
- Exoccipital.—*exocc.*, [Gk. *exo-*, out of, outside of + ML. *occipitalis*, from L. *occipit*, *occiput* + *-alis*, *-al*, back formation.] An endochondral bone forming the posterior end of the braincase, posterior to the prootic and around the foramen magnum. The exoccipital is usually fused with the prootic in adult anurans.
- External naris.—*ext. nar.*, [L. akin to L. *nasus*, nose.] The nostril or the opening of the cavum principale of the olfactory capsule to the exterior.

- Fontanelle.—*fon.*, [ME. *fontinelle*, from MF. *fontenele*, little spring, diminutive of *fontaine*, spring.] A gap(s) in cranial roofing bones.
- Foramen.—*f.*, [L. from *forare*, to bore, pierce.] The aperture or opening through a bone or membrane for the passage of blood vessels and/or nerves.
- Frontoparietal.—*fpar.*, [L. *frons*, forehead + *parietal*, MF. from NL. *pariet-*, *paries*, wall + MF. -al.] Paired dermal roofing bones which overlie the sphenethmoid and prootic in anurans.
- Frontoparietal fontanelle.—*fpar. fon.* A gap in the endochondral cranial roof of anurans formed in the sphenethmoid anteriorly and the prootic posteriorly. The fontanelle is covered by membranous connective tissue. In addition, it may be covered partially or completely by the frontoparietals dorsally.
- Inferior prenasal cartilage.—*inf. pnas. c.* Anterior and ventral nasal capsule cartilage which extends from floor of olfactory capsule anterior to the base of the alary process of the premaxillary.
- Infundibulum.—*inf.*, [NL. from L., funnel, from *infundere*, to pour in.] Any funnel-shaped anatomical structure. Refers here to pocket formed at posterior end of *cavum medium*.
- Intermedia.—*intm.*, [NL. from L., feminine of *intermedius*, intermediate.]
- Internal naris.—*int. nar.*, [L. akin to L. *nasus*, nose.] The choana or the opening of the *cavum principale* and *cavum inferius* into the oral cavity.
- Internasal.—[L. *inter*, between + L. *nasus*, nose + *-alis*, -al.] Dermal roofing bone which lies anterior to nasals and between external nares.
- Jugular foramen.—*jug. f.*, [L. *jugulum*, collarbone, neck, throat akin to L. *jungere*, to join.] Nerve foramen of the prootic and exoccipital. Foramen lies just posterior to the otic capsule and allows passage of glossopharyngeal (ninth cranial nerve; visceral sensory and motor) and vagus (tenth cranial nerve; visceral sensory and motor) nerves from medulla.
- Lamina.—*lam.*, [L. *lamina*, a thin plate.]
- Lamina inferior.—*lam. inf.* A thin plate of cartilage which lies between the *cavum medium* and *cavum inferius* of the olfactory capsule. Anteriorly lamina differentiates from *solum nasi*; posteriorly, the lateral part of the lamina fuses with the *cartilago obliqua* to form the *planum terminale*.
- Lamina perpendicularis.—*lam. perp.*, [from L. *perpendicularis*, from *perpendicularum*, plumb line (from *per-*, through + *pendere*, to hang + *-iculum*, suffix denoting an instrument).] Bony ventral flange of the frontoparietal which forms the dorsolateral corner of the braincase in the region of the synchondrotic union of the sphenethmoid and prootic.
- Lamina superior.—*lam. sup.* A thin plate of cartilage which lies between the *cavum principale* and *cavum medium* of the olfactory capsule. Anteriorly, the lamina differentiates from the *solum nasi*; posteriorly, the lamina is associated with the medial ramus of the septomaxillary.
- Lateral process of parasphenoid.—The basal wing, or that, posterior part of the parasphenoid which invests the otic capsule ventrally.
- Marginalis.—*mar.*, [L. *margo*, border + *-alis*, -al.]
- Maxillary.—*max.*, [L. *maxilla*, jaw, diminutive of *mala*, jawbone.] The principal bone of the upper jaw. Maxillary articulates with the premaxillary anteriorly, and usually the quadratojugal posteriorly.
- Meckel's cartilage.—*Mc. c.*, [Meckel's in reference to Johann Friedrich Meckel, Junior, a German anatomist (died 1833).] The cartilaginous rod of the lower jaw which lies medial to the dentary anteriorly, and lateral and dorsal to the angulosplenic posteriorly. Meckel's cartilage articulates with the cartilaginous quadrate process in the articular region.
- Medial.—[L. *medius*, middle.]
- Medial ramus of the pterygoid.—*med. r. pter.* That branch of the pterygoid which extends toward, and sometimes articulates with, the anteroventral corner of the otic capsule.

- Mentomeckelian.—*mmk.*, [combination form, from L. *mentum*, chin + meckel, in reference to Johann Friedrich Meckel, Junior, a German anatomist + -ian.] A small endochondral bone of the lower jaw. The bone is located lateral to the mandibular symphysis and articulates laterally with the dentary.
- Nasal.—*nas.*, [from L. *nasale*, neuter singular of *nasalis*, nasal, from L. *nasus*, nose + -alis, -al.] Paired dermal roofing bones which cover the olfactory capsule anterior to the sphenethmoid.
- Nasal process.—*nas. proc.* A posterolateral process of the nasal which extends towards and articulates with the pars facialis of the maxillary in some species.
- Nasolacrimal duct.—*nlc. dt.*, [combination form, from L. *nasus* + L. *lacrima*, tear + -alis, -al.] The tear duct extending from the posterolateral corner of the cavum medium to the orbit.
- Occipital crest.—[ML. *occipitalis*, from L. *occipit*, *occiput* + -alis, -al, back formation.] Transverse crest sometimes present at the posterior edge of the frontoparietal.
- Oculomotor foramen.—*ocul. f.*, [combination form, from L. *ocul-* from *oculus*, eye + L. *motus* (past participle of *movere*) to move + -or.] Small foramen located posterior to the optic foramen in the prootic bone. Foramen allows passage of third cranial nerve (somatic motor) from midbrain to inferior oblique, superior, inferior, and internal recti, and some accessory muscles of the eyeball.
- Odontoid.—[Gk. *odontoeides*, from *odont-*, tooth + -*oeides* form, -oid.] A structure which is tooth-like in appearance.
- Olfactory capsule.—[L. *olfactorius*, from *olfactus*, *olefactus* (past participle of *olfacere*, *olefacere* from *olere*, to smell + *facere*, to make, do) + -orius, -ory.] The olfactory bulb, or the entire complex of nasal structures including the nasal cavities and associated cartilages.
- Olfactory eminence.—*olf. em.* A protuberance from the floor of the posterior part of the olfactory capsule. Structurally the olfactory eminence involves the epithelium of the nasal cavity, the cartilaginous support of the solum nasi, and the bony support of a dorsal process of the prevomer.
- Operculum.—*Op.*, [NL. from L. cover, lid, from *operire*, to cover, shut (from *op-*, *ob* to, before + (assumed) -*verire*, to shut) + -*culum*, suffix denoting an instrument).] A plate-like structure which articulates with the pars interna plectri of the columella or stapes and covers the oval window of the internal ear.
- Optic foramen.—*opt. f.*, [MF. *optique* from ML. *opticus* from Gk. *optikos* from *optos* + -*ikos*, -ic.] Large foramen located in cartilage between sphenethmoid and prootic bones. Foramen allows passage of the optic tract of the brain from the diencephalon to the retina.
- Orbit.—*orb.*, [L. *orbita*, circuit.] Cavity, surrounded by cranial bones, in which the eye is located.
- Orbitonasal foramen.—*orbnas. f.*, [combination form, from L. *orbita*, circuit + L. *nasus*, nose.] Conspicuous bony foramen which is located in the sphenethmoid in the anterior end of the orbit, and allows passage of blood vessels and nerves from orbit to snout.
- Otic capsule.—*ot. cap.*, [NL. *oticus*, from Gk. *otikos*, relating to the ear.] That part of the prootic lateral to the braincase, which houses the internal ear consisting of the membranous labyrinth.
- Otic process.—*ot. proc.*, [NL. *oticus*, from Gk. *otikos*, relating to the ear.] A cartilaginous process uniting the anterolateral corner of the crista parotica to the pseudobasal process.
- Palatine.—*pal.*, [F. *palatin*, from (assumed) NL. *palatinus*, from L. *palatum*, palate + -inus, -ine.] Paired dermal bone of support located at anterior end of orbit. Distally, the palatine articulates with the maxillary; medially, the bone usually articulates with the sphenethmoid.

- Palatine process.—*pal. proc.*, [L. *palatum*, palate + *-inus*, *-ine*.] Small, pointed process located posteromedially on pars palatina of premaxillary.
- Parasphenoid.—*psrph.*, [para-, from L., from Gk. *para* (akin to Gk. *pro*, before, ahead) + sphenoid from Gk. *sphen*, wedge + *-oeides*, *-oid*.] Dermal investing bone which is located ventral to the posterior part of the sphenethmoid and the prootic.
- Pars.—*p.*, [L., one that is equal, from *par*, equal.]
- Pars ascendens plectri.—*p. asc. pl.* A small rod of cartilage which extends from the distal part of the columella, the pars externa plectri, to the distal end of the crista parotica dorsally.
- Pars dentalis.—*p. dent.*, [L. *dentatus*, from *dent-*, *dens*, tooth + *-alis*, *-al*.] The tooth-bearing parts of the maxillary and premaxillary.
- Pars externa plectri.—*p. ext. pl.* The distal cartilaginous part of the columella which lies adjacent to the tympanic membrane.
- Pars facialis.—*p. fac.*, [ML. *facialis*, from L. *facies*, form, shape + *-alis*, *-al*.] Dorsomedially inclined flange of bone arising from ventral, longitudinal axis of the maxillary.
- Pars interna plectri.—*p. int. pl.* Proximal, cartilaginous segment of the columella which lies adjacent to the otic capsule and articulates with the operculum posteriorly.
- Pars media plectri.—*p. med. pl.* Medial, ossified part of the columella which lies between the pars interna plectri, medially, and the pars externa plectri, laterally.
- Pars palatina.—*p. pal.* Lingual flange of bone dorsal to pars dentalis of maxillary and premaxillary bones.
- Planum.—*pla.*, [L. *planum*, level surface.]
- Planum antorbitale.—*pla. ant.*, [ant-, ME. from L. *ante*, before, in front of + orbit, L. *orbita*, circuit + *-al*, of, or relating to.] Posterolateral part of the olfactory capsule lying in synchondrotic continuity with the sphenethmoid posteriorly.
- Planum terminale.—*pla. term.*, [L. *termino*, limit, level, end + *-al*, of, or relating to.] Cartilage surrounding lateral part of olfactory capsule posterior to external naris. Planum terminale formed by fusion of lamina inferior and cartilago obliquus.
- Plectri.—*pl.*, [L. from Gk. *plektron*, striking instrument.]
- Posterior acoustic foramen.—*post. acus. f.* See acoustic foramen.
- Posterior arm of squamosal.—That part of the squamosal which extends posteriorly from union of anterior and ventral arms of the squamosal. Posterior arm usually articulates with crista parotica.
- Posterior maxillary process.—*post. max. proc.* Small rod of cartilage which lies medially adjacent to the maxillary between the levels of the planum antorbitale anteriorly and the divergence of the pterygoid and pterygoid process from the maxillary posteriorly.
- Posterior ramus of pterygoid.—That branch of the pterygoid which articulates posteriorly with the quadrate process of the articular region.
- Premaxillary.—*pmax.*, [pre-, ME. from OF. and L. *prae*, before + maxillary from L. *maxilla*, jaw.] Anterior, dermal bone of the upper jaw. Premaxillary bears a dorsal alary process and articulates with the maxillary laterally.
- Prenasal.—*pnas.*, [pre-, ME. from OF. and L. *prae*, before + nasal from L. *nasus*, nose + *-alis*, *-al*.] Dermal bone which lies anterior to premaxillaries, maxillaries, and nasals, and forms the anterior end of the snout.
- Preorbital knob.—*porb. kb.*, [pre-, ME. from OF. and L. *prae*, before + L. *orbita*, circuit + *al*, of, or relating to.] Nasal prominence formed at the posterior end of the canthal ridge at the edge of the orbit.

- Prevomer.**—*pvom.*, [pre-, ME. from OF. and L. *prae*, before + L. *vomis*, *vomer*, plowshare.] Paired dermal investing bones located ventral to the solum nasi of the olfactory capsule. Prevomer bears a dorsal process which provides internal support for the olfactory eminence, and usually a posterior dentigerous process.
- Principale.**—*prin.*, [from L. *principalis*, first, principal.]
- Process.**—*proc.*, [from L. *processus* (past participle of *procedere*, to procede).]
- Prootic.**—*pro.*, [pro-, L. from *pro*, before, in front of + otic, from NL. *oticus* from Gk. *otikos*, relating to the ear.] Endochondral bone which forms otic capsules and braincase posterior to the sphenethmoid.
- Prootic foramen.**—*pro. f.* Large foramen located posterior to oculomotor foramen in prootic bone. This foramen allows the passage of three cranial nerves and their branches from the floor and side of the medulla to various parts of the head. The cranial nerves included are as follow: (1) trigeminal (fifth cranial nerve; mixed somatic and visceral sensory) with three branches, the ophthalmic (to orbit and nasal region), maxillary (to upper jaw and roof of oral and pharyngeal cavities), and mandibular (to lower jaw and floor of oral and pharyngeal cavities); (2) abducens (sixth cranial nerve; somatic motor) to external rectus muscle of eyeball; and (3) facial (seventh cranial nerve; sensory and visceral motor) to taste buds, pharyngeal lining and muscles of hyoid arch.
- Pterygoid.**—*pter.*, [probably from (assumed) NL. *pterygoides* from Gk. *pterygoeides*, winglike.] Paired, triradiate dermal bones of support located in posterolateral part of skull between articular region, otic capsule, and orbit.
- Pterygoid process.**—*pter. proc.* Cartilaginous process associated with the pterygoid and continuous with the posterior maxillary process anteriorly and the quadrate process posteriorly.
- Quadrate process.**—*quad. proc.*, [from L. *quadratum*, from neuter of *quadratus*, square]. Cartilaginous process of the articular region. Quadrate process is continuous with the pterygoid process anteriorly. Posteriorly, it articulates with the quadratojugal, ventral arm of the squamosal, posterior ramus of the pterygoid and Meckel's cartilage.
- Quadratojugal.**—*qj.*, [quadrat-, from L. *quadratus*, square + -o- + -jugal, from L. *jugalis*, from *jugum*, yoke.] Small, dermal bone of upper jaw. Quadratojugal articulates with maxillary anteromedially; posteriorly ossification of the quadratojugal invades cartilage of the quadrate process. The bone is often reduced or lost.
- Ramus.**—*r.*, [from L. *ramus*, branch.]
- Septomaxillary.**—*spmax.*, [sept-, from L. *septum*, partition + -o- + maxillary, from L. *maxilla*, jaw.] Small bone which is internal to olfactory capsule and of uncertain (endochondral or dermal) origin. Septomaxillary is located around cavum medium. A ventral ramus or loop supports the divergence of the nasolacrimal duct from the cavum, whereas dorsal, lateral, and medial rami support the union of the cavum principale and cavum inferius through the posterior end of the cavum medium.
- Septum.**—*sept.*, [L. *septum*, partition.]
- Septum nasi.**—*sept. nas.* Cartilaginous partition between the olfactory capsules. Septum is synchondrotically united with sphenethmoid posteriorly.
- Solum.**—*sol.*, [L. *solum*, floor.]
- Solum nasi.**—*sol. nas.* Cartilaginous floor of olfactory capsules. Ossification is usually present in posterior parts of solum.
- Sphenethmoid.**—*spheth.*, [Gk. *sphen-*, wedge + *ethmoeides*, like a strainer.] Endochondral bone forming anterior end of braincase between olfactory capsules, anteriorly, and prootic, posteriorly.
- Squamosal.**—*sq.*, [L. *squamosus*, squamous + E. -al, scale-like.] Paired, tri-radiate dermal bones located at posterolateral corners of skull. Anterior and posterior arms usually articulate with the crista parotica of the prootic; the ventral arm articulates with the quadrate process of the upper jaw.

- Superior prenasal cartilage.—*sup. pnas. c.* Anterior and dorsal nasal capsule cartilage which extends from alary cartilage anterior to the dorsal part of the alary processes of the premaxillary.
- Synchondrotic.—adjective from synchondrosis, [Gk. *syn*, with + *chondros*, cartilage.] The union of two or more separate cranial elements by cartilage.
- Synosteotic.—also synostotic; adjective from synostosis or synostosis, [Gk. *syn*, with + *osteon*, bone.] Ossification from two or more centers in the same bone.
- Taenia.—*t.*, [L., head, band.]
- Taenia tecta marginalis.—*t. t. mar.* Cartilage of the sphenethmoid bordering the frontoparietal fontanelle.
- Tectum.—*tect.*, [L., roof.]
- Tectum nasi.—*tect. nas.* Cartilaginous roof of the nasal capsule. Tectum nasi is continuous with the septum nasi and gives rise to the cartilago obliquo posterolaterally.
- Tectum synoticum.—*tect. syn.*, [syn-, Gk. *syn*, with, together with + *otikos*, relating to the ear.] Cartilaginous roof of the prootic which unites the otic capsules.
- Trochlear foramen.—*troc. f.*, [NL. *trochlearis*, from *trochlea* + L. *-aris*, *-ar*, sheath of pulleys, from Gk. *trochileia* (akin to Gk. *trochos*, wheel).] Small nerve foramen for fourth cranial nerve (somatic motor). Foramen located dorsal or posterodorsal to optic foramen; it lies within bony margins of optic foramen or in the lamina perpendicularis of the frontoparietal. Allows passage of trochlear nerve from midbrain to inferior oblique, superior, inferior and internal recti, and some accessory muscles of the eyeball.
- Tympanic ring.—*timp. r.*, [L. and NL. *tympanum*, drum + E. *-ic*, from Gk. *tympanon*, drum (akin to Gk. *typtein*, to strike, beat).] Ring of cartilage surrounding tympanic membrane of ear.
- Ventral arm of the squamosal.—*sq.* That part of the squamosal which extends posteroventrally from the union of the anterior and posterior arms of the squamosal, dorsally, to the articular region, ventrally.

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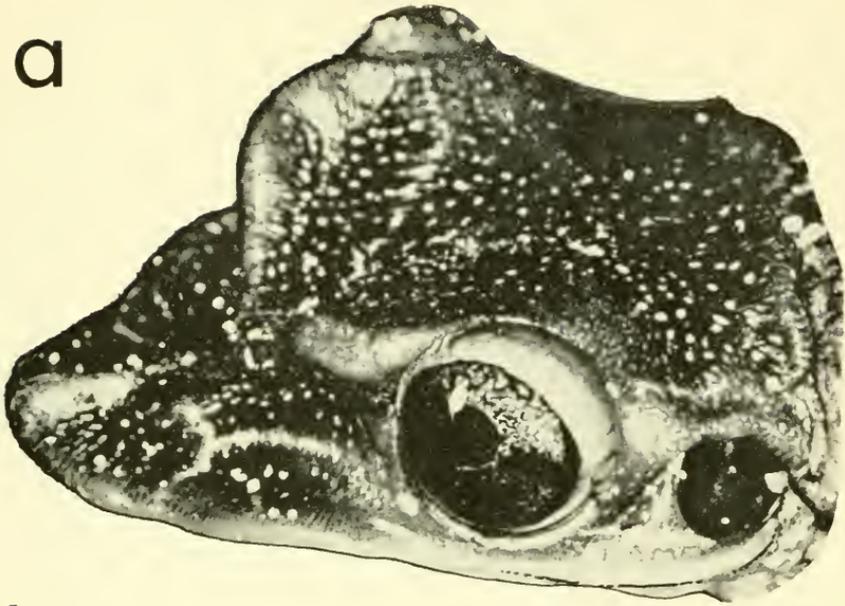
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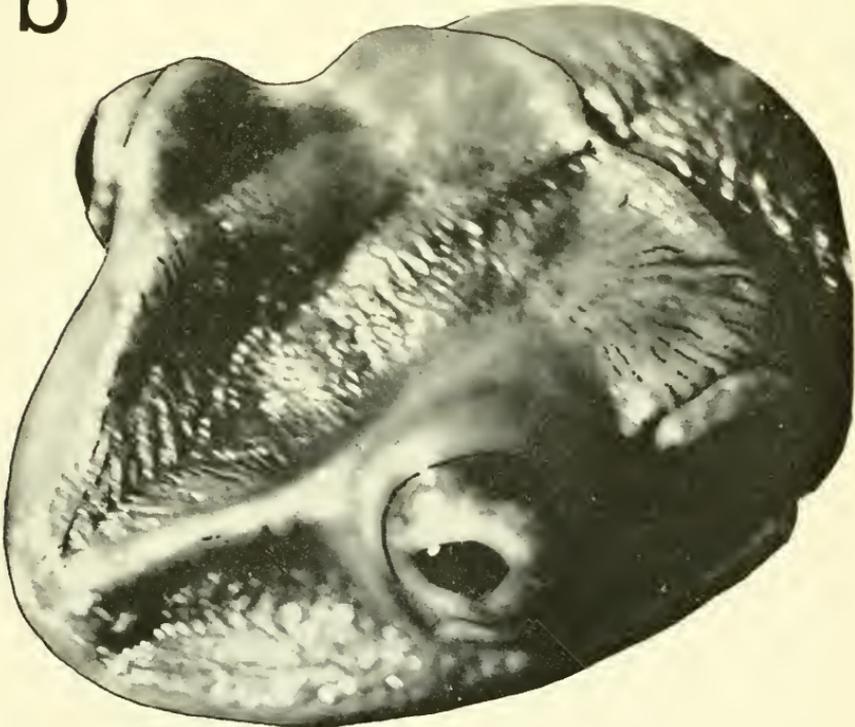
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PLATE 1

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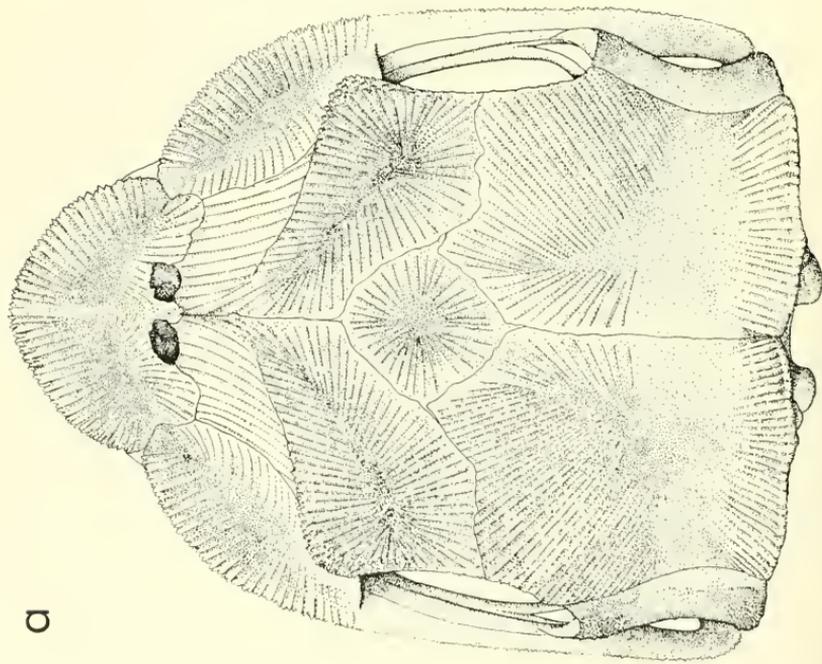


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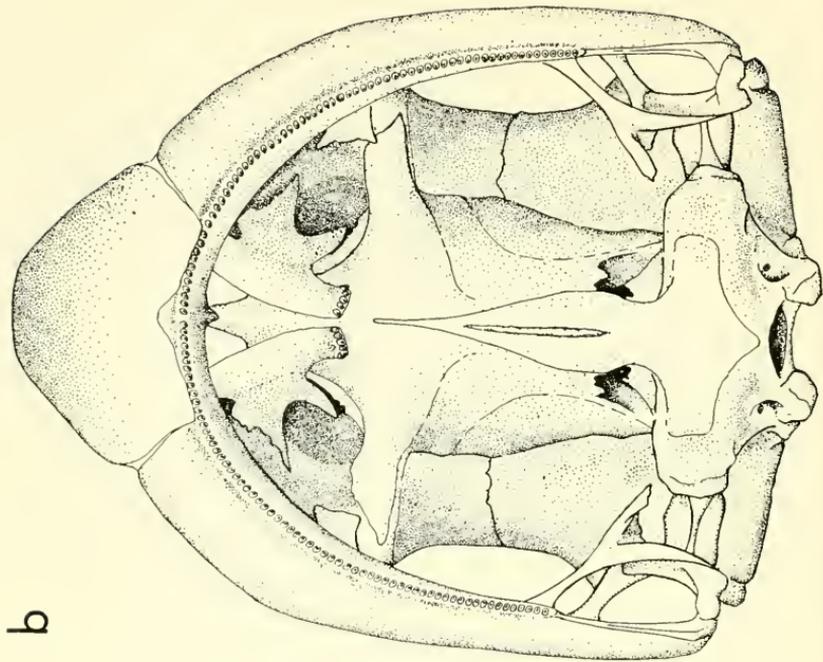


Photographs of two casque-headed, co-ossified hylids. $\times 3$: (a) *Triprion petasatus*, adult female, from 7.5 km. west Escárcega, Campeche, México; (b) *Trachycephalus jordani*, adult male, from an unknown locality in Ecuador.

PLATE 2



a



b

Tripirion petasatus, KU 71780, ♀. $\times 4$. (a) dorsal view; (b) ventral view.

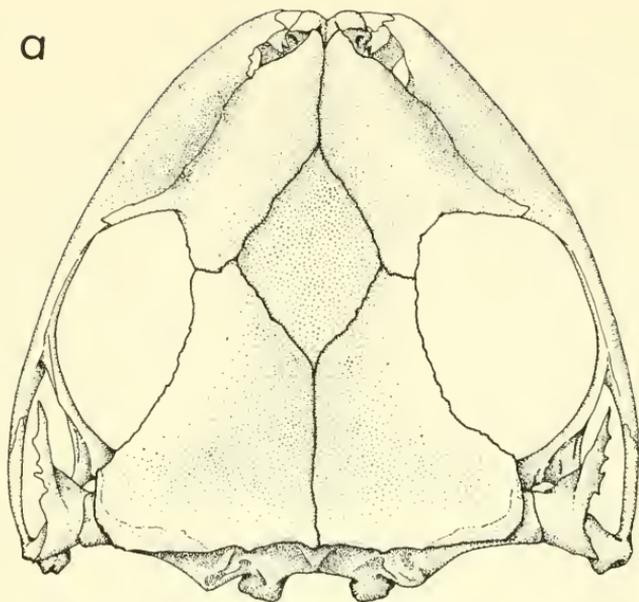
PLATE 3



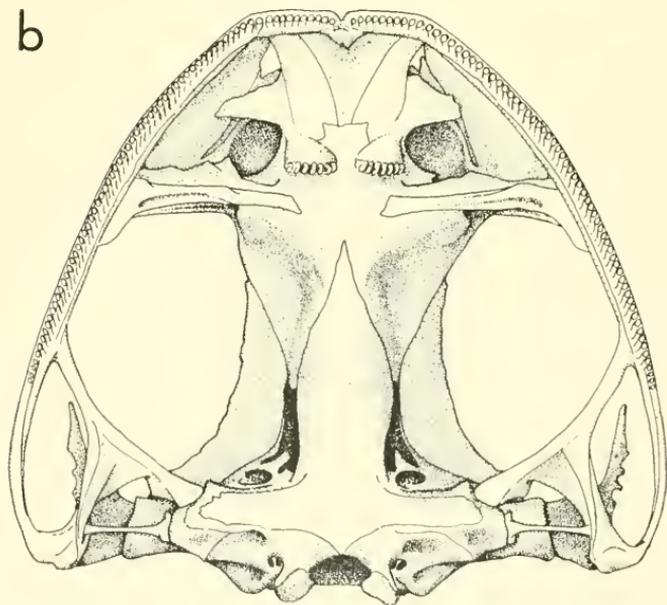
Tripirion petasatus, KU 71780, ♀. × 4. (a) lateral view; (b) posterior view.

PLATE 4

a

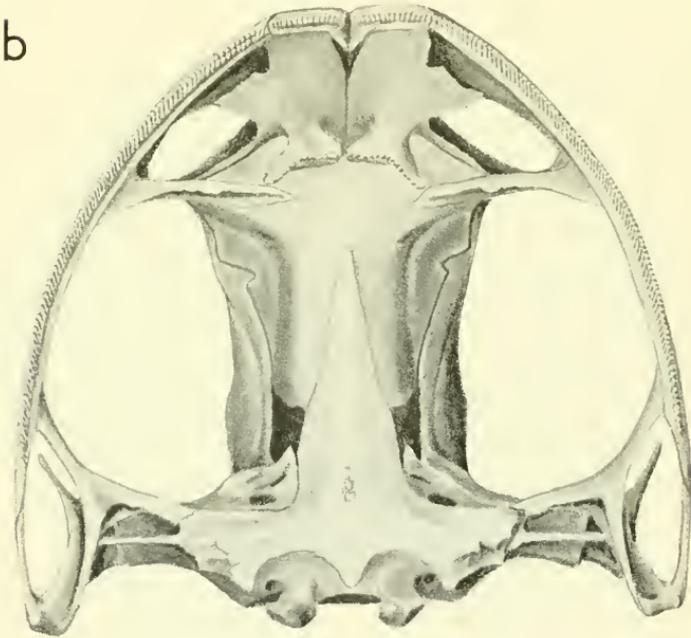
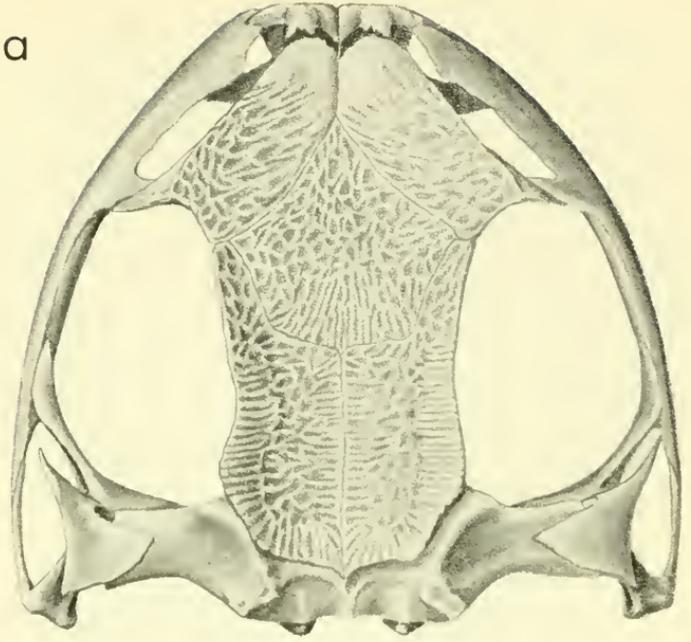


b



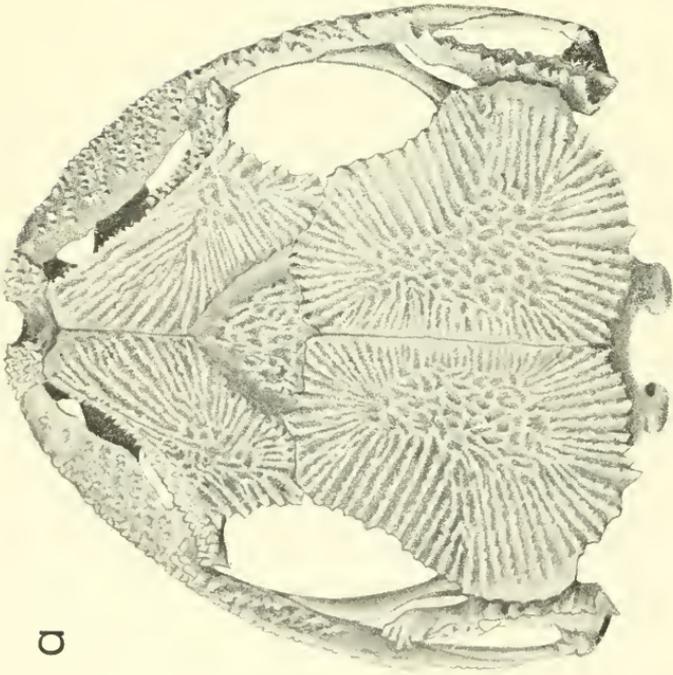
Hyla septentrionalis, KU 72889, ♂. $\times 4.5$. (a) dorsal view;
(b) ventral view.

PLATE 5

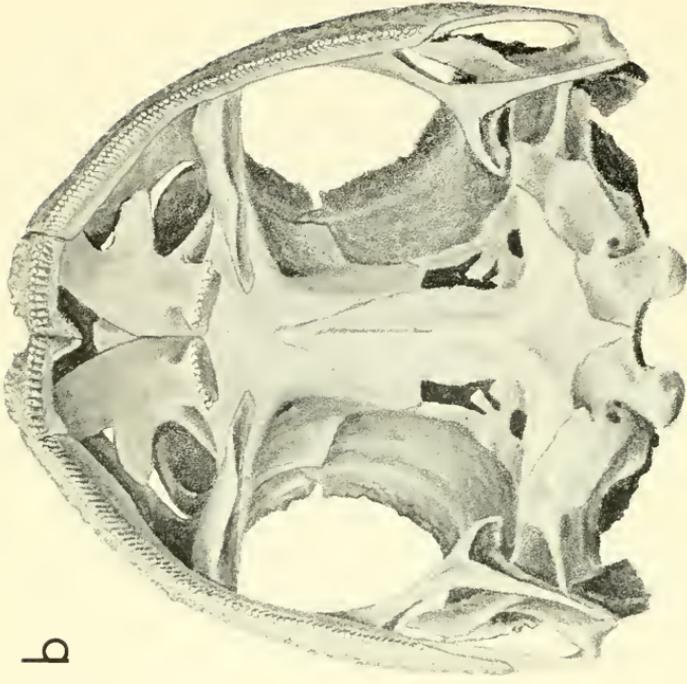


Osteocephalus taurinus, KU 84725. $\times 3.7$. (a) dorsal view;
(b) ventral view.

PLATE 6

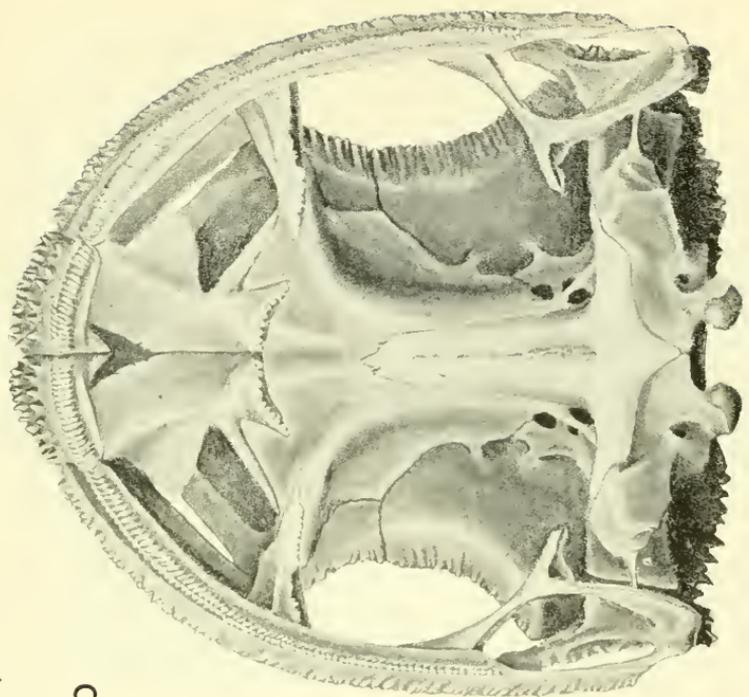


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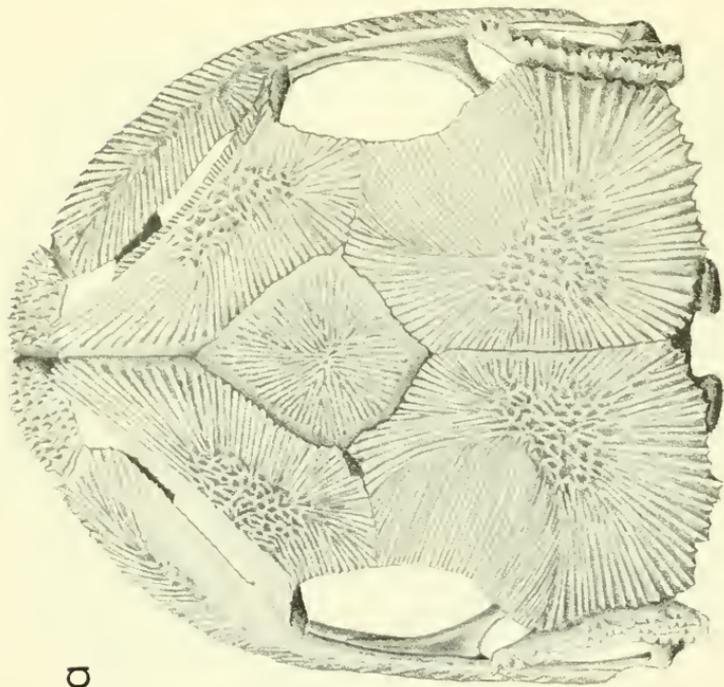


b

Trachycephalus nigromaculatus, CAS 12659, $\times 3.9$. (a) dorsal view; (b) ventral view.



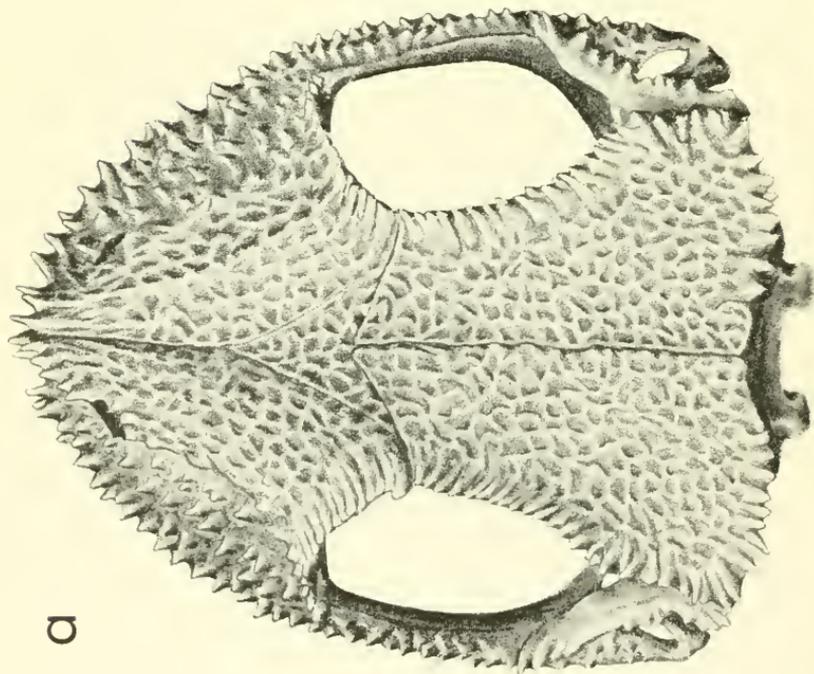
b



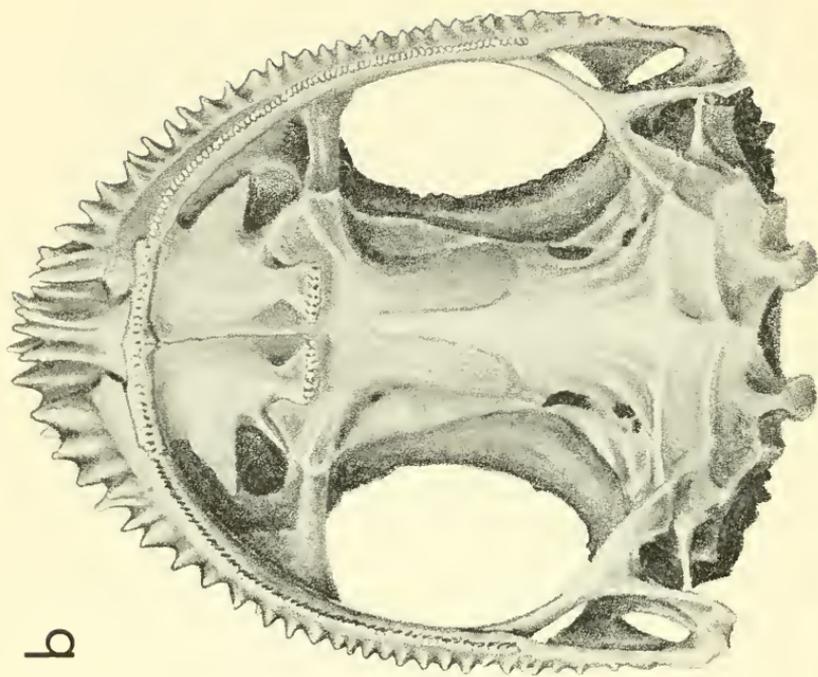
a

Trachycephalus jordani, LBSC 577, $\times 3.5$. (a) dorsal view; (b) ventral view.

PLATE 8



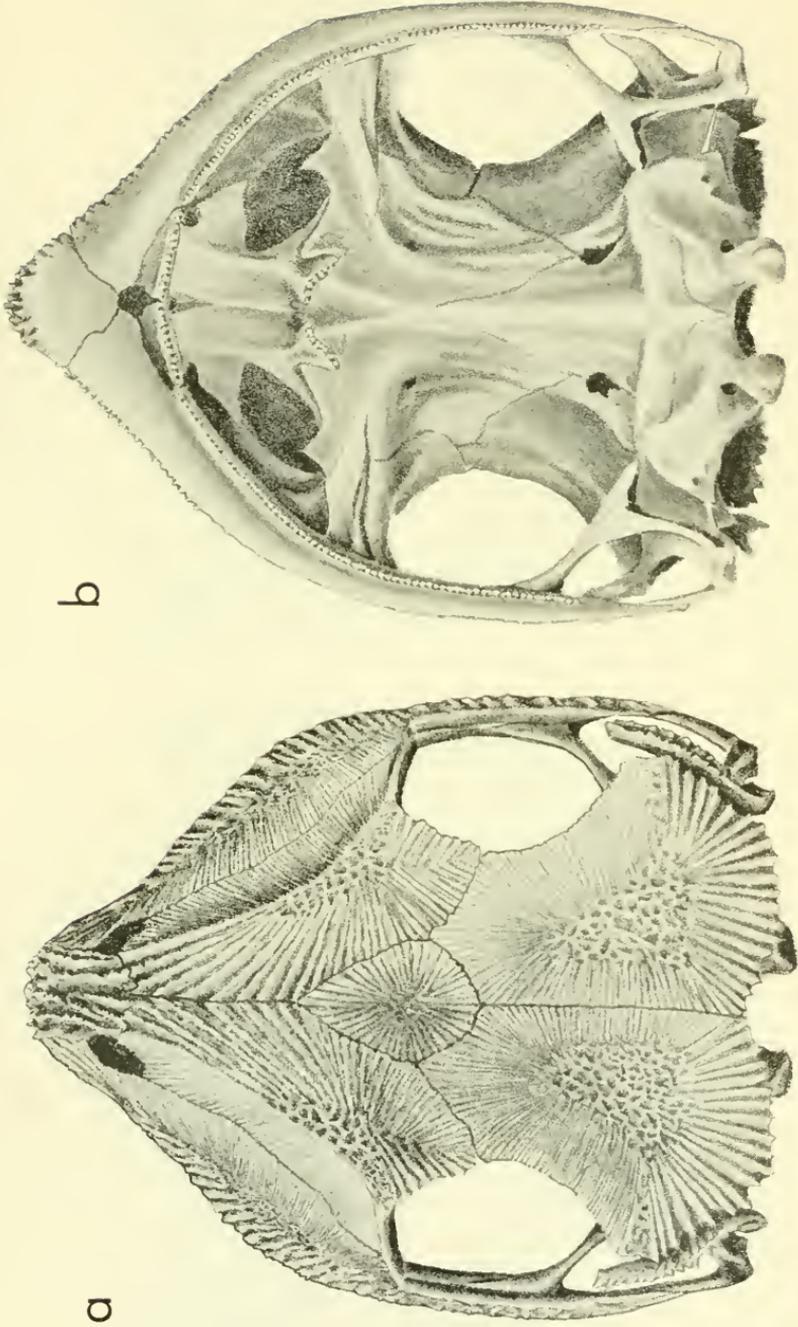
a



b

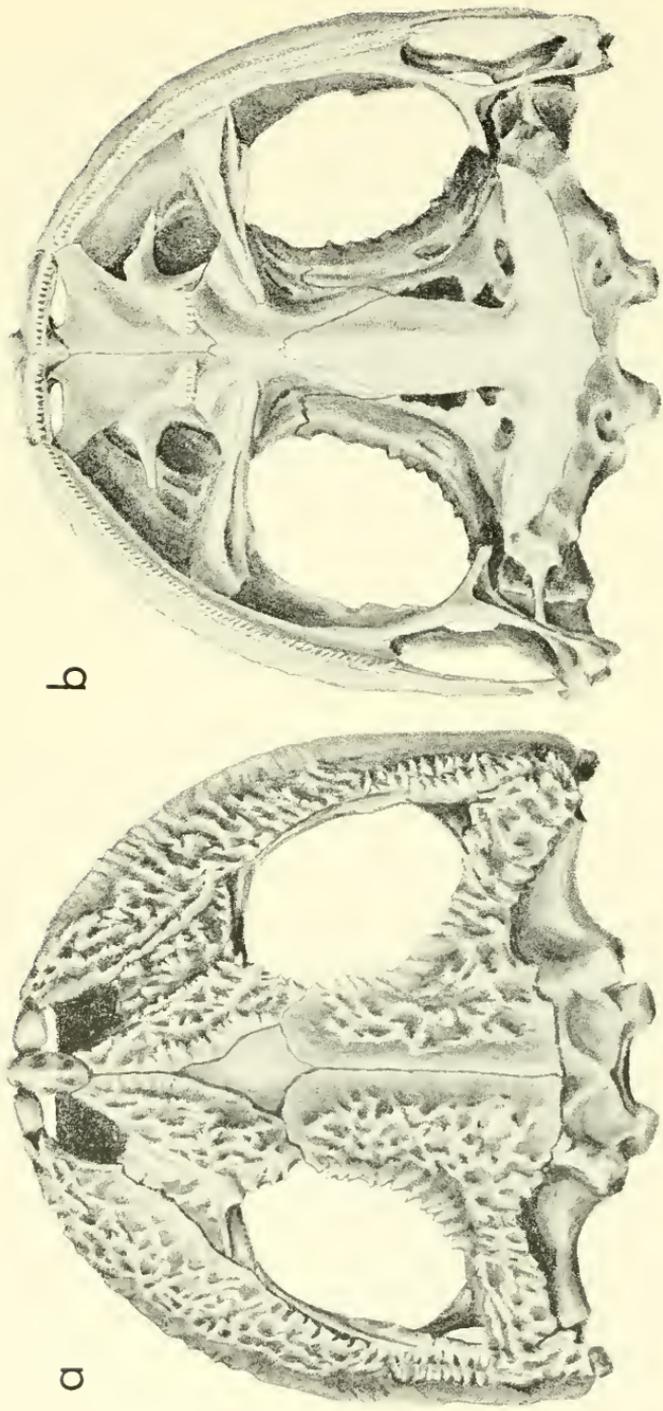
Corythomantis greeningi, KU 92223, ♀. $\times 6.8$. (a) dorsal view; (b) ventral view.

PLATE 9



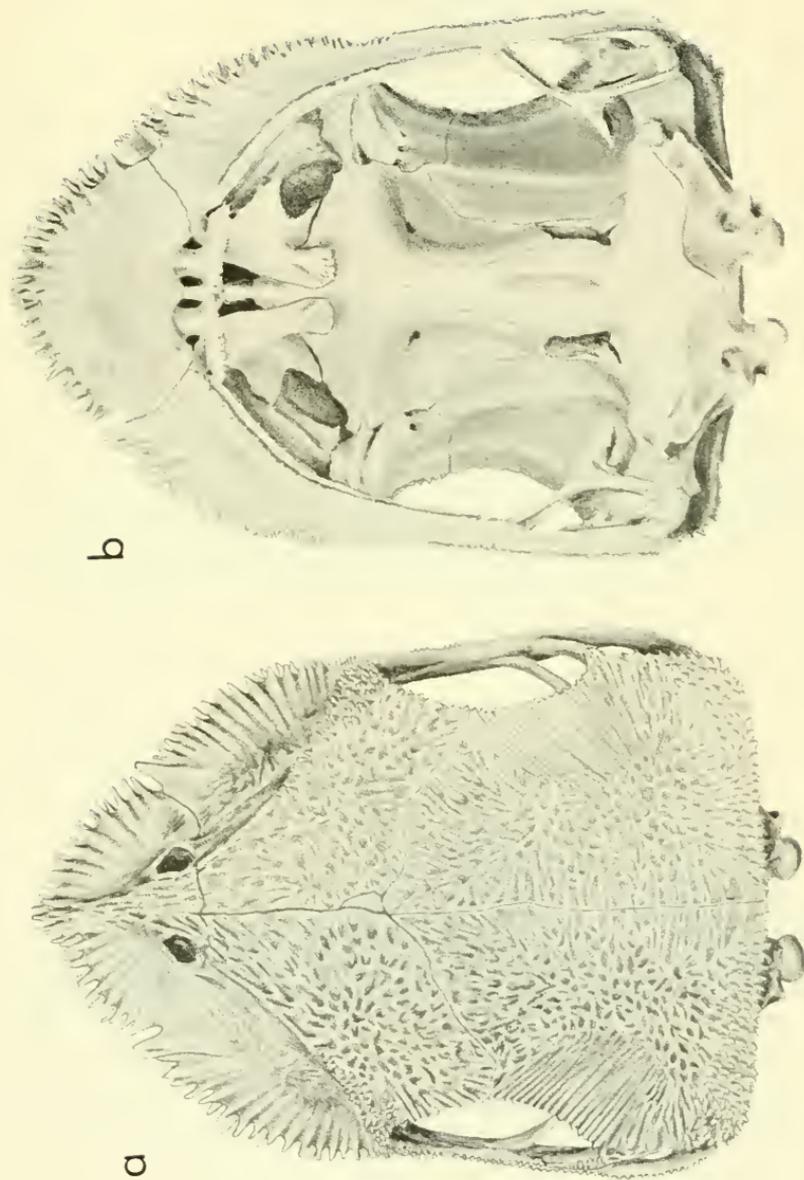
Aparasphiodon brunoi, KU 51326. $\times 3.7$. (a) dorsal view; (b) ventral view.

PLATE 10



Ptarmohyla fodicensis, KU 86614. $\times 5.5$. (a) dorsal view; (b) ventral view.

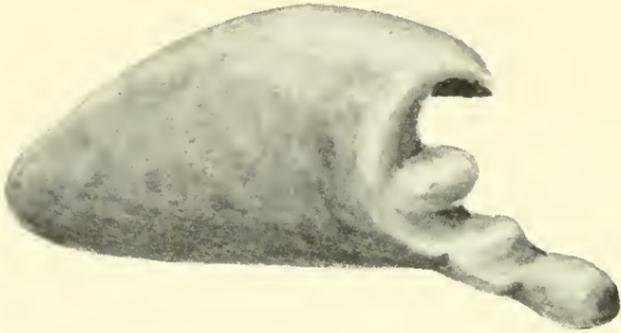
PLATE II



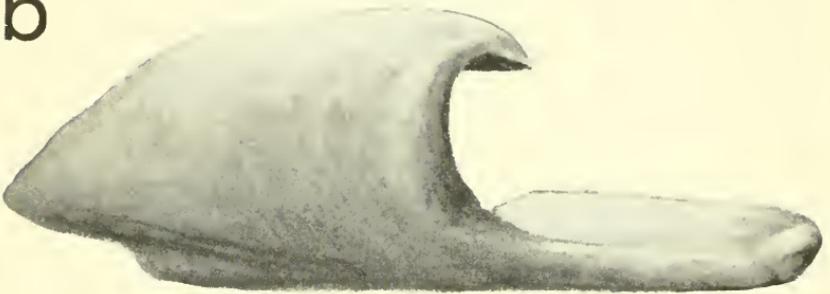
Tripriou spatulatus, KU 84904, ♀. $\times 2.2$. (a) dorsal view; (b) ventral view.

PLATE 12

a



b



c



Anterolateral views of three types of superior prenasal cartilages and their posteriorly associated alary cartilages. $\times 70$. (a) short superior prenasal cartilage characteristic of *Pternoluyia*; (b) long, depressed superior prenasal cartilage characteristic of *Aparasphenodon* and *Corythomantis*; (c) long, compressed superior prenasal cartilage characteristic of *Tripiron*.

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