NUMBER 219
JANUARY 26, 1972

NEW SPECIES OF SALAMANDERS (GENUS *BOLITOGLOSSA*) FROM COLOMBIA, ECUADOR and PANAMA

By ARDEN H. BRAME, JR. AND DAVID B. WAKE

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1964 AIBS Style Manual for Biological Journals is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1964 AIBS Style Manual for Biological Journals in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Changes in the manuscript after galley proof will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

NEW SPECIES OF SALAMANDERS (GENUS *BOLITOGLOSSA*) FROM COLOMBIA, ECUADOR AND PANAMÁ

By ARDEN H. BRAME, JR.[1] AND DAVID B. WAKE[2]

ABSTRACT: Several undescribed species of plethodontid salamanders are reported from South America and Panamá. *Bolitoglossa medemi* is a dark species with rather large, extensively webbed hands and feet and a broad head. It is known from several sites in northwestern Colombia and extreme southwestern Panamá, where it occurs between 50 and 800 m elevation. *Bolitoglossa ramosi* is a somewhat smaller species, with lighter coloration, small but extensively webbed hands and feet, and a broad head. It occurs in sympatry with *Bolitoglossa vallecula* in the Cordillera Central east of Medellín, Colombia, at elevations of about 1930 m. *Bolitoglossa silverstonei* is a slender, long-tailed species with light pigmentation, broad and extensively webbed hands and feet, and a head of moderate breadth. It is known only from a site near Quibdo, in northwestern Colombia, at an elevation of 400 m. *Bolitoglossa walkeri* has less extensively webbed hands and feet and fewer maxillary teeth than the other species. It has dark dorsal and light ventral coloration. This species occurs near Cali, Colombia, at elevations near 2000 m. *Bolitoglossa equatoriana* has more extensively webbed hands and feet than *B. walkeri,* but shares similar low numbers of teeth and coloration. It occurs sympatrically with *B. peruviana* at elevations of about 260 m in Amazonian Ecuador. These new species permit a re-evaluation of relationships among South American members of the genus *Bolitoglossa.* Characters used for analysis of relationships among the twenty-two species are discussed, and five species groups are recognized. The *palmata* and *altamazonica* groups are divided. *B. silverstonei* is assigned to a new *sima* group, along with *B. sima, B. chica,* and *B. biseriata.* The other newly described species are the only members of the *medemi* group.

Salamanders from the Neotropics have been known for over 140 years, but until recently they have been considered to be rare and insignificant. However, it is increasingly evident that the salamander fauna of the New World Tropics is extensive and diverse. The plethodontid salamanders, which range from northern Mexico to Bolivia, account for over 40 percent of all salamander species. This diverse group is of interest to evolutionary biologists

---

[1] Research Associate, Section of Herpetology, Natural History Museum of Los Angeles County; and Supervisor, Eaton Canyon Nature Center, 1750 North Altadena Drive, Pasadena, California 91107.

[2] Research Associate, Section of Herpetology, Natural History Museum of Los Angeles County; and Director, Museum of Vertebrate Zoology, University of California, Berkeley, California 94720.

in that it provides an opportunity to analyze an adaptive radiation in great detail. Many generalized salamanders, probably similar to ancestral forms, survive in extratropical habitats. In addition, many populations intermediate between adaptive extremes are known to occur in the tropics.

A major hindrance to intensive analysis of evolutionary patterns has been the absence of basic biological information concerning the tropical species. Most are poorly known, and are represented in collections by only a few specimens. For some areas, our knowledge of species composition is fragmentary and new populations continue to be discovered. One such area is northwestern South America where the known fauna has increased from one (Dunn, 1926) to nearly twenty species in recent years. In this paper we describe five additional species and discuss the relationships of South American members of the genus *Bolitoglossa.*

Many specimens used for this study were provided by Philip A. Silverstone, who collected salamanders incidental to his work with Colombian frogs. Brame obtained additional specimens in Colombia in the spring of 1971 and W. R. Heyer collected a fine series in Ecuador in the summer of 1971. These specimens are deposited in the Los Angeles County Museum of Natural History (LACM). Specimens also have been loaned to us by the following curators and museums: Charles F. Walker, University of Michigan, Museum of Zoology (UNMZ); Hobart M. Smith and Dorothy M. Smith, University of Illinois Museum of Natural History (UIMNH); William E. Duellman, University of Kansas Museum of Natural History (KU). Additional material is deposited at the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). We thank these curators and institutions for their assistance. We are grateful to William F. Presch for assistance in providing x-rays, and Les Siemens and Gene Christman for assistance with illustrations. Carlos Martinez provided the Spanish summary. Aspects of the work have been supported by NSF grant GB 17112 to David B. Wake.

The first species occurs in low coastal mountains of northeastern Colombia and neighboring Panamá. We are pleased to name it in honor of our good friend, Professor Federico Medem, of the Universidad Nacional de Colombia (Villavicencio), who has aided and encouraged us in our studies of Colombian salamanders.

Bolitoglossa medemi, new species

Figures 1 and 2

Holotype.—LACM 42276, an adult female from Finca Chibiguí, approximately 76° 30′ W, 6° 15′ N, on the Río Arquía, Departamento de Antioquia, Colombia. The specimen was collected on April 23, 1968, by Philip A. Silverstone, Jorge E. Ramos, and Nacianseno Borja. It was active on the ground during daylight hours. Elevation approximately 300 m (980 ft).

Paratypes.–COLOMBIA: LACM 42277-78, same data as holotype; PAS 237 (cleared and stained, LACM 72067), Belén, downstream from Finca Chibiguí, and very near Vegaes on the Río Arquía, Dept. Antioquia, about 100 m (328 ft) elevation; LACM 42280, along trail between Río Opogodó and Río Napipí, near the latter, approximately 77° 10′ W, 6° 43′ N, Dept. Chocó, 30 to 80 m (100-260 ft); LACM 42279, along Río Opogodó at base of eastern slope of the Serranía de Baudó, approximately 77° 18′ W, 6° 50′ N, Dept. Chocó, about 60 m (200 ft); LACM 70565, N slope Alto de Buey, Dept. Chocó, 400 m (1312 ft); LACM 70566, Camino de Yupe, Dept. Chocó, 350 m (1148 ft); LACM 70567, Camino de Yupe, Dept. Chocó, 400-500 m (1312-1640 ft); LACM 70568, Camino de Yupe, Dept. Chocó, 605 m (1984 ft). PANAMÁ: KU 116533-34, Río Jaque, 1.5 km above Río Imamadó approximately 77° 57′ W, 7° 25′ N, Prov. Darién, 50 m (164 ft); KU 116530, Jaque-Imamado divide in Cordillera de Jurado, above Río Jaque, Prov. Darién, 730-800 m (2394-2625 ft).

Diagnosis.—A moderately small species (5 adult males: 33.7–46.7, mean 40.4 mm SL [standard length, measured from tip of snout to posterior angle of vent]; 5 adult females: 34.2–48.2, mean 43.3 mm SL) with moderate numbers of maxillary (mean 41) and vomerine (mean 31) teeth. Distinguished from *B. ramosi* by having fewer maxillary teeth and a darker dorsal ground color; from *B. walkeri* by its broader head, more extensively webbed feet, and longer legs; from *B. equatoriana* by its more numerous maxillary teeth and somewhat longer legs. *Bolitoglossa medemi* is distinguished from other Panamanian and South American species by the combination of large, extensively to completely webbed hands and feet, relatively broad head, long legs, distinctive coloration (very dark, unmarked dorsum, much lighter venter with a few widely scattered, irregular light pigment spots), and size and dentitional features (Table 1).

Description of Holotype.—Adult female with moderately long, somewhat pointed snout and small nostrils. Labial protuberances of nasolabial grooves small, poorly developed. Moderately long canthus rostralis gently arched. Head broad (SL 5.8 times head width) and moderately long (SL 4.2 times snout-gular fold length). Deep groove below eye extends for almost full length of orbit, following curvature of eye, but does not communicate with lip. Large eyes slightly protuberant. Well-defined postorbital groove extends posteriorly from eye as shallow depression for 2.2 mm, then sharply ventrad at level of posterior end of mandible and across gular area as nuchal groove, parallel to, and 4.8 mm anterior to sharply defined gular fold. Vomerine teeth number 23, arranged in single rows that extend to lateral borders of internal nares; rows form slightly curved arches that terminate in center of palate, where they nearly meet. Small maxillary teeth number 41; extend posteriorly to point about two-thirds through eye. No premaxillary teeth can be seen. Relatively short tail (0.75 times SL) has strong lateral compression and is moderately constricted at base. Postiliac glands poorly developed. Limbs long with limb interval (costal folds between appressed limbs) of one; SL 4.0 times right forelimb, 4.0 times right hind limb, 10.0 times right foot width. Webbing of hands and feet nearly complete, but all digital tips extend beyond thin web. Longest digits with long, pointed tips (Fig. 2). Large hands and feet; rather narrow and long compared with those of other extensively webbed species. No subterminal pads. Fingers, in order of decreasing length, 3, 4, 2, 1; toes, in order of decreasing length, 3, 4, 2, 5, 1.

Measurements (in mm) are as follows: Head width, 8.3; snout to gular fold (head length), 11.5; head depth at posterior angle of jaw, 4.0; eyelid length, 3.4; eyelid width, 2.2; anterior rim of orbit to snout, 3.7; horizontal orbital diameter, 2.6; interorbital distance, 3.0; distance between vomerine teeth and parasphenoid tooth patch, 0.8; snout to forelimb, 15.5; distance separating internal nares, 2.1; distance separating external nares, 2.7; snout projection beyond mandible, 0.8; snout to posterior angle of vent (SL), 48.2;

FIGURE 1. Dorsal and ventral views of holotype of *Bolitoglossa medemi* (LACM 42276).

snout to anterior angle of vent, 44.9; axilla to groin, 26.6; tail length, 36.3; tail width at base, 3.0; tail depth at base, 3.7; forelimb length, 12.2; hind limb length, 12.2; width of right hand, 3.6; width of right foot, 4.8.

Coloration of Holotype (in alcohol).–This is a very dark salamander which has the dorsum and upper two-thirds of the lateral sides of the trunk

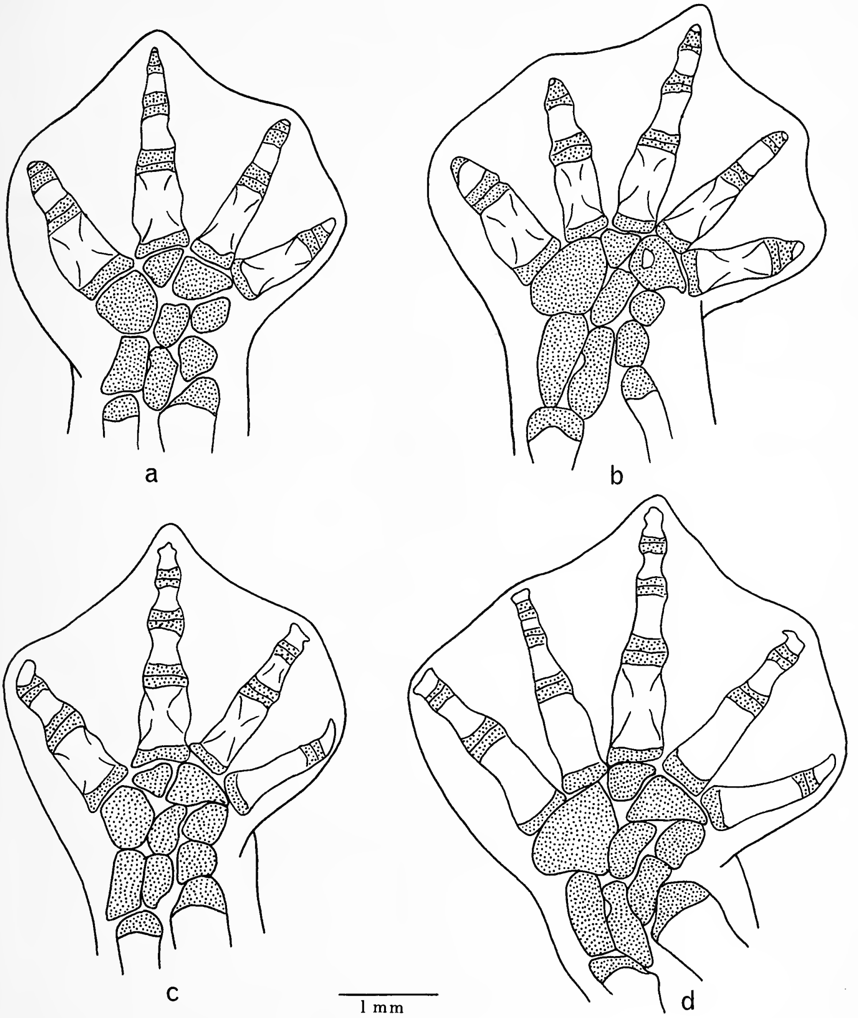


FIGURE 2. Outlines of hands and feet of species of *Bolitoglossa* drawn from cleared and stained specimens through use of microprojector. a. Right hand of *B. ramosi* (LACM 64603). b. Right foot of *B. ramosi* (LACM 64603). c. Right hand of *B. medemi* (LACM 72067). d. Right foot of *B. medemi* (LACM 72067).

uniformly colored a deep, leaden black. The dorsal surfaces of the head, tail, and legs are similarly colored. Small, indistinct guanophores are scattered on the snout, eyelids, and around the insertion of the limbs. Ventral surfaces are distinctly lighter than dorsal ones, and have a general grayish cast. Scattered guanophores are conspicuous on the throat and anterior part of the venter. Posteriorly and on the tail small to moderately sized, irregularly shaped patches of golden cream to grayish silver pigment occur. The ground color of the tail is darker than that of the throat and belly. Ventral surfaces of the limbs are mottled black and light gray, and the hands and feet are medium gray. The iris is golden with melanic mottling.

Variation.—Specimens from the Departamento de Chocó have somewhat lighter venters with fewer light patches that the animals from the Depto. Antioquia. The Panamanian individuals are similar in coloration to the holotype, but lack light ventral patches and have indistinct guanophores. The distinction between the dark dorsal and lateral and lighter ventral coloration is somewhat sharper than in the Colombian specimens.

A total of ten adult specimens are available, nine of which are from Colombia. The single adult from Panamá will be discussed separately. Males have small, well-defined, rounded mental hedonic glands. Females are larger (4 females, 34.2–48.2, mean 42.7 mm SL; 5 males 33.7–46.7 mean 40.4 mm SL) and have longer legs (SL 3.5–4.3, mean 3.9 times hind limb length in females versus 3.4–4.0, mean 3.7 in males) than males. Limb interval is zero to 1.5 in males and one to 1.5 in females. Males have premaxillary teeth which penetrate the upper lip, but females lack them.

The single adult female from Panamá differs from the Colombian females in having premaxillary teeth. It is about the same size as the Colombian specimens but has a narrower head (SL 6.4 times head width) than any Colombian individuals (SL 5.6–6.1, mean 5.8, times head width). The feet of the Panamanian adult are somewhat narrower than those of the Colombian specimens.

The juveniles are uniformly dark dorsally and lighter ventrally, with no distinctive markings.

Osteology.—Information concerning osteology has been derived from one cleared and stained female and from stereoscopic radiographs of all adults available.

The heavily ossified, well sutured skull is as well developed as that of any member of the genus. The premaxilla bone has a dental part that is well developed. It is closely aligned with the maxillae on either side. This alignment is typical of female *Bolitoglossa.* However, the toothless condition of the relatively large premaxilla is unusual. Frontal processes of the premaxilla are stout. They ascend along the margins of the cartilaginous nasal capsule, then proceed posteriorly. Near their tips they are dilated and in close apposition. As a result, the internasal fontanelle is very small and is restricted to the anterior end of the snout. The ascending part of each frontal process bears a winglike, flattened process lying against the anteromedial surface of the cartilaginous nasal capsule. These processes meet similar enveloping processes of the nasal. Posteriorly the frontal processes broadly overlap the expanded anterior part of the frontals in a firm articulation. The processes fall short of the ends of the nasals, but extend beyond the anterior margin of the orbits. Nasal bones are very large and protuberant. They extend far anteriorly where they overlie the enlarged nasal capsules. The area occupied by the nasal and prefrontal of more primitive species of the genus is included within the area of the nasal. Medially and anteriorly the nasals overlap the middle parts of the frontal processes of the premaxilla. The overlapping pieces are in medial contact for a short distance, an unusual arrangement in this genus. Posteriorly the nasals overlap the frontals and terminate in rounded borders beyond the margin of the orbits, approximately at the level of the eyes. Large ventrolateral lobes of the nasals overlap the anterior margin of the relatively large facial processes of the maxillae. The nasal is evacuated posterior and medial to these lobes. The nasolacrimal duct extends from the nasal capsule through this evacuated area, then posteriorly through the lower layers of the skin to the anterior corner of the eye. The route of the duct is free of bone. This bone-free area extends from the anterior end of the evacuation in the nasals, between the nasals and the maxillae to the eyes. The maxillae are well-developed bones that extend posteriorly to the limit of the eyes. Anteriorly the maxillae are produced into a flattened sheet of bone which partially underlies and envelops the cartilaginous nasal capsule. The palatal processes are small, but the facial processes are moderately large and relatively high.

Vomers are well developed and completely separated from each other, except posteriorly where the toothed portions are in slight contact. The intervomerine fontanelle is broad. Preorbital processes extend beyond the lateral margins of the vomerine bodies. Vomerine teeth are in patches which barely extend onto the preorbital processes.

Frontals are large and stout, with a strong sutural joint along the midline. The facial portions are stout, but are not especially large, in contrast to more northern species (Wake and Brame, 1969). No marked lobes are present posteriorly, where the margin is irregular. Parietals are well developed and have the parietal spurs that are characteristic of the genus. The occipito-otic bones bear low crests over the anterior vertical and lateral horizontal semicircular canals. The ridges over the latter form braces for the relatively well-developed, vertically oriented squamosals. The large parasphenoid is very narrow anteriorly. The anterior terminus is blunt, rather than pointed. Where the parasphenoid is narrowest, the orbitosphenoids nearly contact each other on the midline. Posterior vomerine teeth are in large patches on the parasphenoid. They narrowly fail to come into medial contact. The right patch bears 91 and the left, 96 ankylosed, bicuspid teeth, in the single cleared individual. The operculum has no stilus. Quadrates are stout. They are connected to the skull by the cartilaginous parts of the suspensorium, and by the relatively large squamosals. The squamosals are very attenuated dorsally where they fit into a depression in the wall of the otic capsule, and they are broadly expanded where they overlap the quadrates.

The hyobranchial apparatus is typical of other members of the genus (Wake, 1966).

Vertebrae are similar to those of other species of *Bolitoglossa.* The centra are spool-shaped, the intervertebral cartilages are unmineralized, and no articular condyles are formed. There are one cervical, fourteen trunk, one sacral, two caudosacral, and 26 caudal vertebrae in the cleared individual. Caudal vertebrae in other specimens number 25 (LACM 42276, 42279, both adults), 24 (LACM 42278, adult, last 5 regenerated), 22 (LACM 42277, juvenile), 19 (LACM 42280, all regenerated; KU 116534, juvenile), and 17 (KU 116537, all regenerated).

The first caudal vertebra is shorter than the next eleven vertebrae, but is the same length as the second caudosacral. All but the last two trunk vertebrae are longer than the longest caudal vertebrae (two to six), but caudal vertebrae two to ten are longer than the sacral and caudosacral vertebrae. Ribs are present on all but the last trunk vertebrae. One specimen (LACM 42279) has a small rib on one side of the last trunk vertebra. Transverse processes are short on all but the first two or three caudal vertebrae, but they are clearly present on all but the last vertebra. Transverse processes of the first caudosacral vertebra are long and directed almost perpendicularly to the body axis. Those of the second are much shorter and are directed somewhat posteriorly. The large, stout, non-bifurcated processes of the first caudal vertebra arise from the anterior margin of the vertebra (in contrast to the more central location of the caudosacral processes). From their anterior origin the processes extend first anteriorly, then sharply in a lateral direction. They do not cross those of the more anterior vertebra. This distinctive pattern of processes on the first three postsacral vertebrae is one not seen in any related or neighboring species. Processes on succeeding vertebrae arise from anterior positions and are anteriorly directed. They progressively diminish in size posteriorly. Hypapophyseal keels are absent only on the first and last two caudal vertebrae.

Hands and feet are large and distinctive. They are characterized by relative narrowness, accentuated by the presence of inordinately long central digits. Some variation in phalangeal formulae is encountered. The usual formula is 1, 2, 3, 2 for the hands and 1, 2, 3, 3, 2 for the feet. Two adults have a foot formula of 1, 2, 3, 2, 2 on one side, and several other individuals have very small penultimate and terminal phalanges in the fourth digit. Terminal phalanges are rather well developed but are erratically shaped (Fig. 2). There are seven carpals and eight tarsals, the generalized *Bolitoglossa* numbers (Wake, 1966). The tibia bears a prominent, sharp-edged crest, but has no free spur.

Remarks.—PAS 237 (LACM 72067) was captured by Norman J. Scott on a tree leaf where it was exposed at night. Other Colombian specimens were collected during daylight hours, exposed on the surface. KU 116530 was collected in cloud forest (Myers, 1969) where it is sympatric with *B. phalarosoma.*

Range.—The Chocó region of extreme northwestern Colombia, in the Río Atrato (Caribbean) drainage, and the Río Jaque (Pacific) drainage of extreme southeastern Panamá (Fig. 8). The species ranges from about 30 to 800 m (100 to 2624 ft) in elevation.

Bolitoglossa vallecula has been the only species known from uplands of the Cordillera Central of Colombia. A second species was collected in 1968 and 1971. We name it after Jorge Eduardo Ramos, who contributed much toward the success of the Silverstone and Brame–Newcomer trips to Colombia.

Bolitoglossa ramosi, new species

Figures 2 and 3

Holotype.—LACM 64601, an adult male from near Represa de Santa Rita (= Santa Rita Dam Site), Departamento de Antioquia, Colombia. This site is between Guatapé and San Rafael at about 75° 7′ W, 6° 17′ N, ca. 16 km by road NE of Guatapé. The specimen was collected by Brame and Jorge E. Ramos from the rolled-up base of a large palm frond on the ground of a forested hill near the dam construction site, April 3, 1971. Elevation about 1930 m (6330 ft).

Paratypes.—LACM 64600, 64602-03, same data as holotype; LACM 42287-90, collected from bromeliads at the same locality by Philip A. Silverstone and Jorge E. Ramos, June 9, 1968.

Diagnosis.—A moderately small species (5 adult males: 37.1–45.4, mean 40.4 mm SL; 2 adult females: 37.2–46.7, mean 42.0 mm SL) with relatively high numbers of maxillary (mean 47) and vomerine (mean 32) teeth; distinguished from *B. medemi* by its greater numbers of maxillary teeth and lighter dorsal ground color; from *B. equatoriana* and *B. walkeri* by its broader head and more numerous teeth. *B. ramosi* is distinguished from other Panamanian and South American salamanders by the combination of its extensively webbed hands and feet with the third digits long and pointed, its broad head, and distinctive coloration (rich rusty red to medium gray-black dorsally, with a darker venter, and a sprinkling of orange-red color on the dorsum and bright yellow patches on the venter).

Description of Holotype.—Adult male with moderately long, truncate snout and small nostrils. Large mental hedonic gland present (2.9 mm long and 3.3 mm wide). Labial protuberances of nasolabial grooves large and well developed, extending beyond margins of jaw. Moderately long canthus rostralis gently arched. Head moderately broad (SL 6.4 times head width) and moderately long (SL 4.5 times snout-gular fold length). Deep groove below eye extends for almost full length of orbit, following curvature of eye, but does not communicate with lip. Large eyes slightly protuberant. Well-defined postorbital groove extends posteriorly from eye as shallow depression for 1.8 mm; proceeds sharply in ventral direction at level of posterior end of mandible and across gular area as nuchal groove, parallel to, and 3.3 mm anterior to well-defined gular fold. Vomerine teeth number 26, arranged in single rows that become patched laterally. Patches extend slightly beyond lateral margins of internal nares; then row forms gentle arch to center of palate, where it is directed posteriorly. Small maxillary teeth number 55; extending posteriorly

FIGURE 3. Dorsal and ventral views of paratype of *Bolitoglossa ramosi* (LACM 42289).

to point about three-fourths through eye. Premaxillary teeth (2) well anterior to projected curvature of maxillary tooth row; piercing lip. Moderately long tail (0.94 times SL) with strong lateral compression, moderately constricted at base. No postiliac glands evident. Limbs moderately long (limb interval one); SL 4.2 times right forelimb and hind limb, and 9.7 times right foot width. Webbing of hands and feet nearly complete, but tips of longer digits pointed, extending beyond limits of relatively thick web. Third digit unusually long and pointed. Hands and feet moderate in size. No subterminal pads. Fingers, in order of decreasing length, are 3, 2, 4, 1; toes, in order of decreasing length, are 3, 4, 2, 5, 1.

Measurements (in mm) are as follows: Head width, 7.1; snout to gular fold (head length), 11.2; head depth at posterior angle of jaw, 3.8; eyelid length, 2.8; eyelid width, 1.8; anterior rim of orbit to snout, 3.2; horizontal orbital diameter, 2.1; interorbital distance, 2.3; distance between vomerine teeth and parasphenoid tooth patch, 0.6; snout to forelimb, 13.8; distance separating external nares, 2.8; distance separating internal nares, 1.8; snout projection beyond mandible, 1.2; snout to posterior angle of vent (SL), 45.4; snout to anterior angle of vent, 41.2; axilla to groin, 24.2; tail length, 42.8; tail width at base, 3.2; tail depth at base, 3.7; forelimb length, 10.8; hind limb length, 10.8; width of right hand, 3.7; width of right foot, 4.7.

Coloration of Holotype (in life).—This is a brightly colored salamander with a rich rusty red dorsal color on head, trunk and tail. A few dark black spots of ground color show through in some areas (especially on the snout). The venter is a dark gray-black. Ventral surfaces of the throat, trunk, and tail have widely scattered, irregularly shaped small spots and patches. These are bright pale yellow. The head is mottled rusty red and black except for the white-tipped nasolabial protuberances. The borders of the mouth are darkened. Dorsal surfaces of the upper arm and leg are light red, but lower parts of the limbs and the entire ventral side match the respective surfaces of the trunk. Dorsal and ventral surfaces of the webbed pad are relatively dark, and the phalanges tend to be outlined by some darker pigment dorsally. The eyes are dark, with heavy concentrations of melanin.

Variation.—Pertinent data are presented in Table 1. The males have longer snouts than the females. No hedonic glands are evident on the two small males but they are large and prominent on the three large ones. The largest male (the holotype) and the three largest male paratypes have premaxillary teeth which protrude from the lip. One of the small males and also LACM 64603 differ in coloration from the remaining paratypes and the holotype in having a pair of broad, white stripes extending from the tips of the nasolabial protuberances to the eyelids. The paratypes (except LACM 64603) differ from the holotype in having a lighter gray dorsal color and light orange-red patches about the base and first one-third of the tail, and also by having larger pale yellow patches ventrally.

TABLE I. Measurements and data for specimens of new species of *Bolitoglossa*

	Sex	Snout-Vent Length	Axilla-Groin Length	Head Width	Hind Limb Length	Forelimb Length	Tail Length	Numbers of Maxillary Teeth	Numbers of Vomerine Teeth	Limb Interval	Foot Width
B. silverstonei											
LACM 42283[a]	♂	49.3	27.0	7.8	10.8	10.6	55.7	51	24	3	5.3
B. medemi											
LACM 70565	♂	46.7	24.5	8.1	12.5	12.5	47.5	59	34	0.5	5.3
LACM 42278	♂	41.7	21.4	7.4	12.4	12.0	34.6[b]	43	22	0	4.3
LACM 42280	♂	41.3	21.6	6.9	10.6	10.6	17.8[b]	33	32	0.5	3.7
LACM 70567	♂	38.5	20.1	6.3	9.6	9.2	36.2	35	27	1.5	3.9
LACM 42279	♂	33.7	16.7	6.0	9.3	9.4	33.2	41	29	0.5	3.3
LACM 42276[a]	♀	48.2	26.6	8.3	12.2	12.2	36.3	41	23	1	4.8
LACM 72067[c]	♀	47.3	26.0	7.9	11.2	11.3	36.5	50	26	1	4.8
KU 116533	♀	47.0	26.3	7.3	12.0	11.8	16.1[b]	38	50	1.5	4.4
LACM 70568	♀	39.7	19.7	7.0	11.4	10.2	32.3	45	42	1	4.1
LACM 70566	♀	34.2	17.8	6.1	8.9	8.0	28.7	28	27	1	3.3
LACM 42277	juv.	30.0	14.1	5.3	7.3	7.1	20.6	14	20	0.5	2.7
KU 116530	juv.	28.9	16.1	5.5	7.1	7.0	7.0[b]	23	28	1	2.7
B. ramosi											
LACM 64601[a]	♂	45.4	24.2	7.1	10.8	10.8	42.8	55	26	1	4.7
LACM 64602	♂	41.4	21.4	7.1	10.4	10.3	32.2[b]	50	31	1.5	4.1
LACM 64603[c]	♂	40.0	21.3	6.9	10.7	10.7	29.5[b]	38	25	1	4.0
LACM 42290	♂	37.9	19.0	6.7	9.6	9.2	29.8	47	26	1	3.2
LACM 42289	♂	37.1	20.4	6.6	9.4	9.3	33.9	41	31	2	3.2
LACM 64600	♀	46.7	24.7	7.8	11.2	10.8	36.0	50	51	2.5	4.3
LACM 42288	♀	37.2	19.5	6.6	8.8	8.6	29.7	45	37	1.5	3.2
B. walkeri											
UMMZ 128833[a]	♂	40.2	21.3	6.4	10.2	9.8	32.8[b]	29	22	1.5	4.5
MVZ 68628	♀	41.4	23.1	6.3	9.0	8.6	19.2[b]	33	36	2.5	3.7
MVZ 68627	♀	38.9	22.0	6.2	8.7	7.9	37.0	18	28	2.5	3.2
B. equatoriana											
LACM 70561	♂	42.8	22.7	7.1	10.6	10.0	35.8	23	18	2	4.3
LACM 70562	♂	40.2	21.2	7.1	10.7	10.4	33.6	26	24	1.5	4.2
LACM 70550[a]	♀	57.9	32.8	9.1	13.2	13.2	49.6	48	11	3	5.7
UIMNH 54296	♀	45.9	24.4	7.4	11.2	10.2	41.0	27	28	2	4.2
UIMNH 86692	♀	44.0	23.0	7.0	10.6	10.5	35.2	27	26	2	4.1
KU 98951	♀	43.0	22.8	7.5	10.6	10.1	——[b]	23	24	2	4.3
LACM 70552	♀	42.6	23.5	6.7	10.1	9.7	16.3[b]	24	18	3	3.8
LACM 70551	♀	42.4	23.1	7.0	10.3	10.0	34.9	27	21	2	4.0
UIMNH 86694	♀	41.4	22.1	6.7	9.8	9.8	28.7[b]	19	24	2	3.9
LACM 70553	♀	40.3	20.9	6.8	9.4	9.6	33.7	20	19	3	3.9
LACM 70555	♀	39.7	21.8	6.4	9.1	8.9	35.0	27	23	3	3.6
LACM 70556	♀	39.3	21.2	6.7	9.7	9.0	29.9	14	21	1.5	4.0
LACM 70554	♀	39.0	21.7	6.6	10.1	9.9	29.0	24	17	2.5	3.6
UIMNH 86696	♀	38.3	20.6	6.2	9.2	9.1	22.1[b]	23	20	2	3.9
LACM 70557	♀	37.5	21.2	6.3	9.0	8.8	28.2	22	17	3	3.4
LACM 70558	♀	36.8	19.7	6.1	8.9	9.0	29.3	19	17	2.5	3.5
UIMNH 86695	♀	36.5	19.3	6.3	8.7	8.6	29.2	27	23	2	4.0
LACM 70559	juv.	34.0	18.9	6.2	8.6	8.3	28.3	18	16	2	3.3
LACM 70560	juv.	32.4	16.7	5.9	7.9	7.3	25.0	4	16	2	3.0

[a]holotype; [b]regenerated tails or tails missing; [c]cleared and stained.

Osteology.—Information has been derived from one cleared and stained adult male (LACM 64603) and from stereoscopic radiographs of all adults available.

The skull is well formed and bones in the posterior portion are closely sutured. The snout is short and anterior cranial elements are small, with slight or no articulations. In comparison with *B. medemi* the snout region is poorly developed. The premaxilla is small and slender, with short, distally expanded frontal processes. The processes are well separated for their entire length, but the internasal fontanelle is very small. The irregularly expanded terminal parts of the processes are small and barely overlap the anterior ends of the frontals. Lateral parts of the frontals extend anteriorly so that the tips of the processes lie more or less enclosed by the frontals. The processes extend beyond both the anterior border of the orbit and the posterior margin of the nasals. Nasal bones are of moderate size and, relative to the premaxilla, they are strongly protuberant. Their only articulation is by means of a ventrolateral lobe which barely contacts the facial process of the maxilla. The pointed posterior tips of the nasal bones extend to the anterior border of the orbits. The separation between the nasals is great, approximating their length. The posterolateral margins of the nasals and the anterodorsal margins of the facial process of the maxilla are evacuated for the passage of the nasolacrimal duct. Prefrontal bones are very erratic in shape, and they are very small. In the one cleared specimen the prefrontal of one side is an elongate bone with about one-quarter the area of the facial process of the maxilla and less than one-tenth the area of the nasal. On the other side the bone is reduced to a tiny dot that is less than one-tenth the size of its pair. Prefrontals have no contacts with other bones in this species. The maxillae extend about three-quarters through the eye. They are very slender, with well developed facial processes. The anterior ends of the maxillae are flattened, terminating in narrowed points. Palatal processes are poorly developed.

Vomers are of moderate size and are completely separated from each other. The toothed portions are drawn into processes medially, where they converge, but remain well separated. The intervomerine fontanelle is very large. Preorbital processes extend beyond the lateral margins of the vomerine bodies. Vomerine teeth are in a single row that extends beyond the lateral margin of the internal nares.

Frontals are large and well sutured to each other. Facial portions are relatively smaller than *B. medemi.* Posteriorly the bones are well sutured to the parietals. There are slight lateral lobes on the posterior margins of the frontals. Parietals are well developed and closely articulated with each other. There are no crests on the occipito-otics. The nearly vertical squamosals rest in depressions in ridges on the lateral margins of the occipito-otics. The large parasphenoid has a rather narrow, blunt-tipped anterior end. The orbitosphenoids are well separated at their ventral margins. Posterior vomerine tooth patches are not in contact medially. The right patch bears 74 and the left, 82 ankylosed, bicuspid teeth in the cleared specimen. The operculum has no stilus. Quadrates and squamosals are moderately developed.

There are one cervical, fourteen trunk, one sacral, two caudosacral and 28 (LACM 42289, 42290, 64601), 27 (LACM 64600), 25 (LACM 42288), 23 (LACM 6460, tip regenerated), or 19 (LACM 42287, juvenile) caudal vertebrae; the tail of LACM 64603 is regenerated beyond caudal vertebra seventeen. Ribs are present on all but the last trunk vertebra. The transverse processes on the first caudosacral vertebra are very long and are oriented nearly perpendicularly to the body axis. Those of the second caudosacral vertebra are shorter and extend sharply in an anterior direction. The very long, unbranched processes of the first caudal vertebra are slanted anteriorly. The slant is sharper than on the preceding vertebra. Their tips extend nearly to a level equivalent to the anterior end of the second caudosacral vertebra. The processes of these adjacent vertebrae do not overlap. Processes on the second caudal vertebra are much smaller than those on the first, and they become progressively smaller on the remaining vertebrae. The last vertebra to have distinct processes varies from the eighth to the eighteenth. The last caudosacral and first caudal vertebrae are shorter than neighboring vertebrae. Vertebrae in the anterior one-half of the tail are as long as any but the first three trunk vertebrae. The fourteenth caudal is the first vertebra that is shorter than the first caudal.

The tibia has a distinct crest but no spur. Phalangeal formulae are 1, 2, 3, 2 (or 1), and 1, 2, 3, 3 (or 2), 2 (or 1). The more distal phalanges are poorly developed, but there is a tendency for reduction and loss (Fig. 2). Terminal phalanges are extremely small and poorly ossified, with erratic shapes. Penultimate phalanges are reduced in the longer toes. Proximal phalanges are short and stout, often as broad as long. They are somewhat flattened. The distance between bony areas of a given digit is great, and often the cartilage between elements is longer than the adjacent bones. Metatarsals and metacarpals are flattened, with lateral bony webs. The outermost metapodials have characteristic shapes resulting from a large, rounded web along the margin of the bones. There are seven carpals and seven or eight tarsals. In one tarsus, D 4-5 is fused with D 3, and D 1-2 is partly mineralized in several tarsi (Fig. 2).

Remarks.—All specimens were collected either in bromeliads located within a few feet of the surface, or in the rolled bases of palm fronds on the surface of a forested hill. In 1968 the specimens were collected in sympatry with *Bolitoglossa vallecula,* a species that is widespread in the northern part of the Cordillera Central of Colombia (Brame and Wake, 1963). No *B. vallecula* were found associated with *B. ramosi* during the 1971 visit.

Range.—Known only from the type locality in the Cordillera Central of Colombia (Fig. 8).

The following most distinctive of the new species is named in honor of

Philip A. Silverstone, in appreciation of his assistance to us and in recognition of his important contributions to Neotropical herpetology.

Bolitoglossa silverstonei, new species

Figures 4 and 5

Holotype.—LACM 42283, an adult male from Quebrada Bochoramá, Loma de Encarnación, Departamento de Chocó, Colombia, about 51 km (32 mi) SE Quibdo at approximately 76° 23′ W, 5° 20′ N. This site is a "one-hour walk" SE Playa de Oro. The specimen was collected in a rolled plantanillo leaf on a steep hillside near a stream at about 400 m (1312 ft) elevation by Philip A. Silverstone and Jorge E. Ramos on May 31, 1968. The species is known only from the holotype.

Diagnosis.—A moderate-sized species (49.3 mm SL) with moderate numbers of maxillary (51) and vomerine (24) teeth; distinguished from *B. biseriata* by its larger feet and more numerous maxillary teeth; from *B. sima* by its shorter legs and more numerous maxillary teeth. *Bolitoglossa silverstonei* is distinguished from other Panamanian and South American species by the combination of its extensively webbed hands and feet, distinctive ventral coloration (cream with a light peppering of small brownish spots), and size and dentitional features.

Description of Holotype.—Adult male with moderately long, somewhat truncate snout and small (2.0 mm wide), nearly circular mental hedonic gland and small nostrils. Labial protuberances of nasolabial grooves moderately large, extending below lower jaw margin. Head moderately broad (SL 6.4 times head width) and long (SL 4.3 times snout-gular fold length). Deep groove below eye extends for almost full length of orbit, following curvature of eye, but does not communicate with lip. Eyes moderately small, slightly protuberant. Well-defined postorbital groove extends posteriorly from eye as shallow depression for 2.2 mm, then sharply ventrad at level of posterior end of mandible and across gular area as nuchal groove, parallel to, and 4.2 mm anterior to sharply defined gular fold. Vomerine teeth number 24, in moderately patchy rows that extend slightly beyond lateral borders of internal nares. From lateral terminus, rows extend medially in nearly straight line to near center of palate, then bend sharply posteriad and closely approach (1.0 mm separation) parasphenoid tooth patch. Small maxillary teeth number 51; extending posteriorly to point about three-fourths through eye. Large premaxillary teeth (two) pierce lip. Long tail (1.1 times SL) rounded and moderately constricted at base. Postiliac glands indistinct. Limbs moderately short (limb interval three). Standard length 4.6 times right forelimb, 4.5 times right hind limb, and 9.3 times width of right foot. Webbing of hands and feet extensive, nearly complete, with only tips of longer digits extending slightly beyond web (Fig. 5). No subterminal pads present. Fingers, in order of decreasing length, are 3, 2, 4, 1; toes, in order of decreasing length, are 3, 4, 2, 5, 1.

Measurements (in mm) are as follows: Head width, 7.8; snout to gular fold (head length), 11.5; head depth at posterior angle of jaw, 4.8; eyelid length, 3.2; eyelid width, 2.0; anterior rim of orbit to snout, 3.8; horizontal orbital diameter, 2.7; interorbital distance, 3.3; distance between vomerine teeth and parasphenoid tooth patch, 1.0; snout to forelimb, 14.5; distance separating internal nares, 2.4; distance separating external nares, 3.0; snout projection beyond mandible, 0.9; snout to posterior angle of vent (SL), 49.3; snout to anterior angle of vent, 45.1; axilla to groin, 27.0; tail length, 55.7; tail width at base, 3.9; tail depth at base, 3.9; forelimb length, 10.6; hind limb length, 10.8; width of right hand, 4.1; width of right foot, 5.3.

Coloration of Holotype (in alcohol).—This is a rather light-colored salamander. A reddish brown dorsal mottling overlies the blackish purple ground color. The dorsal pigmentation is distinctly darker than that of the ventral surfaces. Lateral surfaces of the trunk and tail are light reddish brown with some scattered melanophores. An indistinct ventrolateral stripe of blackish purple sharply separates the dark dorsal and lateral from the light ventral pigmentation. The broad stripe of the trunk becomes narrow and discontinuous on the tail. All ventral surfaces are light golden cream to grayish white, peppered with minute, widely scattered melanophores that are clearly visible over the entire surface. Some coalescence of melanophores occurs laterally, producing larger spots of pigment. The head is colored like the trunk, dark dorsally and light ventrally. The whitish ventral coloration of the throat extends along the upper lip region and in front of the eyes. The small eyes have a reddish brown iris, with a gold ring surrounding the horizontally elliptical pupil. Limbs are dark dorsally and light ventrally, with other markings similar to the respective parts of the trunk. The hands and feet are light dorsally and ventrally, and there are no obvious ventral melanophores.

Osteology.—Stereoscopic radiographs have provided all of the following information. The skull is comprised of well-articulated bones and is generally well developed. The premaxilla has a very small dental process which is placed well ahead of the maxillae. Frontal processes of the premaxilla are separated for their entire lengths. The processes are large and expanded near their tips. Nasal bones are large and strongly protuberant. No prefrontal bones can be seen. Vomers are well separated on the midline. The preorbital processes of the vomers extend laterally well beyond the limits of the internal nares. No stilus is present on the middle ear bone. Ribs are present on all but the last trunk vertebra. There are one cervical, fourteen trunk, one sacral, two caudosacral, and 38 caudal vertebrae. The transverse processes on the first caudosacral vertebra are very long and slant posteriorly. Those on the second caudosacral vertebra are much shorter and slant slightly in an anterior direction. The long, unbranched processes of the first caudal vertebra arise near its anterior end and extend sharply in an anterior direction. They termi-

Figure 4. Dorsal and ventral views of paratype of *Bolitoglossa silverstonei* (LACM 42283).

nate beyond the point of attachment of the processes of the second caudosacral vertebra. The tips of the processes of the last caudosacral and first caudal vertebrae do not cross. Transverse processes of the remaining caudal vertebrae are progressively smaller. All are located near the anterior end of the vertebrae and are oriented sharply forward. They are discrete on the first 30 vertebrae. As is usual in species with constricted tail bases, the last caudosacral and first caudal vertebrae are shortened, relative to neighboring vertebrae. Posterior to this region the vertebrae are longer. The fourth through seventh caudal vertebrae are as long as the longest trunk vertebrae (two and three). The first vertebra shorter than the first caudal vertebra is the seventeenth caudal. From that point the vertebrae are progressively shorter to the tail tip. No tibial spurs are present. Phalangeal formulae are 1, 2, 3, 2 and 1, 2, 3, 3, 2. All phalangeal elements are small and poorly developed, and the abrupt decrease in size from the proximal to the distal elements in the longest digits is striking (Fig. 5). Terminal phalanges are all minute and unexpanded; most are tiny points of bone. Much cartilage is present at the ends of the metapodials and phalanges, and the distance from one bony area to another is always greater than the length of the distal bony element. Metapodials are dumbbell-shaped with only slight lateral expansion.

Remarks.—Playa de Oro is located in the Chocó forest area of Colombia, in a region identified as wet tropical forest (Holdridge System) by Espinal and Montenegro (1963). Previously only *B. biseriata* has been known from this area, but discovery of *B. silverstonei, B. medemi,* and *B. phalarosoma* from northwestern Colombia and from Panamá suggests that this has been a region of lowland diversification. Two additional species, *B. sima* and *B. chica,* occur in the Ecuadorian portion of the Chocó.

Range.—Known only from the type locality in the lowlands of northwestern Colombia (Fig. 8).

During the past ten years we have been generously aided in our efforts by the cooperation and encouragement of Professor Charles F. Walker of the Museum of Zoology, University of Michigan. It is a pleasure to name the following Colombian species in his honor.

Bolitoglossa walkeri, new species

Figures 5 and 6

Holotype.—UMMZ 128833, an adult male from "Television Tower Mountain," 15 km WNW Cali and 0.9 km S El Jordan, Departamento de Valle, Colombia. The specimen was collected from a bromeliad in cloud forest at an elevation of 2050 m (6724 ft) by Walter Moberly and Kraig K. Adler on July 17, 1965.

Paratypes.—MVZ 68627-28, 4 km NW San Antonio, Depto. Valle, Colombia, 1982 m (6500 ft) elevation.

Diagnosis.—An apparently small species (3' adults 38.9–41.4, mean 40.2 mm SL) with low numbers of maxillary (mean 27) and moderate numbers of vomerine (mean 28) teeth. Distinguished from *B. equatoriana* by its narrower head, less extensively webbed, slightly smaller hands and feet, and ventral coloration (dirty white to gray, with some streaks of darker pigment and an overlay of brassy pigment, but without the encroachment of dark pigment which leaves the large, whitish spots characteristic of *B. equatoriana*); from *B. medemi* by its narrower head, less extensively webbed feet, and shorter legs; from *B. ramosi* by its narrower head and less numerous teeth. *Bolitoglossa walkeri* differs from other Panamanian and South American *Bolitoglossa* by the combination of its extensively webbed hands and feet, color, and its size and dentitional features (Table 1).

Description of Holotype.—Adult male with moderately short, truncate snout and pronounced, rounded, mental hedonic gland; small nostrils. Labial protuberances of nasolabial grooves well developed, extending below lower jaw margin. Strongly arched canthus rostralis moderately long. Head moderately broad (SL 6.3 times head width) and long (SL 4.4 times snout-gular fold length). Deep groove below eye extends for almost full length of orbit, following curvature of eye, but does not communicate with lip. Eyes relatively large, moderately protuberant. Well-defined postorbital groove extends posteriorly from eye as shallow depression for 1.8 mm, then sharply ventrad at

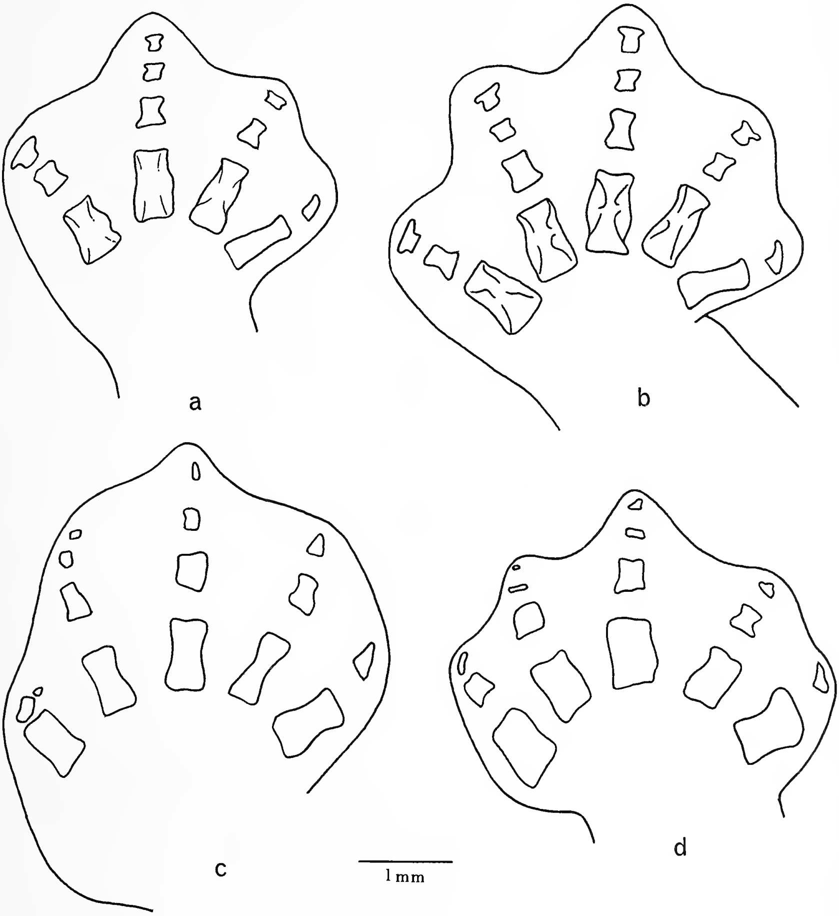


Figure 5. Outlines of hands and feet of three species of *Bolitoglossa*, drawn from radiographs through use of microprojector. Bony parts of digits are outlined. **a.** Right hand of holotype of *B. walkeri* (UMMZ 128833). **b.** Right foot of holotype of *B. walkeri*. **c.** Right foot of holotype of *B. silverstonei* (LACM 42283). The left side of the drawing is distorted as a result of fixation artifact. **d.** Right foot of *B. equatoriana* (KU 98951). The foot is slightly distorted on the left and slightly foreshortened as a result of fixation artifact.

FIGURE 6. Dorsal and ventral views of holotype of *Bolitoglossa walkeri* (UMMZ 128833).

level of posterior end of mandible and across gular area as nuchal groove, parallel to, and 3.2 mm anterior to sharply defined gular fold. Vomerine teeth number 22, arranged in single rows extending from one-half to two-thirds diameter of internal nares; from lateral terminus, rows form moderately strong arches to center of palate, where two rows nearly meet. Small maxillary teeth number 29; extending posteriorly to point about one-half through eye. Single premaxillary tooth pierces lip. Relatively short tail (0.82 times SL) has slight lateral compression and is slightly constricted at base. Postiliac glands small, indistinct. Limb length moderate with limb interval of 1.5. Standard length

4.1 times right forelimb, 3.9 times right hind limb, and 9.0 times width of right foot. Webbing of hands and feet extensive, thin. Tips of all digits discernible, longer digits protruding substantially from web. Digital tips broadly rounded. Hands and feet relatively large. No subterminal pads. Fingers, in order of decreasing length, are 3, 4, 2, 1; toes, in order of decreasing length, are 3, 4, 2, 5, 1.

Measurements (in mm) are as follows: Head width, 6.4; snout to gular fold (head length), 9.2; head depth at posterior angle of jaw, 3.6; eyelid length, 3.2; eyelid width, 1.8; anterior rim of orbit to snout, 3.0; horizontal orbital diameter, 2.3; interorbital distance, 2.8; distance between vomerine and parasphenoid teeth, 0.5; snout to forelimb, 11.8; distance separating internal nares, 2.0; distance separating external nares, 2.7; snout projection beyond mandible, 1.1; snout to anterior angle of vent, 35.8; snout to posterior angle of vent (SL), 40.2; axilla to groin, 21.3; tail length, 32.8; tail width at base, 2.8; tail depth at base, 3.2; forelimb length, 9.8; hind limb length, 10.2; width of right hand, 3.6; width of right foot, 4.5.

Coloration of Holotype.—In life (from field notes of Kraig Adler): "Golden brown above in different shades, with blackish spots and blotches. Cream white streaks running lengthwise, especially over vent and on tail; black "V's" on neck, pointing outwards; some faint reddish pigment on dorsum, especially in midline. Dark golden below, light tan golden between eye and nasolabial groove, nose region speckled with various shades of golden. Belly dirty white overlaid with much brassy pigment; some few black streaks, also at posterior end of anus [sic]; throat heavily flecked with golden, especially at anterior end; mental gland bright golden; soles of hands and feet pinkish (=blood) and golden." After several years in alcohol the brighter pigments have faded, but the pattern remains distinct. The impression is of a rather dark tannish brown animal with a much lighter venter. The whitish ventral pigment is more sharply demarcated from the lateral dark pigment of the tail than of the trunk. The mental gland is light and prominent on the relatively dark throat.

Variation.—Pertinent data are presented in Table 1. The holotype is a male and the two paratypes are females. The paratypes have proportionally shorter limbs (limb interval 2.5 rather than 1.5) and narrower feet (SL 11.2–12.2 times right foot width, rather than 9.0) than the holotype. Both features are sexually dimorphic in similar ways in most species of *Bolitoglossa.* Premaxillary teeth are absent in one paratype and fail to protrude from the lip in the other; these are also female characteristics.

One specimen, MVZ 68628, is colored like the holotype, but has a somewhat darker venter which lacks dark streaks, whereas MVZ 68627 has a lighter dorsal ground color than the holotype, but has a similar ventral coloration. This animal is briefly described in the field notes of the collector, A. H. Miller, as follows: "The light areas of the back, belly and undertail surface were yellow or bronze in life so that the whole animal was distinctly light and bright."

Osteology.—All information has been derived from stereoscopic radiographs. The skull is well developed with well articulated bones. The small, slender premaxilla has relatively short, divergent frontal processes. The dilated tips of these processes fall short of the posterior margin of the nasals. The large, protuberant nasals have distinct lateral lobes that articulate firmly with the maxillae. No prefrontals are evident. Vomers are well separated for their entire lengths, but the toothed parts approach the midline posteriorly. Preorbital processes of the vomers extend well beyond the lateral margins of the internal nares and bear teeth for most of their lengths. Maxillae extend about to the posterior margin of the eyes. The operculum has no stilus. Ribs are present on all but the last trunk vertebra, but those on the next to last vertebra are very small in the holotype. There are one cervical, fourteen trunk, one sacral, two caudosacral and 28 caudal vertebrae in the single specimen that has a complete tail.

The long, stout, transverse processes on the first caudosacral vertebra are nearly perpendicular in orientation, but have a slight posterior slant. The shorter and more slender processes on the second caudosacral vertebra have a sharp anterior slant. These processes are stouter and less slanted in the holotype than in the paratypes. Their tips reach to a point about one-third through the preceding vertebra. The very long processes of the first caudal vertebra are long and sinuous. They slant strongly in an anterior direction. Tips of the processes extend beyond the bases of the processes on the second caudosacral vertebra, but the processes of the adjacent vertebrae do not overlap. The processes are not branched. Processes on succeeding vertebrae are progressively shorter. They are visible to about the nineteenth vertebra, but are minute beyond the seventh. All lie at the anterior end of the vertebrae and slant anteriorly.

The second caudosacral and first caudal vertebrae are shorter than all but the first trunk vertebra, which equals them in length, and the seventeenth and succeeding caudal vertebrae. The second through eighth caudal vertebrae are as long as the longest trunk vertebra (the seventh), and the third caudal vertebra is the longest in the entire column.

No tibial spur is present, but a small ridge is present in mid-shank on the left tibia in the holotype. Phalangeal formulae are 1, 2, 3, 2 and 1, 2, 3, 3, 2. Digits are well developed. Phalangeal elements are increasingly shortened toward the digital tip. Most are dumbbell-shaped. Terminal phalanges are expanded at their tips. Distance between the bony parts of the digits is always less than the length of the shortest phalanx of the digit. Lateral weblike processes of the metatarsals extend into the fleshy web (Fig. 5).

Remarks.—All of the specimens were collected in cloud forest at intermediate elevations. The holotype was taken from a bromeliad. Alden and Virginia Miller collected MVZ 68627 during the day (March 9, 1958) while it was exposed on the surface of a large (five inch) leaf hanging from a flowering epiphyte that was not noticeably moist. Dr. Miller collected the other paratype (MVZ 68628) during the day (September 9, 1958) in a brushy, thick part of the forest. It was apparently dislodged from its position in the foliage, since it was found on the ground as a path was retraced. The individual had, as yet, not righted itself.

Range.—This species is known only from neighboring localities in cloud forest of intermediate elevation (about 2000 m) WNW of Cali, Depto. de Valle, Colombia (Fig. 8).

Examples of an undescribed species of salamander have been collected in sympatry with *Bolitoglossa peruviana* on several occasions. This species, named for its geographic location, is the sixth form discovered in Ecuador.

Bolitoglossa equatoriana, new species

Figures 5 and 7

Holotype.—LACM 70550, an adult female from Limón Cocha, 0° 24′ S, 76° 37′ W, Provinicia de Napo, Ecuador. The specimen was collected at a secondary-primary growth border, 1 m above the ground, on August 5, 1971 by W. Ronald Heyer. Elevation 260 m (850 ft).

Paratypes.—LACM 70551-64 (14 specimens) collected by W. Ronald Heyer between June 11 and August 5, 1971; KU 98951, UIMNH 86692, UIMNH 86694-96 collected by different collectors between July 18 and July 28, 1965 at the type locality.

Diagnosis.—A moderate-sized species (15 females: 36.5–57.9, mean 41.7 mm SL; two males: 40.2–42.8, mean 41.5 mm SL) with low numbers of maxillary (mean 25) and moderate numbers of vomerine (mean 21) teeth. Distinguished from *B. walkeri* by its broader head, more extensively webbed and slightly longer hands and feet, and spotted ventral color pattern; from *B. medemi* by its less numerous maxillary teeth and somewhat shorter legs; from *B. ramosi* by its narrower head and less numerous maxillary teeth; from *B. peruviana* by its broader head, larger hands and feet, and less numerous maxillary teeth, as well as by its spotted ventral color pattern; and from *B. altamazonica* by its broader head, larger hands and feet, and spotted ventral color pattern. *Bolitoglossa equatoriana* is distinguished from all other Panamanian and South American species of *Bolitoglossa* by the combination of its extensively webbed hands and feet, coloration, and its size and dentitional features (Table 1).

Description of Holotype.—Adult female with moderately short, relatively broad, truncated snout. Nostrils rather small, nasolabial protuberances moderately developed. Slightly arched canthus rostralis of moderate length. Head of moderate width (SL 6.4 times head width) and length (SL 4.3 times snout-gular fold length). Deep groove below eye extends for almost full length of orbit, following curvature of eye, but does not communicate with lip. Moderately large eyes only slightly protuberant. Well-defined postorbital groove extends posteriorly from eye as shallow depression for 2.8 mm; then sharply ventrad at level of posterior end of mandible and across gular area as nuchal groove, parallel to, and 5.1 mm anterior to sharply defined gular fold. Vomerine teeth number 11, arranged in single rows that extend to center or to lateral margin of internal nares. Slightly arched rows extend nearly to midline on palate, but have no posterior extension. Small maxillary teeth number 48; extending to point about one-half through eye. Three premaxillary teeth. Relatively short tail (0.86 times SL) is laterally compressed, with strong basal constriction. Postiliac glands not evident. Limbs are of moderate length (limb interval 3); SL 4.4 times right forelimb, 4.4 times right hind limb, and 10.2 times right foot width. Webbing of hands and feet extensive, moderately thick. Finger and toe tips, especially of third digits, protrude substantially from webbed pad. Tips of third fingers and toes pointed, others rounded. No subterminal pads. Hands and feet moderately large. Fingers, in order of decreasing length, are 3, 4, 2, 1; toes, in order of decreasing length, are 3, 4, 2, 5, 1.

Measurements (in mm) are as follows: Head width, 9.1; snout to gular fold (head length), 13.4; head depth at posterior angle of jaw, 4.6; eyelid length, 3.8; eyelid width, 2.0; anterior rim of orbit to snout, 3.7; horizontal orbital diameter, 2.2; interorbital distance, 3.3; distance between vomerine teeth and parasphenoid tooth patch, 0.8; snout to forelimb, 16.7; distance separating internal nares, 2.4; distance separating external nares, 3.1; snout projection beyond mandible, 1.0; snout to posterior angle of vent (SL), 57.9; snout to anterior angle of vent, 53.4; axilla to groin, 32.8; tail length, 49.6; tail width at base, 3.7; tail depth at base, 4.4; forelimb length, 13.2; hind limb length, 13.2; width of right hand, 4.2; width of right foot, 5.7.

Coloration of Holotype (in alcohol).—The dorsal color consists of a distinct though irregular beige to gray dorsal band divided down the middle by a dark blackish brown thin stripe of ground color. The ground color of the lateral surfaces is much darker than that of the dorsal and ventral surfaces. The venter appears somewhat light because of the many tiny bluish white cells covering much of the blackish ground color. The tiny spots are grouped together as patches on the last three-fourths of the tail venter. The front of the head is a medium brown and the back of the head is covered by the anterior end of the dorsal band. The hind limbs have a considerable amount of beige and gray to brown mottling dorsally, but the dorsal area of the front limbs is mostly a blackish brown ground color. The inside half of the hands and feet are covered dorsally with many tiny light colored spots overlying the ground color. The limbs all have some of these spots ventrally but the ventral surfaces of the hands and feet are an immaculate gray-black.

Variation.—Pertinent data are presented in Table 1. The female holotype is considerably larger (57.9 mm SL) than the largest paratype (45.9 mm SL). Most of the paratypes are adult females except for two males and four juveniles. Standard length is from 5.7 to 6.4 (mean 6.1) times head width in the entire sample. Limb length is somewhat variable in the series, and the holotype has relatively broad hands and feet (SL 10.2 times right foot width in holotype, 9.1 to 11.2, mean 10.4 in paratypes). The holotype has the third longest tail (0.86 times SL, versus 0.58 to 0.89, mean 0.79 in paratypes).

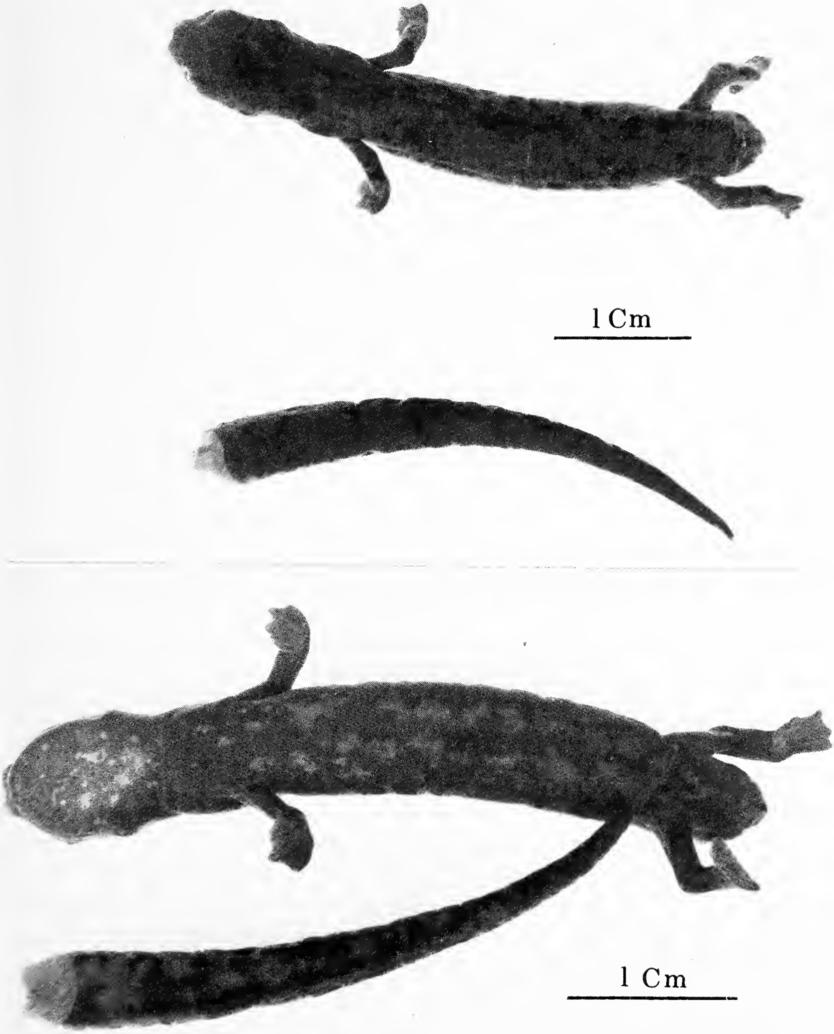


FIGURE 7. Dorsal and ventral views of a paratype of *Bolitoglossa equatoriana* (UIMNH 54296).

Digital tips of the holotype are like most of the paratypes. The tip of digit three is pointed with the other digits having more rounded tips. There is considerable variation in dorsal coloration. The holotype has a distinct though irregular beige to gray dorsal band divided by a dark blackish brown stripe of ground color down the middle; one other specimen has a uniform broad beige dorsal band; six specimens have weak or partial dorsal bands of beige to gray; two have a few dorsal light brown patches; two are uniform blackish brown dorsally. The type series varies in ventral coloration as follows: five specimens have a few to moderate numbers of mostly small, bluish silver to white spots or patches; thirteen have an irregular row of moderate-sized, bluish silver to white patches on either side of the midline (see paratype ventral view, Fig. 7); and the holotype is covered ventrally by hundreds of tiny iridophores.

Osteology.—All information has been derived from stereoscopic radiographs of the type series. The skull is well ossified and the bones are well articulated. The premaxilla is small and slender but frontal processes may be well developed. The frontal processes of UIMNH 54296 are slender and are not expanded at their tips. Those of some other specimens are expanded at their tips. The processes are separated for their entire length in all specimens. The large, protuberant nasals have a strong, extensive articulation with the maxillae. Prefrontals are definitely present in some individuals but absent in others. Vomers are well separated for their entire lengths. Preorbital processes of the vomers extend laterally well beyond the limits of the internal nares. Maxillae are of moderate size and extend about to the posterior margin of the eyeball. There is no stilus on the operculum. All but the last trunk vertebrae bear ribs. There are one cervical, fourteen trunk, one sacral, two caudosacral and from 23 to 30 caudal vertebrae in those specimens with complete tails. The long, stout transverse processes of the first caudosacral vertebra are directed nearly perpendicularly to the body axis, but with a slight posterior slant. The shorter processes on the second caudosacral vertebra slant in an anterior direction. Very long, unbranched processes are present on the first caudal vertebra, and these slant sharply toward the head. They do not cross the processes of the second caudosacral vertebra even though they extend in front of the base of the latter. Processes of succeeding vertebrae are progressively smaller. They lie at the anterior end of each vertebra and slant anteriorly. Caudal transverse processes are visible as far as the seventeenth vertebra in one adult, but they are small and highly variable in degree of development past the tenth vertebra. In the basal part of the tail the vertebrae increase in length, and the fourth and fifth caudal are as long as the longest (anterior two to six) trunk vertebrae in some, but a little shorter in others. About the thirteenth caudal is the first that is shorter than the three vertebrae immediately behind the sacrum. Vertebrae are progressively shorter from that point to the tail tip. No tibial spurs are present. Phalangeal formulae in some individuals are 1, 2, 3, 2; 1, 2, 3, 3, 2. A tendency toward phalangeal reduction is apparent and formulae may be 1, 2, 3, 1 and 1, 2, 3, 2, 1 in extreme instances. Terminal phalanges are usually small and short, often being broader than long. They are rounded at their tips, and usually neither pointed nor expanded. Penultimate phalanges of the longest digits are small and often broader than long. Distance between the bony parts equals or surpasses the length of the penultimate phalanges in the longest digits. Terminal phalanges are shorter and smaller than penultimate ones in most instances. Metapodials are flat and broad, with some lateral bony growth extending into the fleshy web.

Remarks.—Found between 7:30 and 9:30 PM, from 0.5 to 2 m (1½ to 6½ ft) above the ground on broad leaves, palm leaves and stems, along the stream banks in secondary growth, secondary-primary border, and in agricul-

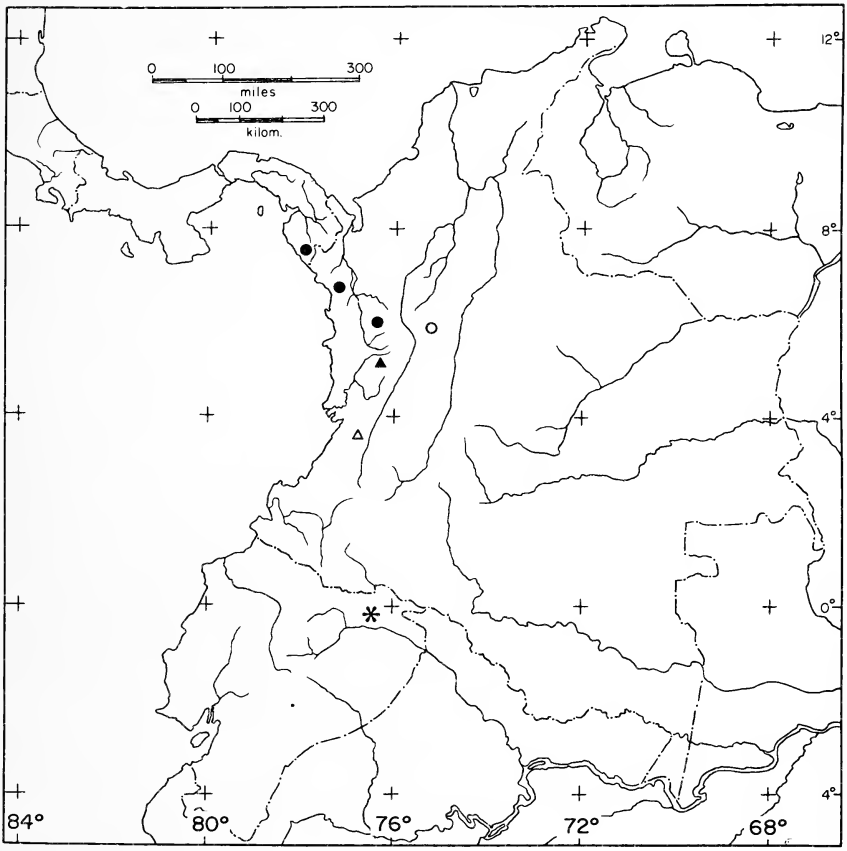


FIGURE 8. Distribution of five new species of *Bolitoglossa* in Panamá, Colombia, and Ecuador. Symbols: ● *Bolitoglossa medemi*; ○ *B. ramosi*; ▲ *B. silverstonei*; △ *B. walkeri*; * *B. equatoriana*.

tural clearings. It occurs in sympatry with the smaller and more slender *B. peruviana.*

Range.—Known only from the type locality in the Amazonian lowlands of Ecuador (Fig. 8).

DISCUSSION

In 1963 we discussed the relationships of the South American members of *Bolitoglossa,* and our views have recently been elaborated (Wake and Brame, 1966; Wake, Brame and Myers, 1970). The continued discovery of new populations and undescribed species points up the tentative nature of such discussions and the need for continuing revision. Nevertheless, it is useful to present our current views concerning species relationships, even in a developmental state, for they may aid in planning research projects and in zoogeographic work. Small samples and incomplete knowledge make full documentation impossible. However, we can present the basis for our character analysis and the kind of reasoning used.

Characters subject to interspecific variation are divided into discrete states for analytical purposes. Direction of character state change is determined in several instances. Usually this is based on out-group comparisons, with conditions that are present in more generalized relatives (such as the extratropical plethodontids) considered to be primitive. In some instances it is possible to identify one or more highly specialized states, but operationally the primitive state is identified by following the trend in specialization back to the simplest or most generalized condition by phenetic methods. Correlation of character state trends with other trends, for example, geographic patterns, is sometimes used in initial analysis. We have come to expect more ancestral states among northern and upland members of a given group, and derived states in species that are southern, lowland, or both. Finally, as a working hypothesis we expect the more derived state of a given character to be present in species in which derived states of many other characters are present. This last criterion involves some circularity in reasoning, and is used only tentatively and when other criteria are not applicable. Our knowledge of the neotropical salamanders is not sufficient to detect all of the parallelism and convergence which we suspect are present, and the fact that few characters are used in our analysis increases our chance of error. Hopefully future work will improve our ability to detect these phenomena, and will also increase the number of characters, thus diminishing the chance of error. Larger series will permit quantification and the use of continuously variable characters.

Characters:

Size.—Average adult size is small (ca. 40 mm SL), moderate (50–60 mm SL), or large (ca. 70 mm SL). Intermediate conditions (e.g., moderately small) are recognized. Moderate size is characteristic of many generalized neotropical salamanders, and is probably close to the ancestral condition.

Either extreme is considered derived, but examples of parallelism are suspected. The character has low reliability on a genus-wide basis, but may be of use within a species group established on other grounds.

Structure of Hands and Feet.—This is one of the most complex and useful sets of characters. Much information can be derived from detailed consideration of both external and internal structure of the appendages. Categories of foot-webbing have been outlined previously (Wake and Brame, 1969). The primitive hand and foot has little webbing, large and discrete digits and a full complement of phalangeal and mesopodial elements. Terminal phalanges are primitively large and well developed, and cutaneous subterminal pads are well developed. Derived characters include increase in webbing, decrease in number and size of phalangeal and mesopodial elements (through loss and fusions) and loss of digital integrity. Many types of reduction trends, all considered to be derived, are found. These include reduction in size, or loss, of the subterminal pads; reduction in size and degree of development of certain phalanges, for example, the terminals; reduction in total phalangeal bone relative to metapodial bone; disproportionate digital reduction, for example the central relative to the first digit. Also important are the shape of the toe tips, the cutaneous outline, the degree of flattening, and the proportions of limbs, feet and digits.

Numbers of Maxillary and Vomerine Teeth.—Numbers of maxillary teeth in adults are low (mean 0–30), moderate (30–60), or high (above 60). Similar categories for vomerine teeth in adults are low (0–20), moderate (20–30), and high (above 30). Moderate numbers characterize generalized relatives and are considered ancestral; both extremes are derived. Teeth increase in number with increasing size, but at different rates in different species. The values given here are not absolutes, but must be considered relative to size of the species. Thus the number of teeth in adults of a small species may be considered to be high, while the same number for a large species might be considered moderate or even low. Eventually we hope to deal with such ontogenetically variable characters in a more satisfactory manner.

Head Width.—Heads are narrow (greater than 6.7 times SL), moderate (6.3–6.6), or broad (less than 6.3). The character must be used with caution, since the proportion changes with age and size, to a degree. Moderate heads are closest to the ancestral condition and either extreme is considered to be derived.

Coloration.—We are unable to break the color continuum into discrete states. Nevertheless, certain features, such as unusual pigmentation, bands, stripes, spotting and streaking patterns, etc., are frequently used when comparing species within groups.

Behavioral Attributes.—Terrestrial habits are considered to be primitive for *Bolitoglossa*. Arboreal habits, varying from a tendency toward arboreality to complete arboreality, are considered to be derived.

Comparative Osteology.—Large numbers of osteological features have potential value in systematic work (see Wake, 1966), but unfortunately the small samples available for most South American species preclude extensive use of such characters. In general, any reduction, fusion, loss or elaboration of the presumed ancestral condition is considered derived. Osteological features that are used for these species include presence or absence of prefrontal bones and tibial spurs, shape of the nasals, premaxillae, maxillae, and vomers, and arrangement of the transverse processes of the caudosacral and caudal vertebrae. Features associated with the hands and feet have been discussed above.

Certain other characters are used within species groups for the purposes of comparing close relatives in some detail. These include some relatively subjective features, such as snout shape and degree of protuberance of the eyes, as well as proportional relationships, such as relative leg, tail, and head lengths.

Most characters have been used in a phenetic manner, and those species which have high similarity are considered to be more closely related than those with low similarity. All of the following groups have been recognized on the basis of total similarity, with group borders recognized by discontinuities. In a fluid situation, such as obtains in the genus *Bolitoglossa* in South America, undescribed species might easily fill one of these discontinuities, necessitating changes in this arrangement in the future. Within the species groups, attention is focused on direction of change in characters, and relative degree of derivation of the various species. Attention is also given to the degree of derivation of one group relative to others.

The genus *Bolitoglossa* is by far the largest in the Order Caudata, with over 60 species. It is convenient to recognize informal species groups, which in turn form major assemblages. The species groups are not of equivalent rank, but are comprised of from one to many species. Most have discrete geographic patterns, and close relatives are not usually sympatric. Many of the species groups appear to have resulted from the fragmentation and diversification of what once were more or less continuously distributed populations. This pattern is apparent in the *helmrichi* group of Nuclear Central America (Wake and Brame, 1969) and in the *adspersa* group of northern South America (Brame and Wake, 1963; Wake, Brame and Myers, 1970). Because of our fragmentary knowledge of South American species we defer characterization of these groups to a later date.

The following species groups and subgroups occur in South America and adjacent Panamá:

A. The *adspersa* group (subgroup 1. *hypacra, adspersa, vallecula, savagei, taylori, borburata, orestes;* subgroup 2. *palmata;* subgroup 3. *nicefori, capitana, pandi*).
B. The *sima* group (*sima, chica, biseriata, silverstonei*).
C. The *medemi* group (*medemi, ramosi, walkeri, equatoriana*).

D. The *altamazonica* group (*altamazonica, peruviana*).
E. The *phalarosoma* group (*phalarosoma*).

The major departures from our arrangement of 1963 are: 1) the description of *B. taylori* and its addition to the *adspersa* group; 2) the dissolution of the *palmata* group and the assignment of *B. orestes* and *B. palmata* to different subgroups of the *adspersa* group; 3) the division of the *altamazonica* group and the uniting of the coastal species (*B. sima, B. chica*) with *B. biseriata,* formerly of the *adspersa* group, to form the *sima* group; 4) the description of *B. silverstonei* as a member of the *sima* group; 5) the description of *B. ramosi, B. medemi, B. walkeri,* and *B. equatoriana,* members of the *medemi* group.

The major division is between the relatively primitive *adspersa* group and the other, more derived groups. The *sima* and *altamazonica* groups share numerous derived features in proportions and foot structure, all perhaps related to lowland, arboreal existence. They are separated by coloration and osteological differences. The *medemi* group is more similar to these two groups than to any other, although it also has some similarity in coloration, proportions and foot structure to *B. phalarosoma.* The *medemi* group is the only one of the four derived groups that contains some relatively primitive, upland species. These species have slight similarities to members of the *adspersa* group, but such species as *B. biseriata* also are similar to members of the *adspersa* group in some features. The *adspersa* group contains the most generalized South American species (*B. hypacra, B. vallecula, B. adspersa*) which resemble highland Middle American species (*B. marmorea, B. cerroensis*) in many features, mostly primitive states. The *adspersa* group contains several highly derived species, both in the lowlands (*B. borburata, B. capitana*) and the highlands (*B. orestes, B. palmata*).

The revised organizational scheme for South American species presented here is based in large part on our expanded knowledge of many species as the result of recent collection. Since our last survey of South American salamanders we have seen, in addition to specimens already reported, good series of specimens that were living, preserved, or both, of the following species: *B. altamazonica, B. peruviana, B. sima, B. chica, B. vallecula, B. adspersa, B. orestes, B. savagei,* and *B. biseriata.* Additionally we have seen a few recently collected specimens of *B. phalarosoma* and both living and preserved specimens of *B. capitana.* Recently many specimens of *B. hypacra* and *B. nicefori,* previously known from their holotypes, have been collected, and living and preserved specimens have been studied. Species which remain poorly known include *B. palmata* and *B. pandi,* the latter known only from the holotype. Further comments in this paper will be focused on the newly described species and their relatives.

Members of the *sima* group share similarity in size, webbing and other features of their hands and feet, head proportions, and coloration. *Bolitoglossa silverstonei* has more teeth than the other three members of the group, and has a broader foot than either *B. chica* or *B. biseriata.* It is larger than *B.*

chica. In South America the group is restricted to the wet forest west of the Cordillera Occidental, but *B. biseriata* is widely distributed in Panamá. All species of the group are restricted to the lowlands, below 1000 m.

Members of the *medemi* group share similarities in proportions, dentition and coloration. *Bolitoglossa medemi* and *B. ramosi* form one subgroup, and *B. walkeri* and *B. equatoriana* another. The former pair are similarly proportioned and have generally similar color patterns. Both have extensively webbed feet with reduced phalangeal numbers and flattened digits. The feet of *B. ramosi* are smaller and much less well developed than those of *B. medemi*. *Bolitoglossa walkeri* and *B. equatoriana* are somewhat more generalized than the other species pair. *Bolitoglossa walkeri* has the least webbing, the most discrete digits, and the most highly developed phalanges of any species of the group. It has a somewhat narrower head than *B. equatoriana*, and there are some color differences, but otherwise the species are similar. While all members of the *medemi* group are allopatric, only *B. walkeri* lacks sympatric associates. *Bolitoglossa walkeri* and *B. ramosi* occur at about 2000 m elevation, and the other species are lowland forms of the Chocó and the Amazonian basin.

The description of these five species brings the total number of species of *Bolitoglossa* known from South America to 21, and another, *B. taylori*, occurs nearly on the Colombian border in Panamá. Of these, three (*equatoriana, peruviana, altamazonica*) are extensively webbed, lowland Amazonian species, six (*medemi, silverstonei, phalarosoma, biseriata, chica, sima*) are extensively webbed, lowland Chocoan species, and three (*hypacra, vallecula, adspersa*) are generalized, slightly webbed upland species from the Cordillera Occidental, Cordillera Central, and Cordillera Oriental, respectively. The remaining species range from diminutive, specialized highland species (*orestes*) to giant species of intermediate elevation (*capitana*), and the degree of diversity is relatively great. Many species inhabit cloud forest formations, and it is these areas that are likely to produce additional populations. While some of the generalized species are terrestrial, most species are occasionally to almost exclusively arboreal. Species known to occur in bromeliads include *B. nicefori, B. savagei, B. ramosi, B. vallecula, B. borburata,* and *B. walkeri*, and most, if not all, of the lowland species are arboreal.

Recent field work has disclosed that sympatry, unknown in 1963, occurs in the following combinations: *B. medemi-B. phalarosoma, B. vallecula-B. ramosi, B. peruviana-B. equatoriana,* and *B. sima-B. chica*. We can expect future field work to yield much additional information concerning ecology and distribution, and, doubtless, new populations and undescribed species will be found.

The five groups of South American *Bolitoglossa* present a rather broad array of species. The *adspersa* group is diverse and its species are allopatric, distributed broadly across Colombia to Panamá, Venezuela, and Ecuador. The *sima* and *phalarosoma* groups are specialized lowland forms of the wet northwestern forests. The *medemi* group is rather broadly distributed, ecologically and geographically, with species in the uplands in areas of Caribbean and Pacific drainage, in the Chocó, and in the Amazonian Basin. Finally, the *altamazonica* group has the most peripheral distribution within the genus, mostly within the Amazonian Basin.

RESUMEN

En el presente reporte se describen nuevas especies de salamandras pletodóntidas para America del Sur y Panamá. *Bolitoglossa medemi* es una especie de color oscuro con manos y pies grandes y extensivamente palmeados y con la cabeza ancha. Se le conoce en varias localidades en el noroeste de Colombia y en el sudoeste de Panamá, donde se le encuentra entre 50 y 800 m. de elevación. *Bolitoglossa ramosi* es una especie de menor tamaño, de color mas claro, con manos y pies pequeños, pero tambien extensivamente palmeados, y con la cabeza ancha. Esta especie es simpátrica con *Bolitoglossa vallecula* en la Cordillera Central al este de Medellín, Colombia, a altitudes de aproximadamente 1930 m. *Bolitoglossa silverstonei* es una especie delgada, de larga cola y color claro, las manos y los pies son anchos y extensivamente palmeados y la cabeza es moderadamente ancha. Ha sido encontrada solo en una localidad cerca de Quibdo, a una altura de 400 m., en el noroeste de Colombia. *Bolitoglossa walkeri* no tiene las extremidades tan palmeadas y generalmente posee menos dientes maxilares que las otras especies. El color es oscuro en el dorso y claro en el vientre. Se le encuentra a elevaciones de cerca de 2000 m., cerca de Calí, Colombia. *Bolitoglossa equatoriana* tiene extremidades más palmeadas que *B. walkeri,* pero tiene como esta última, un numero bajo de dientes y la misma coloracion. Es simpátrica con *B. peruviana* en localidades de una elevación de aproximadamente 260 m. en la Amazonía ecuatoriana. La descripción de estas nuevas especies permite una reevaluación de las relaciones sistemáticas entre los miembros sudamericanos del género *Bolitoglossa.* Se discuten además los caracteres usados en el análisis sistemático de veintidós especies ye se reconocen cinco grupos de ellas. Los grupos *palmata* y *altamazonica* son divididos. *B. silverstonei* es incluída en el nuevo grupo *sima,* junto con *B. sima, B. chica* y *B. biseriata.* Las otras especies nuevas son los únicos miembros del grupo *medemi.*

LITERATURE CITED

BRAME, A. H., JR., AND D. B. WAKE. 1963. The salamanders of South America. Los Angeles Co. Mus., Contrib. Sci. 69: 1-72.

DUNN, E. R. 1926. The salamanders of the family Plethodontidae. Northampton, Mass. Smith College Publ. 441 p.

ESPINAL, L. S., AND E. MONTENEGRO. 1963. Formaciones Vegetales de Colombia. Instituto Geografico, Bogotá, Colombia, 201 p.

WAKE, D. B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. So. Calif. Acad. Sci., Mem. 4: 1-111.

WAKE, D. B., AND A. H. BRAME, JR. 1966. Notes on South American salamanders of the genus *Bolitoglossa*. Copeia 1966, 360-363.

————. 1969. Systematics and evolution of Neotropical salamanders of the *Bolitoglossa helmrichi* group. Los Angeles Co. Mus., Contrib. Sci. 175: 1-40.

WAKE, D. B., A. H. BRAME, JR., AND C. W. MYERS. 1970. *Bolitoglossa taylori*, a new salamander from cloud forest of the Serranía de Pirre, Eastern Panamá. Amer. Mus. Nov. 2430: 1-18.

Accepted for publication August 30, 1971

Printed in Los Angeles, California by Continental Graphics

NUMBER 220
FEBRUARY 8, 1972

A SYNOPSIS OF THE BURROWING LAND CRABS OF THE WORLD and LIST OF THEIR ARTHROPOD SYMBIONTS AND BURROW ASSOCIATES

By DONALD B. BRIGHT AND CHARLES L. HOGUE

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1964 AIBS Style Manual for Biological Journals is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1964 AIBS Style Manual for Biological Journals in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Changes in the manuscript after galley proof will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

A SYNOPSIS OF THE BURROWING LAND CRABS OF THE WORLD AND LIST OF THEIR ARTHROPOD SYMBIONTS AND BURROW ASSOCIATES

By Donald B. Bright[1] and Charles L. Hogue[2]

Abstract: The burrowing land crabs of the world are defined as an ecological group and the burrow or crabhole faunal community is recognized and discussed as such.

Introductory remarks on terminology, relationship of the crabhole habitat to other habitat types, general physical nature of the crabhole, and the major ecological structure of the community as now known are presented. The remainder of the paper consists of two parts: 1) A list of all the species of borrowing land crabs of the world, including notations on distribution, recognition, and ecology. Twenty-four species in the genera *Sesarma, Ocypode, Uca, Ucides, Gecarcoidea, Cardisoma,* and *Gecarcinus* are given. 2) A list of all published records of arthropods found in crab burrows either associated with the crab as a burrow coinhabitant or having symbiotic relationships with it. The vast majority of these are insects, primarily mosquitoes, of which 140 species are noted. For each burrow associate or symbiont, the distribution, recorded crab host, type of relationship (specific, semispecific, transient or accidental) are given.

INTRODUCTION

The present paper represents a literature survey to establish the present state of knowledge on the unique ecological relationship existing between burrowing land crabs and a variety of associated organisms. From our own field studies it is evident that there are many unrecorded species of arthropods occurring in crabholes and undescribed ecological phenomena to be discovered and analyzed. We hope that from this beginning other workers will recognize the land crab burrow as a special habitat and respond to the need for inquiring further into its natural history.

Published data on land crabs consists primarily of species accounts and selected aspects of behavior and natural history; no broad coverage of the basic ecology of any species exists. Likewise, with regard to the burrow associates, no general ecological treatment is available, only taxonomic notes and fragmentary collecting data.

We are presently engaged in a project to study the biology of land crabs and their burrow associates (Hogue and Bright, 1969). One preliminary field survey in Kenya, East Africa (Hogue and Bright, 1971) has been reported. Field studies in Costa Rica, Baja California, Pacific mainland

---

[1] Donald B. Bright, Associate Professor of Biology, California State Colege, Fullerton, California 92631.

[2] Charles L. Hogue, Senior Curator of Entomology, Natural History Museum of Los Angeles County, Los Angeles, California 90007.

Mexico, Panama, Peru, Ecuador, Western Caribbean (Islas San Andrés and Providencia), and Australia will be reported upon in forthcoming papers. All specimens and data collected on this project are given the code LCBA (Land Crab Burrow Associates). Entomological materials are deposited in the Los Angeles County Museum of Natural History, and crustaceans in the Department of Biology, California State College, Fullerton.

DEFINITIONS

Since we make use of terms and concepts originally devised for very different community types, we find it necessary to define certain of our present usages:

Crabhole and crab burrow: Used synonymously.

Burrowing land crab: This term refers to a group of tropical species which dig well-defined burrows above the normal flooding and flushing action of the tides. These species belong to the families Gecarcinidae, Ocypodidae, and Grapsidae. The family Coenobitidae is excluded since the terrestrial hermit crabs are non-burrowers. Thus our attention will be directed to the following taxa:

- Gecarcinidae (all 3 genera of the family)
  - *Gecarcoidea*, all species
  - *Cardisoma*, all species
  - *Gecarcinus*, all species
- Grapsidae (only 1 of 26 genera in the family)
  - *Sesarma*, certain species only
- Ocypodidae (3 of 4 genera in the family)
  - *Ocypode*, certain species only
  - *Uca*, certain species only
  - *Ucides*, certain species only

Several species of land dwelling lobsters (e.g., *Thalassina*), crayfish (*Procambarus, Cambarus*) and freshwater crabs (*Sudanonautes*) also construct burrows supporting an associated fauna. Though we consider these outside our specified limits with burrowing land crabs (and they are omitted from the section on burrowing land crabs), we mention them in our survey of associates because they occur sympatrically with burrowing land crabs and confusion frequently arises in identifying the true owner of a burrow (Scharff and Tweedie, 1942).

Ecological structure of crabhole community: All of the organisms found in the crabhole and associated ecologically with land crabs we refer to as the crabhole community. It is presently possible to evaluate only the gross community structure of arthropod symbionts and burrow associates of land crabs in terms of the general levels of interrelationships and the most conspicuous variations in niches displayed by the arthropod fraction. By niche we mean the total ecological role a species plays in the community, both in regard to its habitual location of occurrence (place niche–microhabitat) and its inter-dependency with other members of the community (functional niche).

Within the crabhole community we find two general levels of interspecific reaction: The first of these, simple *association*, is shown by the assemblage of species whose common occurrence is dictated directly by the spectrum of indigenous limiting factors (physical and biotic) encountered in the crabhole. The second, *symbiosis*, refers to those species not only tied together by these factors but which also depend directly upon some form of intimate (often or usually also involving prolonged physical contact) interaction with one other member of the community, i.e., parasitism or commensalism (no example of mutualism yet having been found). A summary of the general ecological structure of the arthropod fraction of the crabhole community is given in Table 1.

The extent to which a particular organism is dependent on the crabhole as a suitable habitat and to which it is an obligate member of the crabhole community may be further classed:

I. *Specific* (or obligatory)

The species is narrowly adapted to conditions in the crabhole or lives symbiotically with the host or other community member. Such species have specific adaptations to the physical and biological stresses encountered in the burrow (the precise nature of and adaptive significance of which are

TABLE I

SUMMARY OF THE KNOWN ECOLOGICAL STRUCTURE OF THE CRABHOLE COMMUNITY (ARTHROPOD FRACTION)

Level of Interspecies Reaction	Niche		
	Place	Functional	Major Examples
ASSOCIATION	Burrow water	Developing; feeding, breeding, etc.	Immature mosquitoes Diving beetles (*Bidessus*) *Cyclops*
	Burrow chambers and surface of burrow water	Resting, mating, etc.	Adult mosquitoes Adult biting gnats (*Culicoides*)
SYMBIOSIS			
Parasitism	Gill chamber of *Gecarcinus lateralis*	Attaching and feeding	Mite (*Laelaps cancer*)
Commensalism	Peribuccal cavity and renal grooves of *Gecarcinus ruricola*	Attaching to host and feeding on food debris	*Drosophila carcinophila*

presently little known, such as prolonged developmental period, impermeable cuticle, reduced salt absorbing organs, etc.). Examples occur among the following genera: *Deinocerites, Aedes* (*Cancraedes and Geoskusea*), and *Drosophila.*

II. *Semispecific* (or semiobligatory)

The species usually inhabits the crabhole, being adapted at least in part to certain of its conditions but survives well in other habitats. An example is the mosquito *Aedes* (*Skusea*) *pembaensis* which habitually breeds in crabholes but also develops commonly in various other types of coastal ground water accumulations (pools, swamps and even in artificial containers).

III. *Transient* (or facultative)

The species usually inhabits other sites but may take up temporary residence or breed in the crabhole because of its similarity or proximity to the normal habitat. Examples are the many mosquitoes occurring along the seashore such as *Aedes* (*Neomacleaya*) *panayensis* and *Aedes* (*Ochlerotatus*) *taeniorhynchus*; insular treehole breeders, *Aedes* (*Stegomyia*) *polynesiensis*; and indiscriminate breeders, *Culex (Culex) annulirostris.*

IV. *Accidental*

The species is adapted to another habitat and only rarely occurs in and about crabholes for some anomalous reason (e.g., larvae flushed from ground pools during heavy rains, wind blown adults, etc.). For example, adults of *Mansonia* mosquitoes are sometimes found in crabholes but do not develop from larvae and pupae living in the burrow; these mosquitoes require certain aquatic plants to which they attach with special respiratory structures for extracting vascular oxygen. These plants live only in open freshwater pools and ponds.

These four categories of habitat dependence, of course, are provisional. Unfortunately, for no species do we yet know the complete story of its functional niche in the crabhole community.

GENERAL PHYSICAL NATURE OF THE HABITAT

While there is considerable specific variation, in general the land crab burrow is a gently sloping or near vertical tubular excavation ranging from depths of 1.5-3.4 m. The diameter generally is equivalent to the carapace width of the host crab and the depth is determined by the level of the water table.

Normally, the bottom of the burrow is filled with water derived indirectly from ground seepage from nearby sources (streams, estuaries, ponds, open sea, etc.) or directly from rainfall. Thus the water may vary considerably in solute concentrations even from day to day or hour to hour. Like estuarine organisms in general, which are able to accommodate to such changes physiologically, crabhole water dwellers have wide osmoregulatory capacities. Some species, in genera such as *Gecarcinus*, are so well adapted to terrestriality that their burrows often are for physical protection only and penetration to the water table to maintain a supply of water for physiological functions is not necessary. The community of these shallow burrows, lacking the aquatic fraction, is depauperate.

The burrows are located most often in compact alluvial soil well above high tide lines but still close enough to the sea to permit migration for spawning and close enough to a ground water source to maintain a reservoir. Burrows also are often found along large rivers far inland where the fresh water affords the crab's hydrobiotic needs.

LAND CRABS OF THE WORLD

The following genera and species accounts are for those burrowing land crabs listed as hosts in the arthropod portion of this paper or those, based on our field experience, that are likely to be additional hosts.

In several of the species accounts there is question regarding reliable taxonomic and zoogeographic data. This is particularly true for distributional patterns in the Indo-Pacific, e.g., the species of *Cardisoma* and *Sesarma.* (See Tweedie (1950) for a discussion of the problems associated with *Cardisoma.*) Correspondence with a number of workers indicates that revisions are in preparation for *Sesarma, Uca* and *Gecarcinus.* These works should aid future studies on the distribution of land crabs and their burrow associates.

No attempt has been made to provide a complete synonymy. Where there is considerable taxonomic confusion a note to clarify our usage has been included in the species accounts.

In listing the various species we have assumed that the published reports on burrow ownership are correct. Where authors were unable to identify the crustacean but provide descriptions, specific localities and/or habitats, we have sometimes made a provisional determination. It is hoped that in future accounts authors will attempt to determine hosts specifically and include additional remarks on general ecology of the crab and its associates.

The species we define as land crabs are enumerated below followed by a synopsis of important information on each species.

Family: Grapsidae
1. *Sesarma (Sesarma) sulcatum*
2. *Sesarma (Sesarma) meinerti*
3. *Sesarma (Chiromantes) africanum*
4. *Sesarma (Holometopus) ortmanni*
5. *Sesarma (Holometopus) eulimene*

Family: Ocypodidae
6. *Ocypode gaudichaudii*
7. *Ocypode occidentalis*
8. *Ocypode quadrata*
9. *Ocypode ceratophthalma*

10. *Uca pugilator*
11. *Uca subcylindrica*
12. *Uca tangeri*
13. *Ucides cordatus*
14. *Ucides occidentalis*

Family: Gecarcinidae

15. *Gecarcoidea humei*
16. *Cardisoma guanhumi*
17. *Cardisoma crassum*
18. *Cardisoma armatum*
19. *Cardisoma carnifex*
20. *Cardisoma hirtipes*
21. *Gecarcinus planatus*
22. *Gecarcinus ruricola*
23. *Gecarcinus quadratus*
24. *Gecarcinus lateralis*

Family GRAPSIDAE

Genus *Sesarma* Say, 1817

CHARACTERS: Carapace squarish; sides generally straight and parallel; orbits of eye deep, oval and occupy only slightly less than half of the anterior border of the carapace; antennules transverse; epistome well defined; chelipeds thick, and subequal in male, and third pair of legs longest.

DISTRIBUTION: Tropical and subtropical coastal areas of the world.

HABITAT: Coastal marshes, mud flats, banks of drying streams, gravelly mud along lagoons and mangroves.

HABITS: Generally these have well defined burrows which are similar to those of most *Cardisoma* juveniles. These burrows are in muddy, mud-gravel areas extending from the surface down 1 m to the water table. Some do not construct burrows but live under debris (rocks and roots). Most individuals are solitary. In some areas young live in the same burrow with an adult.

REFERENCES[1]: Bott, 1955 (D,T); Campbell, 1967 (D,T); Crane, 1947 (B,D,T,); Crosnier, 1965 (D,T); Gordon, 1934 (D); Macnae, 1966 (B,D); Miers, 1880 (D); Rathbun, 1914 (T); Tesch, 1917 (D,T); Tweedie, 1940 (D,T).

Note: Considerable taxonomic confusion prevails in this taxon, particularly the validity of the subgeneric groupings. Many synonymies are suspected

---

[1] The application of each reference is indicated by a symbol following (T—taxonomy; B—biology, i.e., habits, habitat, life history, physiology; D—distribution; G—general).

because of the inordinate number of species, e.g., 115 in the Indo-Pacific alone. Campbell (1967) and Crosnier (1965) give recent accounts dealing with these problems. Because of the above, some species determinations are questionable.

1. *Sesarma* (*Sesarma*) *sulcatum* Smith, 1870

COLOR: Carapace and legs dark brownish gray; lower portion of male chelae cream yellow; chelae in females cream with a few maroon striations; females with conspicuous yellow line across front.

DISTRIBUTION: Pacific coast of the Americas (San Ignacio Lagoon, Baja California to southern Panama).

HABITAT: Gravelly mud along lagoon shores, tidal marshes, and on the banks of streams and mangroves.

HABITS: They construct straight or slightly sloped burrows or live under debris characteristic of the habitat. Some spend considerable time climbing the branches of marsh plants, e.g., *Sueda, Salicornia* (Baja California) and the roots and pneumatophores of mangroves, e.g., *Rhizophora* and *Avicennia* (Costa Rica and Panama). Individuals are solitary, but in areas where burrow structure is not well developed they tend to occur in groups, e.g., three to six individuals under a rock (Wright, 1966). In drier habitats they commonly use burrows (occupied and unoccupied) of other crabs, e.g., *Cardisoma crassum, Ucides occidentalis* and *Uca* spp. They are often sympatric also with *Goniopsis pulchra.* They are active throughout most of the day (except in drier areas) feeding primarily on plant materials.

COMMON NAMES: Mangrove crab; Marsh crab; Speckled crab.

REFERENCES: Bott, 1955 (D,T); Crane, 1947 (B,D,T,); Garth, 1960 (D); Wright, 1966 (G).

2. *Sesarma* (*Sesarma*) *meinerti* de Man, 1887

COLOR: Carapace black to gray or purple to deep violet, anterior and lateral margin bordered with orange to light yellow; underside a dirty yellow; and chelipeds a striking brilliant red. Cott (1930) gives a good account of this plus a consideration of the theory of warning colors.

DISTRIBUTION: Andamans and Madras, Mozambique, Mauritius, Madagascar; east coast of Africa (south to Port St. John's); across Indo-Pacific to Australia (Cooktown) and north to the Philippines.

HABITAT: Sandy-clay areas and higher, drier, muddy banks associated with estuaries and mangroves.

HABITS: Burrows are well developed and most common in areas where there is dry, relatively hard mud. The burrows are deep and usually extend to the water table. Often the mouth of the burrow has a hood built of mud excavated while enlarging the tunnel or cleaning out. These crabs are retiring, remaining at the mouth of the burrow, and only leave to forage at night. They apparently feed primarily on plant material, but also act as scavengers where they occur in high density. There is no indication of colonialism in areas of high density.

COMMON NAME: Marsh crab?

REFERENCES: Alcock, 1900 (D,T); Chace, 1953 (D,T); Cott, 1930 (G); Crosnier, 1965 (D,T); Hogue & Bright, 1971 (D); Macnae, 1966 (B,D); Millard and Harrison, 1954 (G).

3. *Sesarma (Chiromantes) africanum* H. Milne Edwards, 1837

COLOR: Carapace reddish brown; transverse patches of stiff hairs over carapace and limbs; distal portion of chelae violet-red in color.

DISTRIBUTION: Senegal to Benguela, Angola; also Barbados(?).

HABITAT: Mangroves; salt marshes; and mouths of rivers.

HABITS: Occurs primarily in dense, well shaded areas of mangroves. Juveniles and adults are conspicuous, climbing over vegetation, since they have no burrows or only very small ones. Typically, when threatened, they hide under debris and roots. In open localities, with soft mud, they construct shallow (.3-.6 m) individual burrows. These burrows are not known to intersect. They are presumed to be scavengers.

COMMON NAME: Hairy lagoon crab.

REFERENCE: Rathbun, 1921 (D,T).

4. *Sesarma (Holometopus) ortmanni* Crosnier, 1965

COLOR: Carapace greenish brown and heavily calcified; chelae a dull to bright orange.

DISTRIBUTION: East coast of Africa; Madagascar.

HABITAT: Muddy soil along the margins of mangroves.

HABITS: Constructs shallow burrows among exposed pneumatophores of the mangrove, *Avicennia.*

COMMON NAME: None recorded.

REFERENCES: Crosnier, 1965 (D,T); Macnae and Kalk, 1969 (B,D).

5. *Sesarma (Holometopus) eulimene* de Man, 1898

COLOR: Carapace dull brown and with conspicuous pits; underside a dirty white, chelae of male bright orange-red.

DISTRIBUTION: East coast of Africa from Malindi to Durban.

HABITAT: Mud areas of salt marshes and mangroves.

HABITS: Poorly known. Burrows generally well developed, but shallow, and often associated with the pneumatophores of mangroves. Millard and Harrison (1954) indicate extensive distribution of this species in Richards Bay, South Africa, in areas along the mangrove margins where there is deep, soft mud covered at least once per day by tidal flux.

COMMON NAME: None recorded.

REFERENCES: Barnard, 1947 (D,T), 1950 (D,T); Crosnier, 1965 (D,T); Macnae and Kalk, 1969 (B,D); Millard and Harrison, 1954 (G).

Family OCYPODIDAE

Genus *Ocypode* Fabricius, 1798

CHARACTERS: Carapace deep, somewhat broader than long but generally squarish; orbits large and divided into two chambers; eye stalk often prolonged as a style; antennae small and rudimentary; epistome small; chelipeds shorter than legs and subequal; 4th pair of legs shorter and thinner than others.

DISTRIBUTION: Tropical and subtropical coast of American Atlantic (Rhode Island to Brazil), Mediterranean Sea, coasts of Africa, Red Sea, Indo-Pacific, and eastern Pacific (Turtle Bay, Baja California to Chile).

HABITAT: Sandy beaches with tidal surge; rubble flats; sand-mud areas adjacent to mangrove swamps.

HABITS: Construct simple to complex burrows in the soft substratum of the habitat. In several areas species occur sympatrically but generally are distinguishable on the basis of feeding habits or the presence-absence-degree of development of the style over the eye.

REFERENCES: Alcock, 1900 (D,T); Chace and Hobbs, 1969 (G); Crane, 1941b (B); Garth, 1960 (D); Rathbun, 1918 (D,T); Tweedie, 1950 (D,T).

6. *Ocypode gaudichaudii* H. Milne Edwards & Lucas, 1843

COLOR: Highly variable, coral red to dark brown. Individual color associated with size, sex and the color of substratum of the habitat.

DISTRIBUTION: Pacific coasts of America. Gulf of Fonseca, El Salvador, to Chile; Galapagos Islands.

HABITAT: Common on sandy beaches of protected bays; occasionally on exposed sandy areas when the surge is not high; also occurs along the shores of lagoons.

HABITS: Burrows highly variable; Crane (1941) indicates three types: 1) shallow, simple, oblique; 2) straight with a right angle at 1-3 m depth; and 3) straight for 15-20 cm then extending downward in a gradual spiral. The second type is most common in the center of the range of distribution. All are diurnal and most active following high tide and before flooding midtide. Occasionally occurs sympatrically with *O. occidentalis.* These two species are distinguishable by: 1) *O. gaudichaudii*: carapace length of 17 mm or more and with well developed ocular styles; actively manipulate the substratum feeding on microscopic organic matter (similar to several species of *Uca*); 2) *O. occidentalis*: no ocular style; they are confirmed predators and/or scavengers.

COMMON NAMES: Cart-driver; Carretero (Peru).

REFERENCES: Bott, 1955 (D,T); Crane, 1941b (B); Garth, 1948 (D,T); Rathbun, 1918 (D,T).

7. *Ocypode occidentalis* Stimpson, 1862

COLOR: Upper surface of body and legs generally darkish gray with white marbling. Manus of chelipeds, tips of walking legs and underside of body cream white. Colors tend to vary with substratum except where sand is volcanic (dark black). These crabs are, due to color, conspicuous when found on light colored or dry sand.

DISTRIBUTION: Turtle Bay, Baja California to Ancon, Peru.

HABITAT: Sandy surge-beaten beaches; sandy-silt areas adjacent to rivers where water flow is fairly rapid, e.g., Playas del Coco, Costa Rica.

HABITS: Distinguishable from *O. gaudichaudii* by absence of ocular styles. Burrows similar to common mode for *O. gaudichaudii.* Completely nocturnal in habits except when very young (see remarks in discussion of *O. gaudichaudii*). They are scavengers and their rapid movements when disturbed contribute to their common name, ghost crab. Feeding begins shortly after onset of ebb until about mid-flood tide. Activity greatest during ebbing of tide and at slack water.

COMMON NAME: Ghost crab.

REFERENCES: Bott, 1955 (D,T); Crane, 1941b (B); Garth, 1960 (D); Rathbun, 1918 (D,T).

8. *Ocypode quadrata* (Fabricius, 1787)

COLOR: Upper surface white with small black spots or generally a pale yellow or a grayish white or a speckled brown. Many show a degree of iridescence along the outer areas of the carapace. The general color pattern is apparently associated with the color of the substratum of the habitat, e.g., dark brown at Tortuguero, Costa Rica, while pale yellow at Punta Cahuita, Costa Rica. Chace and Hobbs (1969) give a detailed account of the two color phases found on Dominica.

DISTRIBUTION: Atlantic coasts of America. Rhode Island to Estado do Santa Catharina, Brazil, including most of the islands in the greater and lesser Antilles.

HABITAT: Sandy beach areas from upper tidal level to well beyond supralittoral area. Distance from sea generally associated with distribution of same and associated vegetation.

HABITS: Burrows deep, .45-.75 m. Chace and Hobbs (1969) note two types of burrows: 1) vertical or nearly so; and 2) U-shaped. Throughout most of Central America, the U-shaped are most common with the bottom of the U about .45 m. Burrow construction is initiated by a general scratching using the chelipeds followed by removal of sand for the entrance using the dactyli of the walking legs. Once the burrow is sufficiently deep, sand is then transported in either the right or left cheliped to the surface and then dumped, or it may be tossed out of the burrow using either cheliped. These crabs are scavengers and are probably a geminate species of *O. occidentalis* in the Pacific.

COMMON NAME: Ghost crab. (In the past also called a sand crab, but this name is more commonly applied to members of the unrelated genus *Emerita.*)

REFERENCES: Bott, 1955 (D,T); Chace and Hobbs, 1969 (G); Chace and Holthuis, 1948 (T); Pearse, 1916 (G); Rathbun, 1918 (D,T), 1933 (D,T).

Note: This has until recently been cited by many authors as *O. albicans* Latreille, 1802 (see Chace and Hobbs, 1969).

9. *Ocypode ceratophthalma* (Pallas, 1772)

COLOR: Generally the dorsal appearance is from sage green and yellow to grayish white. Tweedie (1950) gives the color for those found on the Cocos-Keeling Islands as uniform gray, but sometimes olive, and with a splash of yellow on the chelae. The color is highly variable, and associated with the character of the substratum (see Green (1964) for discussion of color changes in Hawaiian forms).

DISTRIBUTION: East coast of Africa (Port St. John), Red Sea, Indo-Pacific North to Kii Peninsula, Japan, including many islands (Mauritius, Maldive and Laccadive Islands, Caroline and Marshall Islands, Tuamotu Islands, Guam and Hawaiian Islands).

HABITAT: Sandy beaches.

HABITS: Burrows are common from the high tide mark to 6-10 m above; less frequently they occur in areas beyond the edge of the sea. They have also been reported along the margins of lagoons. Burrows are generally 37-50 cm deep. In those sites affected by tidal flux the crabs emerge from their burrows during the ebbing of the tide to feed. They are scavengers feeding on debris deposited by the tidal exchange; in the areas above the tidal influence they feed on small organisms, e.g., crickets (Gressitt, 1954). Well defined ocular styles are present in adults of this species.

COMMON NAMES: Ghost crab; Kepiting Mata Panjang (Longeyed crab) (Christmas Island, Indian Ocean).

REFERENCES: Alcock, 1900 (D,T); Barnard, 1950 (D,T); Borradaile, 1902 (B); Dakin et al., 1952 (G); Day et al., 1954 (B,D); George and Knott, 1963 (D,T); Gordon, 1934 (D); Green, 1964 (B); Holthuis, 1953 (D); Miers, 1880 (D); Millard and Harrison, 1954 (G); Sakai, 1940 (D); Tesch, 1918 (D,T); Tweedie, 1950 (D,T); Ward, 1934 (D).

Genus *Uca* Leach, 1814

CHARACTERS: Carapace deep, somewhat broader than long and with antero-lateral area pronounced and/or projected, orbits deep and oblique; antennae large and pronounced; epistome short and distinct; chelipeds of males extraordinarily unequal and large while in female equal and small; ambulatory legs longer than small cheliped of male and both chelipeds of female, last pair of ambulatory legs shorter than rest.

DISTRIBUTION: American Atlantic (Boston to Uruguay), Mediterranean, west coast of Africa (Portugal to Angola), east coast of Africa to Indo-Pacific, including Maury Islands, and eastern Pacific (British Columbia to Valparaiso, Chile).

HABITAT: Associated with a wide variety of mud-sand habitats, e.g., clay tidal flats, salt marshes, mangroves, low tide muddy areas, etc.

HABITS: Most construct well-defined burrows where substratum is moist enough to maintain burrow configuration. Area may be exposed or associated with dense vegetation (e.g., mangroves, *Avicennia*, or pickle weed, *Salicornia*). Many species show a correlation of burrow site with tidal flux whereas others occur widely throughout tidal zone even when burrows may become quite dry. Most species show considerable social behavior. Crane (1941a, 1943b, and 1957) gives a thorough account of display, breeding and relationships of a number of sympatric species of the genus. See Salmon (1965) for an additional account of courtship behavior. There is considerable taxonomic discord associated with this genus due to voids in collections from certain areas and the high degree of variability in color.

REFERENCES: Barnard, 1950 (D,T); Bott, 1954 (D,T); Crane, 1941a (G), b (B), 1943a (D), b (B), 1957 (B); Hagen, 1968 (D); Salmon, 1965 (B); Schmitt, 1921 (D).

10. *Uca pugilator* (Bosc, 1801)

COLOR: Carapace cream white; large cheliped of male buff with apricot at base of movable finger; chelipeds of small males and females white with a grayish cast.

DISTRIBUTION: Boston Harbor, Massachusetts, to Brownsville, Texas.

HABITAT: Sandy areas where sand content is generally more than 40 per cent.

HABITS: They construct well defined, moderately deep burrows showing considerable variation with age and location. See Pearse (1914a) and Dembowski (1925) for details of burrow construction. Feeding, burrow repair-construction and social behavior occur during the low tide period, generally ceasing when the tidal level reaches the burrow entrances; however, some of these events are correlated with sunset and sunrise as well (see Salmon, 1965). This species is restricted by substratum preference. In a typical situation the sand content may increase down a bank from 10 per cent at the top to 60-70 per cent at the low tide level, with the crabs feeding at the lower levels and living near the top. See Teal (1958) for an account of feeding habits as related to sand content.

COMMON NAME: Sand fiddler crab.

REFERENCES: Burkenroad, 1947 (B); Crane, 1943b (B); Dembowski, 1925 (B); Pearse, 1914a (B), b (B); Salmon, 1965 (B); Salmon and Stout, 1962 (B); Teal, 1958 (B).

11. *Uca subcylindrica* (Stimpson, 1859)

COLOR: No record.

DISTRIBUTION: Corpus Christi, Texas to northern Mexico.

HABITAT: Mud-sandy areas in and adjacent to estuarine situations.

HABITS: Burrows are small, slightly twisted, and constructed in loose sandy soil with high moisture content or in muddy areas. Burrows seldom deeper than .75 m. Little other ecological data recorded for this species.

COMMON NAME: Puffed fiddler crab.

REFERENCE: Rathbun, 1918 (D,T).

12. *Uca tangeri* (Eydoux, 1835)

COLOR: Carapace reddish brown to dirty yellow; male large cheliped reddish brown to pale blue; female chelae dirty cream with some pinkish areas.

DISTRIBUTION: Portugal, north and west coasts of Africa to Angola.

HABITAT: Sandy areas adjacent to brackish water; salt marshes; not common on open coasts.

HABITS: Burrows which extend downward for about 30 cm or so are located from the mean tide to highest high tide level. The top of the burrow is generally plugged with 7.5-10 cm of excavated substratum by the time the burrow is covered by the tide. As the tide recedes the plug is removed and the crab emerges to feed, etc. Habits vary from solitary to colonial. In colonial situations, e.g., salt marsh flats, the burrows are still simple, but they often intersect. See Hagen (1961) and Hediger (1934) for additional details.

COMMON NAMES: Fiddler crab; Calling crab.

REFERENCES: Altevogt, 1959 (B), 1962 (B); Barnard, 1950 (D,T); Hagen, 1961 (D), 1962 (B); Hediger, 1933 (B), 1934 (B); Rathbun, 1921 (D,T).

Note: This was described by Eydoux in 1835 as *Gelasimus tangeri,* and is recorded as such by some authors.

Genus *Ucides* Rathbun, 1897

CHARACTERS: Interorbital distance a little more than one-half the greatest width of the carapace; orbits deep but not much larger than the eyes; antennules oblique; epistome small but prominent; legs stout.

DISTRIBUTION: East and west coasts of the Americas.

HABITAT: Common inhabitants of muddy shores and mangrove swamps where there is a moderate degree of tidal flux.

HABITS: Burrows constructed below the highest high tide level most commonly at midtide level so that burrows covered daily by tidal surge. Burrows not uniform, generally shallow, relatively straight, and frequently with multiple entrances; almost always filled with ground water to the level of the burrow mouth. Juveniles occur in dense numbers per unit area within an interchange of intersecting burrows or in burrows of less density per unit area but where the burrow is directly adjacent and/or attached to those of adults.

REFERENCES: Bright, 1966 (G); Rathbun, 1918 (D,T).

Note: Until recently this genus was placed among the members of the family Gecarcinidae but Chace and Hobbs (1969) placed it among the members of the family Ocypodidae.

13. *Ucides cordatus* (Linnaeus, 1763)

COLOR: Carapace pale yellow with cervical groove and urogastric lobe rusty brown; walking legs red-violet; tips of chelae cream. Young with a tendency to have a dark gray area along the median anterior margin of the carapace. Color is variable throughout the range of distribution primarily associated with the nature of the habitat substratum.

DISTRIBUTION: Atlantic coasts of America. Southern Florida (Biscayne Bay) to Santos, Brazil, including the West Indies.

HABITAT: Areas, frequently flooded by tidal surge, in mangroves along mouths of rivers and brackish water marshes adjacent to the sea.

HABITS: This crab constructs burrows in very soft mud in areas where there is an absence of low ground vegetation (shrubs). Primary sites are mangroves with burrows concentrated along the upper edge of distribution of the red mangrove (*Rhizophora mangle*). Burrows are wide, mostly straight and relatively shallow. Young and adults construct their burrows in close proximity. At both ends of the range there is some indication that burrows are shallower and often nothing more than depressions. This is a twin species of *U. occidentalis* in the Pacific.

COMMON NAMES: Pagurus; Kaburi (Cuba); Uçá (Brazil).

REFERENCES: Bott, 1955 (D,T); Bright, 1966 (G); Chace and Hobbs, 1969 (G); Garth, 1960 (D); Manning and Provenzano, 1961 (D); de Oliveira, 1946 (B); Rathbun, 1918 (D,T), 1933 (D,T).

14. *Ucides occidentalis* (Ortmann, 1897)

COLOR: Carapace reddish gray with orange-red on the lateral margin; however, older forms tend to become rust red due to staining from the mud in the burrow. The last three ambulatory legs and most of the chelipeds dark red; dactyli of chelipeds reddish white; underside brownish white. Molt condition not predictable from color change.

DISTRIBUTION: Pacific coast of America (Espíritu Santo Island, Baja California to Rio Tumbes, Peru).

HABITAT: Mud of mangrove areas, mouths of rivers and brackish water marshes.

HABITS: This species maintains burrows in areas which are generally covered by high tide at least once per month. Burrows are most common along the mud-water margin of mangroves; may be associated with salt marsh vegetation, e.g., *Salicornia, Sueda*, etc. Burrows are shallow and often with more than one entrance. Typically, there is a small side chamber or tunnel paralleling the surface just inside the mouth of the burrow. Juveniles are most often found in small pockets connecting to the burrows occupied by the adults. Burrows do not generally extend more than 50 cm below the surface. This is a geminate species of *U. cordatus* which occurs in the Atlantic.

COMMON NAMES: Wide red land crab, Cangrejo amarillo (Peru).

REFERENCES: Bright, 1966 (G); Garth, 1960 (D); Rathbun, 1918 (D,T).

Family GECARCINIDAE

Genus *Gecarcoidea* Milne Edwards, 1837

CHARACTERS: Fronto-orbital border less than half the greatest breadth of carapace; orbits deep; antennae very small and excluded from the orbit; epistome sunken and quite hairy; chelipeds equal or nearly so in both sexes; legs stout.

DISTRIBUTION: Indo-Pacific Islands.

HABITAT: Moist soil or muddy areas in the jungle areas adjacent to the sea.

HABITS: Burrows shallow and not well developed.

REFERENCES: Calman, 1911 (B); Gibson-Hill, 1947 (B); Keilin, 1921 (D); Rathbun, 1918 (D,T); Tweedie, 1947 (D,T); Webb, 1922 (B).

15. *Gecarcoidea humei* (Wood-Mason, 1873)

COLOR: Dorsal surface a relatively uniform red-violet with some indication of red near the base of the chelae; claws white-brown with reddish violet tinge; scars on carapace yellow or yellowish white.

DISTRIBUTION: Indo-Pacific Islands (Nicobars, Andamans, New Britain, Celebes, Christmas (Indian Ocean), Philippines, Loyalties, Formosa, New Guinea, Pulu Weh, and Talauts.

HABITAT: Moist areas along the coasts of islands, typically within the jungle.

HABITS: Burrows not well developed; generally shallow 15-60 cm in length; mostly parallel with the surface; burrows principally for retreat. Found only where there is a constant source of water to keep soil moist. Andrews (1900) gives a good account of selected aspects of the life history of this species. Gibson-Hill (1947) reports extensive migrations to the sea during spawning together with an account of the aspects of development of the young.

COMMON NAME: None recorded.

REFERENCES: Andrews, 1900 (B); Calman, 1909 (B); A. Milne Edwards, 1879 (T); H. Milne Edwards, 1834 (T), 1837 (T); Ortmann, 1894 (D,T); Pocock, 1888 (D); Rathbun, 1918 (D,T); Sakai, 1940 (D); Tweedie, 1947 (D,T), 1954 (B); Wood-Mason, 1873 (T).

Note: This is frequently listed as *Gecarcoidea lalandii* H. Milne Edwards, 1837. The genus was erected by H. Milne Edwards (1837) for *G. lalandii* which was erroneously recorded from Brazil, and then renamed by the same author in 1853 as the genus *Pelocarcinus*. Wood-Mason (1873), de Man (1879), and Pocock (1888) all described this under a number of genera and species. Ortmann (1890) reduced all these species to synonymy with *Gecarcoidea lalandii* except Pocock's *natalis*. Tweedie (1947) gives a good review of this taxonomic snarl and concludes that *G. lalandii* must be regarded as indeterminable on the basis of an incorrect type locality. We use the name *humei* on the advice of Wood-Mason (1873). Tweedie (1947) also supports the position that because these are generally island forms there are several variants which can be recognized as subspecies, e.g., the crab found on Christmas Island (Indian Ocean) is *G. humei natalis* (Pocock).

Genus *Cardisoma* Latreille, 1825

CHARACTERS: Fronto-orbital distance much more than half the greatest width of the carapace; orbits deep with eyes filling half of the orbit; antennules folded; epistome short and well defined; legs stout.

DISTRIBUTION: Tropical America, Cape Verde Islands, west coast of Africa, Indo-Pacific from Port St. Johns, Africa to Hawaiian Islands.

HABITAT: Commonly inhabits muddy shores, mangrove swamps and saline lowland soils near the coast.

HABITS: Constructs well defined deep burrows in soft soils where ground water is available during the dry season. Often they plug the burrow mouth with mud during the dry season to keep the lower portions of the burrow moist. Burrow sites are always above the mean high tide level. They return to the sea to spawn and to introduce the pre-zoea to the required sea water environment. All are primarily herbivorous but feed on carrion also.

REFERENCES: Barnard 1950 (D,T); Behre, 1949 (B); Bright, 1966 (G); Gifford, 1963 (G); Herreid and Gifford, 1963 (B); Holthuis, 1959 (D); Rathbun, 1918 (D,T); Tesch, 1918 (D,T).

16. *Cardisoma guanhumi* Latreille, 1825

COLOR: Carapace deep violet in young, but tends to become bluish gray with age or approach to molt; ambulatory legs deep blue with larger cheliped dirty white. Local variation may be due to the type of soil characteristic of habitat.

DISTRIBUTION: Atlantic coasts of America, central east coast of Florida, Louisiana, Texas to Florianópolis, Brazil, including the West Indies.

HABITAT: Open fields, margins of mangrove swamps, along margins of rivers, in forests, along roads and under houses. In all known situations the soil is saline.

HABITS: All are typically found within a few hundred yards of a brackish or saltwater source. The young are found under debris, e.g., coconut husks, palm fronds, flotsum, etc., directly adjacent to salt water (generally above the highest high tide level) or in the burrows of adults. Adults construct burrows of varying depth and structural complexity, depending upon their age and the location of the burrow with respect to available ground water. Large aggregations of adult crabs are often found in areas where the substratum is soft yet still suitable for burrows, and where there is little ground cover. Although adults occur several hundred meters from the sea, they are most common within about 200 meters of the tidal zone. Inland dwelling individuals migrate to the sea in great numbers during the breeding season to shed their eggs. This is a twin species of *C. crassum* which occurs in the Pacific.

COMMON NAMES: Great land crab; White land crab, Juey, Cangrejo; Guanhumi; Mulatto land crab; Guaiamú, guaraní, guayamu (Brazil).

REFERENCES: Behre, 1949 (B); Bott, 1955 (D,T); Bright, 1966 (G); Chace and Holthuis, 1948 (T); Feliciano, 1962 (B); Gifford, 1963 (G); Herreid, 1963 (B), 1967 (B); Herreid and Gifford, 1963 (B); de Oliveira, 1946 (B); Pearse, 1916 (G); Peyton et al., 1964 (D); Rathbun, 1933 (D,T).

17. *Cardisoma crassum* Smith, 1870

COLOR: Carapace deep blue; dactyli of walking legs red; large cheliped pale yellow to dirty white; underside cream-white.

DISTRIBUTION: Pacific coasts of America. Todos Santos, Baja California to the Rio Chira, Peru.

HABITAT: Open fields, margins of mangrove swamps, along roads and fence-rows, margins of rivers and streams, under houses and in cultivated fields; generally in saline lowland soils near the coast.

HABITS: These show habits similar to those of *C. guanhumi* in areas adjacent to brackish or salt water sources. In contrast to *C. guanhumi* the young construct separate shallow burrows along river banks and edges of mangroves. Adult burrow construction parallels that of *C. guanhumi*. During the dry season, adults with burrows in open, exposed areas close the top of the burrow with a plug of mud. Some reports have indicated that closure of the burrow also occurs prior to the onset of ecdysis (shedding). Adult migrations to the sea during the spawning period are common in Mexico, Costa Rica, Panama, and Ecuador. This is a geminate species of *C. guanhumi* which occurs in the Atlantic.

COMMON NAMES: Mouthless crab, Cangrejo sin boca (Peru), Cajo (Mexico).

REFERENCES: Bott, 1955 (D,T); Bright, 1966 (G); Garth, 1948 (D,T), 1960 (D); Murphy, 1944; Pesta, 1931 (D,T); Rathbun, 1918 (D,T).

18. *Cardisoma armatum* Herklots, 1851

COLOR: Young, newly molted individuals with violaceous carapace; tips of chelae and walking legs bright red; with age and approach to molt carapace turns dirty yellow with occasionally slight reddish spots dorsally.

DISTRIBUTION: Western coast of Africa from St. Louis to Baia dos Tigres, Angola, Africa and Cape Verde Islands.

HABITAT: Moist sandy areas above the mean high tide level; mangroves, mouth of rivers, under houses, in cultivated areas adjacent to permanent sources of brackish or sea water; and inland areas of larger islands.

HABITS: Youngest juveniles are in small depressions or newly dug shallow burrows directly adjacent to water; older juveniles found in smaller compartments within the burrows of adults. Adults construct deep burrows, and often these are part of a large colony where the burrows intersect. Both juveniles and adults are nocturnal scavengers, often moving considerable distance from their burrows to feed on palmnuts, coconuts, dead fish and scraps of vegetation. Spawning activities have not been recorded in the literature for this species.

COMMON NAME: Edible land crab.

REFERENCES: Barnard, 1950 (D,T); Cheesman, 1922 (B), 1923 (B); Dalziel, 1920 (D); Rathbun, 1921 (D,T); Wanson, 1935 (D).

19. *Cardisoma carnifex* (Herbst, 1794)

COLOR: Carapace dark purple; chelipeds light purple to dark cream.

DISTRIBUTION: East coast of Africa, whole of Indo-Pacific, north eastern Australia and north toward Japanese Mainland (Loo Choo), including Mauritius, Madagascar, Andaman Islands, Malay Archipelago, Polynesia and Melanesia.

HABITAT: Common inhabitants of muddy shores, mangrove swamps or Kuli and saline lowland soils near the coast. Not uncommon in the jungle adjacent to the sea. All around the Indian Ocean it is most commonly found between the high tide mark and just beyond the extreme highest high tide line.

HABITS: Constructs well defined burrows in soft soils where ground water is available during the dry season. Habits generally parallel other members of the genus. On coral atolls it is common among coconut husks, under rubble piles and in mixed forest areas adjacent to plantations.

COMMON NAMES: Land crab; Kepiting Balong (Cocos Island), Papaka Tupa (Tuamotu Islands).

REFERENCES: Alcock, 1900 (D,T); Barnard, 1950 (D,T); Borradaile, 1902 (B); Forest and Guinot, 1961 (D); Hogue and Bright, 1971 (B); Holthuis, 1953 (D); Macnae, 1963 (B,D), 1966 (B,D); Miyake, 1939 (D,T); Silas and Sankarankutty, 1960 (B); Stebbing, 1910 (D); Tesch, 1918 (D,T); Tweedie, 1950 (D,T).

Note: Over much of the range this occurs in sympatry with *C. hirtipes* (see Miyake, 1939).

20. *Cardisoma hirtipes* Dana, 1851

COLOR: Carapace generally dark violet and chelae bright cinnamon red. There is considerable color variation throughout the Indo-Pacific, e.g., Tweedie (1947) notes that on Christmas Island (Indian Ocean) the carapace is light bluish gray and the chelae are dirty white.

DISTRIBUTION: Occurs in sympatry with *C. carnifex* from east coast of Africa throughout whole of Indo-Pacific. Miyake (1939) gives a good account of the distinguishing species characteristics.

HABITAT: Moist saline soils; mud banks in the immediate neighborhood of fresh-water. Where soil is dense or crusted they frequently scratch-out a space under a treeroot or rock.

HABITS: Normally the crab digs burrows in the soft mud directly adjacent to streams. The burrows are only 50-75 cm below ground level. Considering our preliminary studies on related species it seems likely that this species can abide in areas where there is more ground water than is characteristic for *C. carnifex.* Perhaps it is the ecological equivalent of the American species of the genus *Ucides.* A few weeks after the onset of the rainy season in January or February spawning occurs. Copulation occurs at the edge of the sea just prior to the time the female sheds the previous batch of eggs. They are primarily plant feeders, occasionally causing crop damage to melons and pumpkins (Esaki, 1940), but in areas associated with human habitation they are carrion feeders as well.

COMMON NAME: Land crab.

REFERENCES: Alcock, 1900 (D,T); Esaki, 1940 (D); Gibson-Hill, 1947 (B); Gordon, 1934 (D); Miyake, 1939 (D,T); Sakai, 1940 (D); Tesch, 1918 (D,T); Tweedie, 1947 (D,T).

Note: Tweedie (1950) restored *Cardisoma frontalis* H. Milne Edwards, 1853, to specific status from synonymy with *Cardisoma hirtipes.* He gives the distribution of *C. frontalis* as Loyalty Islands, northern Daitozima, Japan, and Cocos-Keeling Islands, and further states that examination of series presently considered as *C. hirtipes* would probably result in extension of this distribution. However, until there is an extensive revision of the genus with clarification of the number of island endemics we will herein consider these still to be *C. hirtipes.*

Genus *Gecarcinus* Leach, 1814

CHARACTERS: Fronto-orbital distance half or less than half of the greatest width of the carapace; orbits deep with eyes nearly filling the orbits; antennae very short; epistome linear; legs stout, the second pair being longest.

DISTRIBUTION: Tropical America, Bermudas, Ascension Island, West and South Africa, Australasia.

HABITAT: Drier areas above the tidal margins of mangroves; river mouths and adjacent coastal sandy and saline soil areas.

HABITS: Burrows always shallow and devoid of ground water, except during rain storms. Many utilize debris as a source of protection in lieu of a burrow. In the extreme northern and southern portions of the distribution the burrows are deep 1.2 m and often with mouth plugged during the dry season.

REFERENCES: Bright, 1966 (G); Finnegan, 1931 (D); Garth, 1948 (D,T); Chace and Hobbs, 1969 (G); Villalobos and Cabrera, 1964 (B).

21. *Gecarcinus planatus* Stimpson, 1860

COLOR: Body and legs generally an orange-red; tips of walking legs often dark red; tips of chelae cream with small flecks of brown.

DISTRIBUTION: Pacific coasts of America. Restricted to islands from west coast of Mexico to Colombia.

HABITAT: Rocky areas, under roots and in soft soils above highest high tide mark on slopes up to 120 m, often associated with beach strand vegetation.

HABITS: Adults and older juveniles scratch out shallow burrows under rocks, roots or debris. Burrow serves primarily as a hiding place. Young hide in natural crevices and small spaces providing natural protection. Burrows have no standing water. Newly metamorphosed juveniles hide along the shore under debris, often gregariously. They are nocturnal feeders, and commonly move considerable distance from their burrows. Bold when on feeding excursions, ambling over almost anything in their path, e.g., sleeping scientists, food lockers, young birds, etc. This is a geminate species of *G. ruricola* occurring in the Atlantic.

COMMON NAMES: Island crab; Big red crab; Cangrejo rojo (Panama).

REFERENCES: Garth, 1948 (D,T), 1960 (D); Rathbun, 1918 (D,T).

22. *Gecarcinus ruricola* (Linnaeus, 1758)

COLOR: Body and legs generally black with purplish tinge; small light yellowish spot on the posterior margin of the carapace; last two joints of legs red; red and yellow patch below the orbit of the eye; abdomen light yellow with violet hue; older individuals or those undergoing late preecdysial changes are overall much lighter in color.

DISTRIBUTION: Atlantic coasts of America. Restricted to islands: Bahamas; southern Florida; greater and lesser Antilles; Curaçao, and Cayman Islands.

HABITAT: Low and marshy areas not far from the sea; lower slopes of island mountains up to 500 meters.

HABITS: They hollow out obliquely inclined shallow burrows, which are quite frequently under a tree or the edge of a large rock. After metamorphosis, the young are found in large numbers just above the high tide level, however, very shortly after the second or third molt they move to areas well above the highest high tide. Along the shore edge, they are often found sympatrically with *Gecarcinus lateralis.* On larger islands, e.g., Isla Providencia, Colombia, they are common along mountain slopes and cliffs adjacent to the beach and to heights of 500 meters and as far as a thousand meters from the shore. They are more secretive than most of the gecarcinids. During the rainy season they are reported to move in large numbers to the sea to breed. This is a geminate species of *G. planatus* in the Pacific.

COMMON NAMES: Black crab; Mountain crab; Blue land-crab, Red tourlourou.

REFERENCES: Chace and Hobbs, 1969 (G); Chace and Holthuis, 1948 (T); Rathbun, 1918 (D,T).

23. *Gecarcinus quadratus* Saussure, 1853

COLOR: Carapace brownish red with two white spots in the cardiac region, intestinal region orange-red; large chelipeds with light purple tinge;

merus of maxilliped light yellow; underside sooty white.

DISTRIBUTION: Primarily Pacific coasts of America. (Atlantic side of Colombia). Not known to occur on permanently isolated islands. Acapulco, Mexico to La Libertad, Ecuador; Turbo.

HABITAT: Above the highest tide zones of sandy beaches in moist forest and mangrove areas where there is low growing vegetation or debris.

HABITS: All occur in drier areas directly adjacent to mangroves or the ocean. They are most common along the uppermost areas of sandy beaches from 1.5 - 15 m above the supratidal area where there is a dense covering of debris, e.g., coconut husks and fronds, or low growing beach strand vegetation, e.g., *Ipomoea* (family Convolvulaceae). Burrow construction is correlated with the length of the dry season. Crabs at both extremes of the distribution tend to construct simple burrows, 7-50 cm deep, while at mid-range, burrows are not common. Non-burrowers tend to occupy small depressions under vegetation debris, houses, etc. This is a geminate species of *G. lateralis* in the Atlantic.

COMMON NAMES: Red land crab; Whitespot crab.

REFERENCES: Bright, 1966 (G); Finnegan, 1931 (D); Garth, 1948 (D,T); Pesta, 1931 (D,T).

24. *Gecarcinus lateralis* (Freminville, 1835)

COLOR: Carapace dark red with small white spots just posterior to the eyes and a pair of white spots in the cardiac region; underside cream-white; chelipeds reddish gray; dactyli sooty gray. Pattern of dark red carapace highly variable throughout range of distribution and in distinct (isolated) populations.

DISTRIBUTION: Atlantic coasts of America. Bahamas; Florida Keys; South Padre Island, Texas; Yucatan; to Macuto, Venezuela. Also occurs on islands in the West Indies.

HABITAT: Along the upper dry zone of sandy beaches and adjacent low hills, 6 to 9 m above highest high tide level; associated with a variety of beach strand vegetation, e.g., coconuts, and low growing vines, e.g., *Ipomoea.*

HABITS: All occur in nearly dry areas, i.e., where there is no standing water but a good bit of interstitial soil moisture. Burrow construction is as for *G. quadratus.* There is also a tendency for the depth of the burrow to be correlated with the length of the dry season. Burrows are deeper on the extremes of the range of distribution.

COMMON NAMES: Black land-crab; Common land-crab.

REFERENCES: Bliss, 1964 (B); Bott, 1955 (D,T); Bright, 1966 (G); Cabrera, 1965 (B); Chace and Hobbs 1969 (G); Chace and Holthuis, 1948 (T); Pearse, 1916 (G); Rathbun, 1918 (D,T), 1933 (D,T); Ray, 1967 (D).

ARTHROPOD INHABITANTS OF LAND CRAB BURROWS

The following list represents an attempt to cite all published records of arthropods found in land crab burrows. Because the host was not identified in all cases and there is frequent confusion in usage of the terms land crab, crab, lobster, mud lobster, crayfish, etc., references to all are included. Accounts of dubious validity are also included for completeness and to establish the need for verification.

Some explanation is in order regarding certain assumptions made and conventions used in compiling the list. 1) Identifications and associations with the host crab, i.e., the determinations of the real crab owner of the burrow from which the associates were collected, are assumed to be correct. The list has been read by various specialists and it is hoped that errors of identification, erroneous records and synonymies have been largely detected. 2) The type of association and degree of dependence (see Table I and discussion of the Crabhole Community above) of the species on the crabhole were ascertained or inferred from all available information on the biology of the species. Dubious decisions and the criteria for allocation to a category are explained where relevant.

INSECTS

Order DIPTERA

Family CULICIDAE

We found it impossible to scour the voluminous literature on mosquitoes for all records of species utilizing crabholes. Fortunately, for most regions, comprehensive (though not always current) reviews including ecological data are available (Belkin, 1962: South Pacific; Steffan, 1966: Papuan Region; Hopkins, 1952: Ethiopian Region; Dyar, 1928: tropical America; Delfinado, 1966: Philippines; Barraud, 1934: India; Mattingly, 1958, 1959: Indomalayan Region).

Presently 140 species of mosquitoes are recorded as either resting as adults or breeding in crabholes. To this list could be added several more from unpublished works known to us and no doubt others from other studies now under way. Surprisingly no culicidologist has attempted previously an exclusive investigation of this habitat. Most authors, with a few notable exceptions, seem to regard the crabhole as an aberrant breeding site being utilized by only a handful of specially adapted species. Our bibliographic research would indicate that, whereas those taxa specifically adapted to crabholes are indeed few, the number of transient species is much larger than previously suspected. We feel that much more attention should be paid to crabholes in general mosquito surveys than has been customary in the past (see remarks of Peyton, 1970:2-3). Crabholes are easily sampled using the crabhole pump and collection methods described by Belkin et al. (1965: 37-38).

Most of these transient crabhole breeders are salt water adapted or tolerant species which are general ground pool breeders along the coast.

Their usual normal habitats consist of salt marshes, mangrove pot holes, tidal pools, puddles, coral rock pools, etc. A considerable number of container breeding species (tree holes, especially in mangroves, and artificial containers) also are found in the crabhole. From this it seems probable that the specific crabhole mosquito fauna is of mixed origin derived from both of these more primitive categories through convergent adaptations (van den Assem, 1961:19).

The nature of these adaptations is virtually unstudied. Some characteristics frequently observed in crabhole species are as follows: 1. Stubby or vestigial anal papillae on the larvae. This condition is common, but by no means universal, among larvae which develop in waters with high salt content. 2. Short head hair 1-C, the adaptive significance of which is totally obscure. 3. Prolonged developmental period. 4. Very specialized and aberrant reproductive behavior such as pupal attendance and lack of swarming in *Deinocerites* (Provost and Haeger, 1967) and oviposition directly on the host crab in *Aedes pembaensis* (Goiny et al., 1957).

At least a few crabhole mosquitoes are of known public health importance. Two primary vectors of serious diseases in Africa, while not specific or even semispecific members of the crabhole community, nevertheless may develop in tremendous numbers in this habitat and may even find refuge there during eradication programs designed to treat only the more usual breeding sites. These species are *Aedes aegypti* and *Anopheles gambiae* (? *melas, merus*) for both of which there are several well authenticated records of breeding in crabholes (see list). Vectors of filariasis on the east African coast, *Aedes pembaensis*, and in the south Pacific, *Aedes polynesiensis*, are semispecific members of the crabhole community. The former species has also been found to harbor several kinds of viruses of unknown but possible pathogenicity (Heisch et al., 1956), as have various other mosquitoes which develop in crabholes, including *Deinocerites*. The eastern Equine, Venezuelan and St. Louis encephalitis viruses have all recently been isolated from *D. pseudes* in Panama (Galindo, 1967; Templis and Galindo, 1970:175; Grayson, 1967). Trypanosome organisms have also been recently isolated from wild adults of this species in Panama (Gorgas Mem. Lab., 1970). While *Deinocerites* do not appear to be strongly anthropophilic they may act as important agents in maintaining virus reservoirs in coastal animal populations (silent cycles) and which may enter the human population via other vectors.

Genus *Aedes*

Subgenus *Aedimorphus*

A. abnormalis (Theobald, 1910)

DISTRIBUTION: Tropical Africa; interior and coastal.
CRAB HOST: *Cardisoma armatum*.

TYPE: Transient. Adults only. Probably breeds in ground and rock pools.

REFERENCE[1]: Wanson, 1935:576.

A. albocephalus (Theobald, 1903)

DISTRIBUTION: Tropical Africa, Madagascar, Seychelles; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Accidental. Normally breeds in grassy swamps, pools, etc., in interior; saline seepage pools on coast.

REFERENCES: Hopkins, 1952:182; Ingram and Macfie, 1917:142 (and as *minutus*).

A. caliginosus (Graham, 1910)

DISTRIBUTION: Nigeria; coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Adults only. Recorded also from borrow pits and stream pools.

REFERENCE: Dalziel, 1920:253.

Note: Identification dubious.

A. centropunctatus Theobald, 1913

DISTRIBUTION: Sudan, British West Africa; interior by watercourses (?).

CRAB HOST: *Sudanonautes africanus.*

TYPE: ? Bionomics insufficiently known.

REFERENCE: Hanney, 1960:99.

A. domesticus (Theobald, 1901)

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in grassy swamps, borrow pits, etc.

REFERENCE: Wanson, 1935:576-577, 579.

A. durbanensis (Theobald, 1903)

DISTRIBUTION: Africa, Arabia; primarily coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in fresh water ground pools.

REFERENCE: Wanson, 1935:576-578.

A. fowleri (Charmoy, 1908)

DISTRIBUTION: Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

---

[1] Unless followed by symbols indicating additional significant information (T–taxonomy; B–biology; D–distribution; G–general), the references cite only records of the occurrence of the species in crabholes.

TYPE: Transient. Usually breeds in rock pools and grassy ground pools.

REFERENCE: Wanson, 1935:576-577, 579 (as *nigeriensis*).

A. irritans (Theobald, 1901)

DISTRIBUTION: West and Central Africa; primarily coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Semispecific. Breeds also in small brackish pools along the coast. Strongly anthropophilic.

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119-120 (B); Dalziel, 1920:251-253; Dunn, 1928:249; Ingram & Macfie, 1917:135; Kumm, 1931:65; Wanson, 1935.

A. nigricephalus (Theobald, 1901)

DISTRIBUTION: West Africa; coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Semispecific. Also breeds in ground pools.

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119; Dalziel, 1920: 251; Dunn, 1928:249; Kumm, 1931:65; Wanson, 1935.

A. punctothoracis (Theobald, 1910)

DISTRIBUTION: West tropical Africa; primarily coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Accidental. Adults only. Normally breeds only in ground pools.

REFERENCES: Dalziel, 1920:253; Wanson, 1935:576.

A. tarsalis (Newstead, 1907)

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in rock and ground pools.

REFERENCES: Kumm, 1931:65 (as *sudanensis*); Macfie and Ingram, 1916:7 (as *sudanensis*); Wanson, 1935:576-577.

Note: May be confused with *centropunctatus.*

Subgenus *Cancraedes*

GENERAL REFERENCE: Mattingly, 1958.

All species for which the immatures are known (*) are found breeding primarily in crabholes from which all have been taken as adults. The entire subgenus appears to be adapted to this habitat and comprises a specific or semispecific member of the crabhole community though mangrove pot holes and coastal ground pools may serve as secondary breeding sites. All species have a coastal distribution or are found on small islands. None of the crab hosts has been identified.

A. cancricomes Edwards, 1922

DISTRIBUTION: Andaman Islands.

**A. curtipes* Edwards, 1915

DISTRIBUTION: Borneo, Philippines, Malaya, ? Thailand.

**A. indonesiae* Mattingly, 1958

DISTRIBUTION: Java, Sumatra, east Gulf of Siam.

A. kohkutensis Mattingly, 1958

DISTRIBUTION: Thailand.

A. mamoedjoensis Mattingly, 1958

DISTRIBUTION: Celebes.

**A. masculinus* Mattingly, 1958

DISTRIBUTION: Malaya, ? Philippines.

A. palawanicus Mattingly, 1958

DISTRIBUTION: Philippines.

A. penghuensis Lien, 1968

DISTRIBUTION: Taiwan.

A. simplex (Theobald, 1903)

DISTRIBUTION: Ceylon.

A. thurmanae Mattingly, 1958

DISTRIBUTION: Celebes.

Subgenus *Geoskusea*

GENERAL REFERENCES: Mattingly, 1959; Belkin, 1962:332-339.

As with the preceding, crabholes in coastal areas are the primary breeding places of all species in this subgenus for which the immatures are known (*); the adults of all species have been taken from this habitat. Thus all can probably be classified as specific or semispecific members of the crabhole community. None of the crab hosts has been identified.

A. baisasi Knight and Hull, 1951

DISTRIBUTION: Philippines.

A. becki Belkin, 1962

DISTRIBUTION: Solomons.

**A. daggyi* Stone and Bohart, 1944

DISTRIBUTION: New Hebrides, Solomons.

A. daliensis (Taylor, 1916)

DISTRIBUTION: Australia.

A. fimbripes Edwards, 1924

DISTRIBUTION: Bismark Archipelago, New Guinea.

**A. kabaenensis* Brug, 1939

DISTRIBUTION: Celebes.

**A. longiforceps* Edwards, 1929

DISTRIBUTION: Solomons.

Note: Adults have been observed feeding on mud skippers (*Periophthalmus musgravei*) resting on mangrove roots in the Solomon Islands (Sloof and Marks, 1965).

A. perryi Belkin, 1962

DISTRIBUTION: Solomons.

A. tonsus Edwards, 1924

DISTRIBUTION: Moluccas.

Subgenus *Howardina*

A. inaequalis (Grabham, 1907)

DISTRIBUTION: Jamaica; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Most commonly breeds in treeholes and broken bamboo.

REFERENCE: Berlin, 1969:48.

A. walkeri Theobald, 1901

DISTRIBUTION: Jamaica, interior and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Normally breeds in bromeliads.

REFERENCE: Berlin, 1969:35.

Subgenus *Levua*

A. suvae Stone and Bohart, 1944

DISTRIBUTION: Fiji; coastal.

CRAB HOST: Not recorded, "crab and lobster holes."

TYPE: Specific. No other recorded breeding site.

REFERENCES: Amos, 1944:32; Belkin, 1962:400 (G).

Subgenus *Mucidus*

A. aurantius chrysogaster (Taylor, 1927)

DISTRIBUTION: Australia, New Guinea; coastal.

CRAB HOST: Not recorded, "crab pot hole."

TYPE: Transient. Usually breeds in various types of ground pools in coastal areas. Larva predaceous.

REFERENCE: Steffan, 1966:206.

A. scatophagoides (Theobald, 1901)

DISTRIBUTION: India, Ceylon, Burma, China, tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in transient ground pools and marshes. Larva predaceous.

REFERENCE: Wanson, 1935:576-577, 579.

Subgenus *Neomacleaya*

A. dux Dyar and Shannon, 1925

DISTRIBUTION: Southeast Asia; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Adults only. Usually breeds in puddles and hoof prints near the coast; prefers saline water?

REFERENCE: Delfinado, 1967:20.

A. panayensis Ludlow, 1914

DISTRIBUTION: Philippines, Moluccas, New Guinea; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Adults only. Usually breeds in marine littoral ground pools.

REFERENCES: Delfinado, 1968:33; Steffan, 1966:214.

Subgenus *Neomelanoconion*

A. lineatopennis (Ludlow, 1905)

DISTRIBUTION: Oriental Region, tropical Africa, Australia; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Adults only. Breeds usually in vegetated ground pools.

REFERENCE: Wanson, 1935:576.

Subgenus *Ochlerotatus*

A. perventor Cerqueira and Costa, 1946

DISTRIBUTION: Brazil; interior and coastal.

CRAB HOST: *Cardisoma guanhumi.*

TYPE: Probably transient. Bionomics poorly known. Only breeding records from crabholes.

REFERENCES: Forattini, 1958: 177-178; Forattini et al., 1958:37 (B).

A. taeniorhynchus (Wiedemann, 1821)

DISTRIBUTION: American coasts and interior saline areas.

CRAB HOST: *Cardisoma guanhumi.*

TYPE: Transient. Salt water breeder, usually found in coastal salt marshes, tide pools, etc., and inland saline sinks. Strongly anthropophilic.

REFERENCES: Belkin et al., 1970:49 (G); Forattini, 1958:175-177 (B); Lutz, 1912:19 (as *Culex taeniorhynchus*) (B); Montchadsky and Garcia, 1966:42; de Oliveira, 1946:297.

Subgenus *Paraedes*

A. bonnae Mattingly, 1958

DISTRIBUTION: Malaya; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in ground pools (palm fronds also recorded).

REFERENCE: Mattingly, 1958:34.

Subgenus *Pseudarmigeres*

A. albomarginatus (Newstead, 1907)

DISTRIBUTION: Central tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: ? Single breeding record, from crabhole.

REFERENCE: Wanson, 1935:577.

Subgenus *Pseudoskusea*

A. lunulatus King and Hoogstraal, 1946

DISTRIBUTION: New Guinea; coastal.

CRAB HOST: Not recorded, "crayfish hole."

TYPE: ? Single breeding record, from crayfish hole in shaded rain forest, 250 feet elevation.

REFERENCE: King and Hoogstraal, 1946a:97.

Subgenus *Rhinoskusea*

A. longirostris (Leicester, 1908)

DISTRIBUTION: Indomalayan, north Australian and Papuan Regions; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in numerous other marine littoral ground pool habitats, especially mangrove swamp pools, and artificial containers.

REFERENCES: Colless, 1957:144; Leicester, 1908:8 (as *Ficalbia longirostris*); Mattingly, 1958:39-40.

A. pillaii Mattingly, 1958

DISTRIBUTION: Malaya; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in numerous other marine littoral ground pool habitats.

REFERENCE: Reid *in litt.* after Mattingly, 1958:40.

Subgenus *Skusea*

A. pembaensis Theobald, 1901

DISTRIBUTION: East Africa, Madagascar, Seychelles; coastal.

CRAB HOSTS: *Sesarma meinerti, S. eulimene.*

TYPE: Semispecific. Predominantly breeds in crabholes; also commonly utilizes ground pools and swamps and rarely natural and artificial containers. The females deposit their eggs on the legs and body of the host. (Goiny et al., 1957; Hogue and Bright, 1971). Females are strongly anthropophilic and vectors of filiariasis in east Africa (Heisch, Goiny and Ikata, 1957).

REFERENCES: Brook Worth et al., 1961 (B); Hopkins, 1952:224; Lumsden, 1955: 170-171 (B).

Subgenus *Stegomyia*

A. aegypti (Linneaus, 1962)

DISTRIBUTION: Cosmopolitan; interior and coastal.

CRAB HOSTS: *Cardisoma armatum, Sesarma africanum.*

TYPE: Transient. Usually breeds in various artificial container habitats. Strongly anthropophilic and vector of yellow fever.

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:120; Cheneveau, 1934:590-593; Dalziel, 1920:248, 251-252; Dunn, 1928:249; Riqueau, 1929; Symes, 1960:5, 8; Wanson, 1935:576 (as *argenteus*).

A. africanus (Theobald, 1901)

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Accidental. Normally breeds in treeholes. Anthropophilic and vector of yellow fever.

REFERENCE: Wanson, 1935:576-577.

A. luteocephalus (Newstead, 1907)

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient or accidental. Normally breeds in treeholes (also in cut bamboo, rockholes and temporary ground pools).

REFERENCES: Dalziel, 1920:251-252; Wanson, 1935:576.

A. polynesiensis Marks, 1951

DISTRIBUTION: South Pacific islands; coastal.

CRAB HOSTS: *Cardisoma carnifex, C. hirtipes.*

TYPE: Semispecific. Usually breeds in containers of various sorts. Strongly anthropophilic and vector of filariasis and dengue. Crabholes important breeding sites when other habitats absent as on low coral islands.

REFERENCES: Belkin, 1962:468, pl. 2; Burnett, 1960; Symes, 1960:5, 8; Tamashiro, 1964:10-11 (B).

A. pseudoscutellaris (Theobald, 1910)

DISTRIBUTION: Fiji; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in containers of various sorts.

REFERENCE: Belkin, 1962:470, pl. 2.

Subgenus *Verralina*

A. butleri Theobald, 1901

DISTRIBUTION: Indomalayan Region; coastal.

CRAB HOST: Not recorded.

TYPE: Probably semispecific. Most commonly known from ground pools in mangroves and nipa palm axils.

REFERENCES: Edwards, 1928:346 (as *umbrosus*); Leicester, 1908:8.

A. parasimilis King and Hoogstraal, 1947

DISTRIBUTION: New Guinea; primarily coastal?

CRAB HOST: Not recorded, "crayfish hole."

TYPE: Transient. Usually breeds in various types of ground pools.

REFERENCES: King and Hoogstraal, 1947:125; van den Assem, 1961:25.

Genus *Anopheles*

Subgenus *Anopheles*

A. tigertti Scanlon and Peyton, 1967

DISTRIBUTION: Thailand; interior.

CRAB HOST: Not recorded. Fresh water species.

TYPE: Semispecific or specific.

REFERENCE: Scanlon and Peyton, 1967.

Subgenus *Cellia*

A. gambiae Giles, 1902, complex.

DISTRIBUTION: Africa; interior and coastal.

CRAB HOSTS: *Cardisoma armatum, Sesarma africanum.*

TYPE: Transient. Usually breeds in a wide variety of artificial and natural ground habitats. Anthropophilic and a vector of malaria.

REFERENCES: Aders, 1917:393-394; Bruce-Chwatt and Fitz-John, 1951:120; Cheneveau, 1934:590-593 (as *costalis*); Dalziel, 1920:251-253; Dunn, 1928:249; Ingram and Macfie, 1917:135 (as *costalis*); Macfie and Ingram, 1916:7; Wanson, 1935:576, 578.

Note: The salt water species (?) *merus* (Donitz, 1902) or *melas* (Theobald, 1903) may be found ultimately to be those associated with crabholes (see Coluzzi, 1964).

Subgenus *Nyssorhynchus*

A. albimanus Wiedemann, 1821

DISTRIBUTION: Tropical America, South America; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Accidental. Flushed into crabhole by heavy rains; normally breeds in vegetated ground pools and sluggish streams.

REFERENCES: Shropshire and Zetek, 1927:338 (as *tarsimaculata* in part); Belkin et al., 1970:49.

Genus *Armigeres*

A. breinli (Taylor, 1914)

DISTRIBUTION: New Guinea, Bismark Archipelago, Solomons; primarily coastal.

CRAB HOST: Not recorded.

TYPE: Accidental. Adults only. Species breeds in plant containers and rarely ground pools.

REFERENCES: Peters, 1963:10; Steffan, 1966:215.

Genus *Culex*

Subgenus *Aedinus*

C. bisulcatus (Coquillett, 1906)

DISTRIBUTION: Guadeloupe Island, Lesser Antilles; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Accidental. Normally breeds in bromeliads.

REFERENCE: Floch and Abonnenc, 1945:39.

Note: Probably adults only in crabholes or burrows.

C. corrigani Dyar and Knab, 1907

DISTRIBUTION: Panama; coastal and interior.

CRAB HOST: Not recorded.

TYPE: ? Bionomics poorly known. Type series from bamboo joints.

REFERENCE: Dyar, 1928:347.

C. latisquama (Coquillett, 1906)

DISTRIBUTION: Tropical America; coastal (Atlantic only?)

CRAB HOST: Not recorded.

TYPE: Specific. Multiple collections, all from crabholes.

REFERENCE: Howard, Dyar and Knab, 1915:305.

Subgenus *Culex*

C. annulioris prob. ssp. *consimilis* Newstead, 1907

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in ground pools.

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119; Dalziel, 1920:253; Wanson, 1935:576, 578.

C. annulirostris Skuse, 1889

DISTRIBUTION: Southern and western Australasian Region, Indonesia, Philippines; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Indiscriminate breeder; usually breeds in ground pools but also occurs commonly in almost all other habitats.

REFERENCE: Belkin, 1962:pl. 2.

C. carcinoxenus Castro, 1932

DISTRIBUTION: Brazil; coastal.

CRAB HOSTS: *Cardisoma guanhumi, Ucides cordatus.*

TYPE: Specific or semispecific. Known only from crabholes.

REFERENCES: Castro, 1932:97; Forattini, Rabello and Heredia, 1956:85.

C. corniger Theobald, 1903

DISTRIBUTION: American Mediterranean Region.

CRAB HOST: *Ucides cordatus.*

TYPE: Transient. Indiscriminate breeder.

REFERENCES: Howard, Dyar and Knab, 1915:246; Lutz, 1912:19.

C. decens Theobald, 1901

DISTRIBUTION: Ethiopian Region; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Indiscriminate breeder.

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119; Dalziel, 1920:251, 253; Dunn, 1928:249.

Note: May be confused with *invidiosus.*

C. duttoni Theobald, 1901

DISTRIBUTION: Ethiopian Region; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in a wide variety of ground habitats as well as in containers.

REFERENCE: Wanson, 1935:576, 578.

C. foliaceus Lane, 1945

DISTRIBUTION: Brazil; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Probably transient. Bionomics poorly known.

REFERENCE: Stone, 1950:239.

C. habilitator Dyar and Knab, 1906

DISTRIBUTION: Antilles and Trinidad; coastal.

CRAB HOST: Not recorded.

TYPE: Semispecific. Most records from crabholes; also breeds in ground pools and pot holes.

REFERENCES: Bonne and Bonne-Webster, 1925:189; Dyar, 1928:362; Howard, Dyar and Knab, 1915:262 (as *eremita*); Pratt and Seabrook, 1952:27.

C. inflictus Theobald, 1901

DISTRIBUTION: Tropical America; coastal.

CRAB HOST: Not recorded.

TYPE: Specific or semispecific. All records from crabholes.

REFERENCES: Dyar, 1928:391; Hogue and Wirth, 1968:6; Howard, Dyar and Knab, 1915:327 (as *extricator*); Knab, 1910:868-869 (as *extricator*).

Note: A complex of species.

C. invidiosus Theobald, 1901

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Indiscriminate breeder.

REFERENCE: Wanson, 1935:576, 578-579.

Note: May be confused with *decens.*

C. janitor Theobald, 1903

DISTRIBUTION: Greater Antilles; coastal.

CRAB HOST: Not recorded.

TYPE: Specific. Not recorded from other sites.

REFERENCE: Belkin et al., 1970:49; Grabham, 1905:406-407; Hill and Hill, 1948:55.

C. nigripalpus Theobald, 1901

DISTRIBUTION: Tropical America; coastal (Atlantic).

CRAB HOST: Not recorded.

TYPE: Transient. General ground pool breeder, sometimes found in crabholes.

REFERENCES: Belkin et al., 1970:49; Branch and Seabrook, 1959:216; Martini, 1914:70 (as *prasinopleurus*); Pratt et al., 1945:246.

C. perfuscus Edwards, 1914

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in ground pools.

REFERENCE: Wanson, 1935:576, 578-579.

C. philipi Edwards, 1929

DISTRIBUTION: Western tropical Africa; interior? and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Type series bred from larvae found in crabholes. Also found in vegetated pools.

REFERENCE: Edwards, 1929:327.

C. pipiens quinquefasciatus Say, 1823

DISTRIBUTION: Cosmopolitan; interior and coastal.

CRAB HOSTS: *Cardisoma armatum, Sudanonautes africanus.*

TYPE: Transient. Usually breeds in foul ground pools and ditches and large artificial containers. Vector of filariasis over wide areas of world.

REFERENCES: Dunn, 1928:249; Hanney, 1960:99; Wanson, 1935:576, 578-579.

C. pruina Theobald, 1901

DISTRIBUTION: Western and central Africa; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in ground pools with decaying leaves.

REFERENCE: Dunn, 1928:249.

C. scimitar Branch and Seabrook, 1959

DISTRIBUTION: Bahamas, small islands.

CRAB HOST: Not recorded.

TYPE: Transient? Bionomics poorly known; recorded also from ground pools.

REFERENCE: Branch and Seabrook, 1959:216.

C. sitiens Wiedmann, 1828

DISTRIBUTION: Oriental Region, east Africa and western Pacific; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Normally breeds in saline or brackish coastal ground waters. Anthropophilic.

REFERENCE: van Someren et al., 1955:487.

C. thalassius Theobald, 1903

DISTRIBUTION: Tropical Ethiopian Region; coastal.

CRAB HOST: *Cardisoma armatum, Uca tangeri, Sesarma africanum.*

TYPE: Semispecific. Multiple records from crabholes. Also breeds commonly in saline ground pools and artificial containers. Strongly anthropophilic.

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119-120; Dalziel, 1920:251-253; Hopkins, 1952:286; Ingram and Macfie, 1917:147-149; Wanson, 1935:576, 578-579.

Subgenus *Culiciomyia*

C. cinerellus Edwards, 1922

DISTRIBUTION: Ethiopian Region; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Semispecific or transient. Numerous records from crabholes.

REFERENCES: Dalziel, 1920:251-253 (as *nebulosus*); Dunn, 1928:249; Edwards, 1929:327; Wanson, 1935:578.

C. nailoni King and Hoogstraal, 1946

DISTRIBUTION: New Guinea; interior and coastal.

CRAB HOST: Not recorded, "crabhole in rain forest."

TYPE: ? Bionomics insufficiently known. One record from crabhole.

REFERENCE: King and Hoogstraal, 1946b.

C. ruthi Peters, 1958

DISTRIBUTION: New Guinea; coastal.

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known. Adults only, captured at the entrance of small crabholes in partial shade on the beach. Immatures unknown.

REFERENCE: Steffan, 1966:219.

C. spathifurca (Edwards, 1915)

DISTRIBUTION: Oriental and Indomalayan Regions; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Adults only. A general ground pool breeder.

REFERENCE: Carter and Wijesundara, 1948:145 (as *stylifurcatus*).

Subgenus *Lophoceraomyia*

C. becki Belkin, 1962

DISTRIBUTION: Solomons; small islands.

CRAB HOST: Not recorded.

TYPE: Specific. Known only from crabholes.

REFERENCE: Belkin, 1962:266, pl. 2.

C. infantulus Edwards, 1922

DISTRIBUTION: Oriental (including Japan) and Indomalayan Regions; primarily coastal (?)

CRAB HOST: Not recorded.

TYPE: Transient. A general ground pool and container breeder.

REFERENCE: Bram, 1967:61.

C. pholeter Bram and Rattanarithikul, 1967

DISTRIBUTION: Thailand; interior.

CRAB HOST: Not recorded.

TYPE: Specific. Collected repeatedly and exclusively from small crabholes in secondary rain forests in mountainous terrain.

REFERENCE: Bram and Rattanarithikul, 1967:13.

C. reidi, Colless, 1965

DISTRIBUTION: Singapore, Selangor; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in shaded pools at margin of tidal zone.

REFERENCE: Colless, 1965:280.

C. rubithoracis (Leicester, 1908)

DISTRIBUTION: Indomalayan Region, Japan; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Ground pool breeder.

REFERENCE: Macdonald, 1957:29.

C. variatus (Leicester, 1908)

DISTRIBUTION: Indomalayan Region; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in ground pools but also utilizes containers near the ground.

REFERENCE: Colless, 1965:273.

Subgenus *Lutzia*

C. tigripes Grandpre and Charmoy, 1901

DISTRIBUTION: Ethiopian Region; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Indiscriminate breeder. Larva predaceous.

REFERENCE: Wanson, 1935:578.

Subgenus *Melanoconion*

C. opisthopus Komp, 1926

DISTRIBUTION: Tropical America; coastal (Atlantic).

CRAB HOST: *Cardisoma guanhumi.*

TYPE: Accidental. Probably normal breeding site deep seepage channels or solution holes in coral.

REFERENCES: Pratt et al., 1945:246; Stone and Hair, 1968:41 (as *cedecei*); Belkin, 1969 (T).

C. carcinophilus Dyar and Knab, 1906

DISTRIBUTION: Dominican Republic, ? Guatemala, Cuba; coastal.

CRAB HOST: *Cardisoma guanhumi.*

TYPE: Specific.

REFERENCES: Dyar and Knab, 1906:220; Montchadsky and Garcia, 1966:46.

C. iolambdis Dyar, 1918

DISTRIBUTION: Tropical America; primarily coastal (Atlantic).

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in coastal ground pools shaded by mangroves.

REFERENCE: Pratt and Seabrook, 1952:27.

C. nicaroensis Duret, 1967

DISTRIBUTION: Cuba; coastal.

CRAB HOST: Not recorded.

TYPE: ?

REFERENCE: Duret, 1967:80.

Subgenus *Mochthogenes*

C. inconspicuosus (Theobald, 1908)

DISTRIBUTION: Ethiopian Region; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in nearly stagnant pools, in streams and in ground pools.

REFERENCE: Dalziel, 1920:251-252, 254.

C. laureli Baisas, 1935

DISTRIBUTION: Philippines; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in small vegetated ground pools.

REFERENCE: Delfinado, 1966:133.

Subgenus *Neoculex*

C. insignis (Carter, 1911)

DISTRIBUTION: Africa; interior and coastal.

CRAB HOST: *Sudanonautes africanus, Cardisoma armatum.*

TYPE: Transient. Usually breeds in foul water in pooled streams.

REFERENCES: Dalziel, 1920:251-253; Dunn, 1928:249; Hanney, 1960: 99; Macfie and Ingram, 1916:11.

C. rima Theobald, 1901

DISTRIBUTION: West and central Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Specific or semispecific. Multiple records only from crabholes.

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119; Dalziel, 1920: 251-253; Philip, 1931:192; Surtees, 1958:90; Wanson, 1935:576, 578.

C. salisburiensis Theobald, 1901

DISTRIBUTION: Ethiopian Region; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Transient. Usually breeds in forest ground pools and streams.

REFERENCE: Dalziel, 1920:251-253.

Genus *Deinocerites*

GENERAL REFERENCES: Adames, 1971; Belkin and Hogue, 1959.

Deinocerites normally breeds in crabholes. Referred to as "Crabhole Mosquitoes" in the literature they unquestionably are specific members of the crabhole community, being found breeding outside this habitat only very rarely in such related or proximate places as mangrove treeholes, mangrove pot holes and coastal ground pools.

The genus ranges throughout the American tropics, each species having a completely Atlantic or Pacific (with a few exceptions) distribution. Curiously, in spite of the occurrence of suitable habitats and hosts (*Cardisoma* and *Ucides*) along the entire Brazilian coast to São Paulo, the most southernly Atlantic record is on the coast of the State of Maranhão (Cerqueira, 1938: 291). This apparent truncation in the distribution may be due only to lack of collecting.

All stages exhibit unique characteristics among the Culicidae; some are definitely functional in their relationship to the crabhole habitat and community. The peculiar pupal attendance and mating behavior first described in detail in *Deinocerites cancer* (Downes, 1966; Provost and Haeger, 1967) represents an adaptation correlated with a non-dispersing evolutionary trend in this line of mosquitoes. Among the immatures the larvae of all species have lateral head pouches of unknown function and the pupae of some have three float hairs (these and others discussed by Belkin and Hogue, 1959:421).

Only occasional specimens are observed biting man. The normal food is probably reptile, amphibian or bird blood (Templis and Galindo, 1970).

Deinocerites cancer, at least in Florida (Haeger and Phinizee, 1959), is known to be autogenous.

D. atlanticus Adames, 1971

CRAB HOST: Not recorded. Known from small crabholes.

D. barretoi Adames, 1971

CRAB HOST: Not recorded.

D. belkini Adames, 1971

CRAB HOST: Not recorded, *Uca* (?)

D. cancer Theobald, 1901

CRAB HOST: *Cardisoma guanhumi.*

REFERENCES: Downes, 1966 (B); Haeger and Phinizee, 1959 (B); Komp, 1956; Provost and Haeger, 1967 (B).

D. colombianus Adames, 1971

CRAB HOST: Not recorded.

D. costaricensis Adames and Hogue, 1970

CRAB HOST: *Cardisoma crassum.*

D. curiche Adames, 1971

CRAB HOST: Not recorded.

D. dyari Belkin and Hogue, 1959

CRAB HOST: Not recorded.

D. epitedeus (Knab, 1907)

CRAB HOST: Not recorded.

D. howardi Belkin and Hogue, 1959

CRAB HOST: Not recorded.

D. mathesoni Belkin and Hogue, 1959

CRAB HOSTS: *Uca pugilator, U. subcylindrica, Gecarcinus lateralis.*

REFERENCES: Fisk, 1941 (as *spanius*) (B); Peyton et al., 1964 (B).

D. magnus (Theobald, 1901)

CRAB HOST: Not recorded.

D. melanophyllum Dyar and Knab, 1907

CRAB HOST: Not recorded.

D. mcdonaldi Belkin and Hogue, 1959

CRAB HOST: Not recorded.

D. nicoyae Adames and Hogue, 1970

CRAB HOST: *Ucides occidentalis.*

D. panamensis Adames, 1971

CRAB HOST: Not recorded.

D. pseudes Dyar and Knab, 1909

CRAB HOSTS: *Cardisoma crassum, C. guanhumi, Uca subcylindrica, Gecarcinus lateralis.*

REFERENCES: Galindo, 1967 (B); Hogue and Wirth, 1968; Peyton et al., 1964 (B).

D. spanius (Dyar and Knab, 1909)

CRAB HOST: Not recorded.

Genus *Eretmapodites*

E. quinquevittatus Theobald, 1901

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Accidental. Adults only. Apparently normally breeds in empty *Achatina* shells (land snails).

REFERENCE: Wanson, 1935:576.

Genus *Galindomyia*

G. leei Stone and Barreto, 1969

DISTRIBUTION: Colombia; coastal.

CRAB HOST: Not recorded.

TYPE: Probably specific, though adults only known from crabholes.

REFERENCE: Stone and Barreto, 1969.

Genus *Hodgesia*

H. nigeriae Edwards, 1930

DISTRIBUTION: West tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE: Accidental. Biology not known; probably breeds in vegetated jungle pools like its relatives.

REFERENCE: Wanson, 1935:576-577, 579.

Genera *Mansonia* and *Coquillettidia*

All occurrences of *Mansonia* and *Coquillettidia* are resting adults only and constitute accidental utilization of the crabhole habitat. The larvae of all members of these genera are associated strictly with floating and emergent water plants from which they obtain oxygen with a specially modified, piercing siphon.

C. aurites (Theobald, 1901)

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

REFERENCE: Wanson, 1935:576.

Note: Anthropophilic.

M. africana (Theobald, 1901)

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

REFERENCE: Dalziel, 1920:253.

Note: Anthropophilic and vector of yellow fever and filariasis.

M. uniformis (Theobald, 1901)

DISTRIBUTION: Widespread throughout Old World Tropics; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

REFERENCE: Wanson, 1935:576.

Note: Anthropophilic and important vector of filariasis.

Genus *Psorophora*

P. confinnis (Lynch Arribalzaga, 1891)

DISTRIBUTION: Eastern and southern United States, Caribbean, eastern South America to Argentina; interior and coastal.

CRAB HOST: *Cambarus diogenes ludovicianus.*

TYPE: Transient. Usually breeds in shallow ground pools.

REFERENCE: Evan, 1962.

Note: A complex of species.

Genus *Uranotaenia*

Nearly all the records in this genus are from the burrows of freshwater crabs. See Peyton, 1970.

U. alboabdominalis Theobald, 1910

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: *Sudanonautes africanus.*

TYPE: Transient. Adults only. A ground pool breeder.

REFERENCE: Hanney, 1960:99.

U. annulata Theobald, 1901

DISTRIBUTION: Western tropical Africa; interior and coastal.

CRAB HOSTS: *Cardisoma armatum, Sudanonautes africanus.*

TYPE: Specific or semispecific. Many records and collections, all from crabholes.

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:119; Dalziel, 1920: 251, 253 (as *fasciata*); Dunn, 1928:249; Hanney, 1960:99; Hopkins, 1952:59; Macfie and Ingram, 1916:7; Philip, 1931:192; Surtees, 1958:91.

U. atra Theobald, 1905

DISTRIBUTION: New Guinea, Bismark Archipelago; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in plant and artificial containers and ground pools and in sago palm swamps.

REFERENCES: van den Assem, 1961:25; Steffan, 1966:203.

U. bilineata var. *fraseri* Edwards, 1912

DISTRIBUTION: Tropical Africa; interior and coastal.

CRAB HOST: Not recorded.

TYPE: Accidental? Probably normally breeds in grass-grown ground pools.

REFERENCE: Dalziel, 1920:251-253.

U. bicolor Leicester, 1908

DISTRIBUTION: Southeast Asia; interior.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in a wide variety of ground pools.

REFERENCE: Peyton, 1970:3 and personal communication.

U. caliginosa Philip, 1931

DISTRIBUTION: Nigeria; interior.

CRAB HOST: Not recorded.

TYPE: ?

REFERENCE: Philip, 1931:190.

U. husaini Qutubuddin, 1946 (1947)

DISTRIBUTION: India; interior.

CRAB HOST: Not recorded.

TYPE: ? Adults only. Bionomics insufficiently known.

REFERENCE: Qutubuddin, 1946 (1947):118.

U. koli Peyton, 1970

DISTRIBUTION: Cambodia, Thailand; interior.

CRAB HOST: Not recorded. Fresh water species.

TYPE: Specific or semispecific.

REFERENCE: Peyton and Klein, 1970:248.

U. lateralis Leicester, 1908

DISTRIBUTION: Indomalayan, north Australian and Papuan Regions; coastal.

CRAB HOST: Not recorded.

TYPE: Transient. Usually breeds in slightly brackish open pools behind beaches, although may be very common in crabholes.

REFERENCE: Leicester, 1908:8, 217 (as *cancer*).

U. mashonaensis Theobald, 1901

DISTRIBUTION: Tropical Africa, Madagascar; interior and coastal.

CRAB HOST: *Sudanonautes africanus.*

TYPE: Accidental. Adults only. Breeds in various ground habitats (swamps, rockpools, pools, etc.).

REFERENCE: Hanney, 1960:99.

U. mattinglyi Qutubuddin, 1951

DISTRIBUTION: India; interior.

CRAB HOST: Not recorded.

TYPE: ? Adults only. Bionomics insufficiently known. "Habitat: caught from crabholes in an old pond in the Public Garden, Hyderabad (Deccan) City, India, in October, 1943."

REFERENCE: Qutubuddin, 1951:107.

U. montana Ingram and de Meillon, 1927

DISTRIBUTION: Natal, Transvaal, Cape Province; coastal?

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known. A single record from crabholes. The larva recorded by Hopkins was collected from a crabhole and lived in captivity for 4½ months before pupating.

REFERENCE: Hopkins, 1952:58.

U. nivipous Theobald, 1912

DISTRIBUTION: Tropical Africa; coastal? or interior by large rivers?

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known. Two records only from crabholes.

REFERENCES: Ingram and de Meillon, 1927 (as *candidipes*); Surtees, 1958:91 (as *candidipes*).

U. philippinensis Delfinado, 1966

DISTRIBUTION: Philippines; interior.

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known.

REFERENCE: Peyton, 1970:3 and personal communication.

U. rossi Delfinado, 1966

DISTRIBUTION: Philippines; interior.

CRAB HOST: Not recorded.

TYPE: Specific or semispecific. Numerous collections all from crabholes.

REFERENCE: Peyton, 1970:3 and personal communication.

Family CHAOBORIDAE

The larvae of phantom midges are all aquatic, usually being encountered in fresh water ponds and lakes. Those of two species in the genus *Corethrella* are recorded from crabholes.

Genus *Corethrella*

C. stonei Lane, 1942

DISTRIBUTION: Panama; coastal.

CRAB HOST: *Cardisoma* sp. (*guanhumi?*)

TYPE: ? Bionomics insufficiently known. Adults only, taken at mouths of crabholes.

REFERENCE: Lane, 1942:119.

C. tripunctata Lane, 1942

DISTRIBUTION: Trinidad, Puerto Rico, Brazil; coastal?

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known. Larvae found in crabholes beneath rocks, 100 feet elevation.

REFERENCE: Lane, 1942:120.

Family CERATOPOGONIDAE

A few species of this family, all in the genus *Culicoides*, are recorded as breeding in crabholes. Certainly many more of these coastal, salt marsh and tidal flat-loving flies will be found utilizing the crabhole habitat.

Genus *Culicoides*

C. arubae Fox and Hoffman, 1944

DISTRIBUTION: American Tropics; coastal.

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known.

REFERENCE: Fox and Hoffman, 1944:109.

C. cancer Hogue and Wirth, 1968

DISTRIBUTION: Costa Rica; coastal (Pacific).

CRAB HOSTS: *Cardisoma crassum, Ucides occidentalis.*

TYPE: Specific. The species has been collected in all stages numerous times and in very large numbers only from crabholes.

REFERENCE: Hogue and Wirth, 1968 (G).

C. cancrisocius Macfie, 1946

DISTRIBUTION: Fiji Islands; coastal.

CRAB HOST: Not recorded.

TYPE: ? Bionomics insufficiently known.

REFERENCES: Macfie, 1946; Wirth and Arnaud, 1969:517-518.

C. distinctipennis Austen, 1912

DISTRIBUTION: Nigeria, Uganda, Gold Coast, Senegal; interior and coastal.

CRAB HOST: *Cardisoma armatum.*

TYPE:? Bionomics insufficiently known.

REFERENCE: Wanson, 1935:579, 584 (as *wansoni*).

C. insignis Lutz, 1913

DISTRIBUTION: Mesoamerica; coastal.

CRAB HOST: *Ucides cordatus.*

TYPE: Transient. Usually breeds in coastal marshes.

REFERENCES: Forattini et al., 1956:197 (B,D); Forattini et al., 1958: 37 (B, D).

C. reticulatus Lutz, 1913

DISTRIBUTION: Brazil, Panama; coastal.

CRAB HOST: *Cardisoma guanhumi.*

TYPE: Specific or semispecific. Numerous collections, all from crabholes.

REFERENCES: Forattini et al., 1957:312 (B,D); Lutz, 1912:19, 1913: 50 (B).

Family DROSOPHILIDAE

Two species of *Drosophila* have developed a symbiotic association with land crabs of the genus *Gecarcinus.* The larvae live on the crabs and even pupate (in one species) on the third maxilliped. The adult flies have been observed to remain on the crab, running over and hovering about the carapace. Though the food of the larvae is not known with certainty, it probably consists of food leavings of the host in one case and the host's tissues in the other.

Genus *Drosophila*

D. carcinophila Wheeler, 1960

DISTRIBUTION: Greater and Lesser Antilles, Bahamas, Providencia; islands only (coastal on large islands).

CRAB HOST: *Gecarcinus ruricola.*

TYPE: Commensal, larva in renal grooves and peribuccal region.

REFERENCES: Carson, 1967 (B,D); Wheeler, 1960 (B,D).

D. endobranchia Carson and Wheeler, 1968

DISTRIBUTION: Cayman Islands; small islands.

CRAB HOSTS: *Gecarcinus ruricola* and *lateralis.*

TYPE: Parasitic, larva on host's gills.

REFERENCE: Carson and Wheeler, 1968 (B,D).

MISCELLANEOUS DIPTERA

A number of shore inhabiting flies have been taken, usually as adults only, from the mouths of crabholes. Others (species largely unidentified) are known in the immature stages from water in the burrow.

Family CHIRONOMIDAE

Species undetermined.

LOCALITIES: Lagos, Nigeria; Banana, Congo.

CRAB HOST: *Cardisoma armatum.*

TYPE: ?

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:118; Wanson, 1935: 578.

Family CHLOROPIDAE

Genus *Lasiopleura* sp.

LOCALITY: Not specified.

CRAB HOST: Not recorded.

TYPE: ?

REFERENCE: Wheeler, 1960:210.

Family DOLICHOPODIDAE

Asydetus carcinophilus Parent, 1937

DISTRIBUTION: Hawaii; coastal.

CRAB HOST: *Ocypode ceratophthalma.*

TYPE: Transient. Adults rest and hide in the burrow mouth. Immatures undoubtedly develop elsewhere.

REFERENCES: Wheeler, 1960:210; Williams, 1938:126-129.

Family EMPIDIDAE

Chersodromia hawaiiensis Melander, 1938

DISTRIBUTION: Hawaii; coastal.

CRAB HOST: Not recorded, probably *Ocypode.*

TYPE: Transient. Adults found on the beach in the near vicinity of burrows.

REFERENCE: Melander, 1938:57.

Family EPHYDRIDAE

Hecamede sp.

LOCALITY: Not specified.

CRAB HOST: Not recorded.

TYPE: ?

REFERENCE: Wheeler, 1960:210.

Undetermined "larva A"

LOCALITY: Admiralty Islands.

CRAB HOST: *Cardisoma hirtipes.*

TYPE: Symbiosis? Larvae found in branchial chambers of preserved crabs.

REFERENCES: Baylis, 1915; Keilin, 1921.

Undetermined "larva B"

LOCALITY: Christmas Island (Indian Ocean).

CRAB HOST: *Gecarcoidea lalandii (humei).*

TYPE: Symbiosis? Larvae found in branchial chambers of preserved crabs.

REFERENCES: Baylis, 1915; Keilin, 1921.

Family TETHINIDAE

Rhicnoessa sp.

LOCALITY: Not specified.

CRAB HOST: Not recorded.

TYPE: ?

REFERENCE: Wheeler, 1960:210.

Order COLEOPTERA

Family DYTISCIDAE

Bidessus rogersi Young, 1941

DISTRIBUTION: Florida; interior.

CRAB HOST: *Procambarus rogersi rogersi.*

TYPE: Transient. Primarily a flatwoods species occurring in slow streams, ditches, cypress swamps, ponds, and other lenitic situations.

REFERENCE: Young, 1954:17, 64-65.

Family HELODIDAE

Helodes ? sp.

LOCALITY: Costa Rica.

CRAB HOST: *Cardisoma crassum.*

TYPE: ? Bionomics insufficiently known. Larva only.

REFERENCE: Hogue and Wirth, 1968:6.

MISCELLANEOUS INSECTS

Order HEMIPTERA

Family GELASTOCORIDAE

Mononyx grandicollis Germar, 1840

DISTRIBUTION: West Africa; interior and coastal?

CRAB HOST: *Sudanonautes africanus.*

TYPE: Transient or accidental. A streamside mud flat inhabitant.

REFERENCE: Hanney, 1960:100.

Family VELIIDAE

Microvelia oraria Drake, 1952

DISTRIBUTION: Costa Rica.

CRAB HOST: Not recorded.

TYPE: ?

REFERENCE: Drake, 1952:14-15.

Family CYDNIDAE

Sehirus tibialis Stal, 1853

DISTRIBUTION: West Africa; interior and coastal?

CRAB HOST: *Sudanonautes africanus.*

TYPE: Accidental. Ground burrowing species.

REFERENCE: Hanney, 1960:100 (as *Legnotus tibialis*).

Order ACARINA

Two mites of different families are known as symbiotic associates of certain land crabs:

Family TYROGLYPHIDAE

Rhizoglyphus sp.

DISTRIBUTION: Dry Tortugas Islands; small islands.

CRAB HOST: *Gecarcinus lateralis.*

TYPE: Commensal or parasitic. Single nymphal specimen known.

REFERENCE: Pearse, 1929:230.

Family LAELAPTIDAE

Laelaps cancer Pearse, 1929

DISTRIBUTION: Dry Tortugas Islands; small islands.

CRAB HOST: *Gecarcinus lateralis.*

TYPE: Commensal or parasitic. All stages found in branchial chambers and on gills.

REFERENCES: Pearse, 1929:229-230; 1932:112.

Family UNDETERMINED

Species Undetermined

LOCALITY: West Indies.

CRAB HOST: *Gecarcinus ruricola.*

TYPE: ?

REFERENCE: Carson, 1967:342.

Class CRUSTACEA

Apart from the crab host itself, certain other aquatic crustacea appear to be members of the crabhole community.

Order COPEPODA

Cancrincola jamaicensis Wilson, 1913

DISTRIBUTION: Jamaica, Key West; coastal.

CRAB HOST: *Cardisoma guanhumi.*

TYPE: Parasitic? Cling to gill filaments of crab with their second antennae and maxillipeds. Probably feed on host's blood or secretions.

REFERENCES: Pearse, 1932:112; Wilson, 1913:264-268.

Order EUCOPEPODA

Cyclops sp.

LOCALITIES: Lagos, Nigeria; Banana, Congo.

CRAB HOST: *Cardisoma armatum.*

TYPE: ?

REFERENCES: Bruce-Chwatt and Fitz-John, 1951:118; Wanson, 1935: 578.

ACKNOWLEDGMENTS

For direct assistance and contributions to the preparation of this paper the authors wish especially to thank the following individuals: Drs. John N. Belkin, University of California, Los Angeles; Jocelyn Crane, New York Zoological Society; John S. Garth, Allan Hancock Foundation, University of Southern California; D. J. D. Griffin, Australian Museum; William Macnae, University of Witwatersrand; E. L. Peyton and Botha de Meillon, Southeast Asia Mosquito Project; Shivaji Ramalingam, University of Malaya; and William Stephenson, University of Queensland. We are also indebted to many institutions and persons who have offered assistance and guidance in connection with our field trips through Central and South America, East Africa and Australia, from which were derived the original portions of this paper. Most significantly these are: the American Philosophical Society; California State College, Fullerton; National Geographic Society; Los Angeles County Museum of Natural History Foundation; and Mr. Richard Dwyer, Dr. David Grajeda, and Dr. Purvis L. Martin.

LITERATURE CITED

ADAMES, A. J. 1971. Mosquito studies (Diptera, Culicidae) XXIV. A revision of the crabhole mosquitoes of the genus *Deinocerites*. Contrib. Amer. Entomol. Inst. 7:1-154.

ADERS, W. M. 1917. Insects injurious to man and stock in Zanzibar. Bull. Entomol. Res. 7:391-401.

ALCOCK, A. 1900. Materials for a carcinological fauna of India. No. 6. The Brachyura Catometopa or Grapsoidea. J. Asiatic Soc. Bengal 69:279-456.

ALTEVOGT, R. 1959. Okologische und ethologische studien an Europas einziger Winkerkrabbe *Uca tangeri* Eydoux. Zeit. Morph. Okol. Tiere 48:123-146.

————. 1962. Akustische epiphanomene im sozialverhalten von *Uca tangeri* in Sudspanien. Sond. Verh. Deutschen Zool. Ges. Wien 22:309-315.

AMOS, D. W. 1944. Mosq. Control. Training Manual. Suva, Fiji. 43 p.

ANDREWS, C. W. 1900. Land crustacea. *in* A monograph of Christmas Island (Indian Ocean). British Museum Natur. Hist., London XIII, 337 p., 22 pl.

BARNARD, K. H. 1947. Descriptions of new species of South African Decapod Crustacea, with notes on synonomy and new records. Ann. Mag. Natur. Hist., Ser. 11, 13:361-392.

————. 1950. Descriptive catalogue of South African Decapod Crustacea. Ann. S. Afr. Mus. 38:1-837.

BARRAUD, P. J. 1934. Family Culicidae. Tribes Megarhinini and Culicini. The fauna of British India, including Ceylon and Burma. Diptera 5:1-463.

BAYLIS, H. A. 1915. A parasitic oligochaete and other inhabitants of the gill-chambers of land crabs. Ann. Mag. Natur. Hist., Ser. 8, 15:378-381.

BEHRE, E. H. 1949. Notes on the occurrence of *Cardisoma guanhumi* Latreille at Grand Isle, Louisiana. Proc. Louisiana Acad. Sci. 12:19-22.

BELKIN, J. N. 1962. The mosquitoes of the South Pacific. Univ. of Calif. Press, Berkeley. 608 p. + 412 pl.

————. 1969. *Culex* (*Melanoconion*) *annulipes* invalid. Mosq. Syst. Newsletter 1:68.

————, S. J. HEINEMANN, and W. A. PAGE. 1970. The Culicidae of Jamaica (Insecta, Diptera). Contrib. Amer. Entomol. Inst. 6(1):1-458 (also Inst. Jamaica, Bull. Sci., Ser. 20).

________, and C. L. HOGUE. 1959. A review of the crabhole mosquitoes of the genus *Deinocerites* (Diptera, Culicidae). Univ. Calif. Pub. Entomol. 14:411:458.

________, C. L. HOGUE, P. GALINDO, T. H. G. AITKEN, R. X. SCHICK, and W. A. POWDER. 1965. Mosquito studies (Diptera, Culicidae) II. Methods for the collection, rearing and preservation of mosquitoes. Contrib. Amer. Entomol. Inst. 1(2):19-78.

BERLIN, O. G. W. 1969. Mosquito studies (Diptera, Culicidae) XII. A revision of the neotropical subgenus *Howardina* of *Aedes*.. Contrib. Amer. Entomol. Inst. 4(2):1-190.

BLISS, D. D. 1964. Environmental regulation of growth in the Decapod Crustacean *Gecarcinus lateralis*. Gen. Comp. Endocrinol. 4:15-41.

BONNE, C., and J. BONNE-WEBSTER. 1925. Mosquitoes of Surinam. A study of Neotropical mosquitoes. Mededeeling Koloniaal Instituut te Amsterdam 21, Afdeeling Tropische Hygiene, No. 13. 558 p. + 84 figs.

BORRADAILE, C. A. 1902. Land Crustaceans. Gardiner's fauna and geography of the Maldive and Laccadive Archipelagoes. 1:9-100.

BOTT, R. 1954. Dekapoden (Crustacea) aus El Salvador. 1. Winkerkrabben (*Uca*). Senck. Biol. 35:155-180.

________. 1955. Dekapoden (Crustacea) aus El Salvador. 2. Litorale Dekapoden, ausser *Uca*. Senck. Biol. 36:45-72.

BOYCE, R. 1909. Mosquito or man? Murray, London xvi, 267 p. + 44 fig.

BRAM. R. A. 1967. Contributions to the mosquito fauna of southeast Asia. II. The genus *Culex* in Thailand (Diptera: Culicidae). Contr. Amer. Entomol. Inst. 2(1):1-296.

________, and M. RATTANARITHIKUL. 1967. Six new species of the *Culex* (*Lophoceraomyia*) *mammilifer* group from Thailand (Diptera: Culicidae). Proc. Entomol. Soc. Wash. 69:1-17.

BRANCH, N., and E. L. SEABROOK. 1959. *Culex* (*Culex*) *scimitar*, a new species of mosquito from the Bahama Islands. (Diptera, Culicidae). Proc. Entomol. Soc. Wash. 61:216-218.

BRIGHT, D. B. 1966. The land crabs of Costa Rica. Rev. Biol. Trop. 15:183-203.

BROOKE WORTH, C., J. DE SOUSA, and M. P. WEINBREN. 1961. Studies on the life-history of *Aedes* (*Skusea*) *pembaensis* (Theobald) (Diptera, Culicidae). Bull. Entomol. Res. 52:257-261.

BRUCE-CHWATT, L. J., and R. A. FITZ-JOHN. 1951. Mosquitoes in crab-burrows on the coast of West Africa and their control. J. Trop. Med. Hyg. 54:116-121.

BURKENROAD, M. 1947. Production of sound by the fiddler crab, *Uca pugilator* Bosc, with remarks on its nocturnal and mating behavior. Ecology 28:458-462.

BURNETT, G. F. 1960. Filariasis research in Fiji, 1957-1959. J. Trop. Med. Hyg. 63:153-162.

CABRERA, J. A. 1965. Contribuciónes carcinólogicas. I. El primer estadio zoea en *Gecarcinus lateralis* (Freminville) (Brachyura Gecarcinidae) procedente de Veracruz, Mexico. Ann. Inst. Biol. Mex. 36:173-187.

CALMAN, W. T. 1909. On Decapod Crustacea from Christmas Island, collected by Dr. C. W. Andrews. Proc. Zool. Soc. London 1909:703-713, 1 pl.

________. 1911. The life of Crustacea. London, Methuen and Co. XVI, 289 p.

CAMPBELL, B. M. 1967. The Australian Sesarminae (Crustacea: Brachyura): five species of *Sesarma* (*Chiromantes*). Mem. Queen. Mus. 15:1-19.

CARSON, H. L. 1967. The association between *Drosophila carcinophila* Wheeler and its host, the land crab *Gecarcinus ruricola* (L.). Amer. Mid. Natur. 78:324-343.

________, and M. R. WHEELER. 1968. *Drosophila endobranchia,* a new drosophilid associated with land crabs in the West Indies. Ann. Entomol. Soc. Amer. 61:675-678.

CARTER, H. F., and D. P. WIJESUNDARA. 1948. Notes on some Ceylon culicine mosquitoes. Ceylon J. Sci. 23:135-151.

CASTRO, G. M. DE OLIVEIRA. 1932. Estudo sobre uma especie de *Culex*, que se cria em buracos de guayamú. (Dipt., Culicidae). Rev. Entomol. 2:97-105.

CERQUEIRA, N. 1938. Nota sobre o genero *Deinocerites*: A sua presenca no Estado do Maranhão, Brasil (Dipt., Culicidae). Rev. Entomol. 8:289-291.

CHACE, F. A. 1953. Zoological results of a fifth expedition to East Africa. VI. Decapod Crustacea. Bull. Mus. Comp. Zool. 110:427-443.

————, and H. H. HOBBS. 1969. The freshwater and terrestrial Decapod Crustaceans of the West Indies with special reference to Dominica. Bull. U. S. Nat. Mus. 292:1-258.

————, and L. B. HOLTHUIS. 1948. Land and freshwater Decapod Crustacea from the Leeward Group and Northern South America. *in* Hummelinck, Studies on the fauna of Curaçao, Aruba, Bonaire and the Venezuelan Islands 3:21-28.

CHEESMAN, L. E. 1922. Observations on the land crab, *Cardisoma armatum*, with especial regard to the sense organs. Proc. Zool. Soc. London 1922:361-363.

————. 1923. Notes on the pairing of the land crab, *Cardisoma armatum*. Proc. Zool. Soc. London 1923:173.

CHENEVEAU, R. 1934. Note sur les trous de crabes a Anecho (Togo). Bull. Soc. Pat. Exot. 27:590-593.

COLLESS, D. H. 1957. Notes on the culicine mosquitoes of Singapore III.—Larval breeding-places. Amer. Trop. Med. Parasitol. 51:102-116.

————. 1965. The genus *Culex*, subgenus *Lophoceraomyia*, in Malaya (Diptera: Culicidae). J. Med. Entomol. 2:261-307.

COLUZZI, M. 1964. Morphological divergences in the *Anopheles gambiae* complex. Riv. Malariol. 43:197-232.

COTT, H. B. 1930. The zoological society's expedition to the Zambesi, 1927: No. 2. Observations on the natural history of the land crab *Sesarma meinerti*, from Beira, with special reference to the theory of warning colours. Proc. Zool. Soc. London 1929:679-692.

CRANE, J. 1941a. Eastern Pacific expeditions of the New York Zoological Society XXVI. Crabs of the genus *Uca* from the West Coast of Central America. Zoologica 26:145-207.

————. 1941b. Eastern Pacific expeditions of the New York Zoological Society XXIX. On the growth and ecology of Brachyuran crabs of the genus *Ocypode*. Zoologica 26:297-310.

————. 1943a. Crabs of the genus *Uca* from Venezuela. Zoologica 28:33-44.

————. 1943b. Display, breeding and relationships of fiddler crabs (Brachyura, genus *Uca*) in the Northeastern United States. Zoologica 28:217-223.

————. 1947. Eastern Pacific expeditions of the New York Zoological Society XXXVIII. Intertidal Brachygnathous crabs from the west coast of tropical America with special reference to ecology. Zoologica 32:69-95.

————. 1957. Basic patterns of display in fiddler crabs (Ocypodidae, genus *Uca*). Zoologica 42:68-82.

CROSNIER, A. 1965. Crustacés Decapodes Grapsidae et Ocypodidae. Faune de Madagascar 18:1-143.

DAKIN, W. J., I. BENNETT, and E. C. POPE. 1952. Australian Seashores. Sydney, Angus and Robertson. xii, 372 p.

DALZIEL, J. M. 1920. Crabholes, trees, and other mosquito sources in Lagos. Bull. Entomol. Res. 11:247-270.

DAY, J. H., N. MILLARD, and G. J. BROEKHUYSEN. 1954. The ecology of South African estuaries. Part IV. The St. Lucia System. Trans. Roy. Soc S. Afr. 34:129-156.

DELFINADO, M D. 1966. The culicine mosquitoes of the Philippines, tribe Culicini (Diptera, Culicidae). Mem. Amer. Entomol. Inst. 7:1-252.

———. 1967. Contributions to the mosquito fauna of southeast Asia.—I The genus *Aedes*, subgenus *Neomacleaya* Theobald in Thailand. Contrib. Amer. Entomol. Inst. 1(8):1-56.

———. 1968. Contributions to the mosquito fauna of southeast Asia.—III The genus *Aedes* subgenus *Neomacleaya* Theobald in southeast Asia. Contrib. Amer. Entomol. Inst. 2(4):1-74.

DEMBOWSKI, J. 1925. On the "speech" of the fiddler crab, *Uca pugilator*. Trav. Inst. Nenchi 3:48.

DOWNES, J. A. 1966. Observations on the mating behavior of the crabhole mosquito *Deinocerites cancer* (Diptera, Culicidae). Can. Entomol. 98:1169-1177.

DRAKE, D. J. 1952. Two new *Microvelia* Westwood (Hemiptera; Veliidae). Bull. Brook. Entomol. Soc. 47:13-15.

DUNN, L. H. 1928. Further observations on mosquito breeding in tree-holes and crabholes. Bull. Entomol. Res. 18:247-250.

DURET. J. P. 1967. Dos especies nuevas de *Culex* (*Melanoconion*) (Diptera-Culicidae). Neotropica 13:77-84.

DYAR, H. G. 1928. The mosquitoes of the Americas. Carnegie Inst., Washington. 616 p.

———, and F. KNAB. 1906. The larvae of Culicidae classified as independent organisms. J. New York Entomol. Soc. 14:169-230.

EDWARDS, F. W. 1928. The early stages of some Singapore mosquitoes. Bull. Entomol. Res. 18:337-357.

———. 1929. Mosquito notes.—VIII. Bull. Entomol. Res. 20:321-343.

ESAKI, T. 1940. A preliminary report on the entomological survey of the Micronesian Islands under the Japanese Mandate, with special reference to the insects of economic importance. Proc. Sixth Pacific Sci. Congr. 4:407-415.

EVAN, B. R. 1962. Survey for possible mosquito breeding in crawfish holes in New Orleans. Mosq. News 22:255-257.

FELICIANO, C. 1962. Notes on the biology and importance of the land crab, *Cardisoma guanhumi* Latreille of Puerto Rico. Spec. Contrib. Inst. Marine Biol., Univ. Puerto Rico. iii, 29 p.

FINNEGAN, S. 1931. Report on the Brachyura collected in Central America, the Gorgona and Galapagos Islands, by Dr. Crossland on the "St. George" expedition to the Pacific, 1924-25. J. Linn. Soc. London, Zool. 37:607-673.

FISK, F. W. 1941. *Deinocerites spanius* at Brownsville, Texas, with notes on its biology and a description of the larva. Ann. Entomol. Soc. Amer. 34:543-550.

FLOCH, H., and E. ABONNENC. 1945. Les moustiques de la Guadeloupe (II), les genres *Megarhinus*, *Aedes*, *Culex*, *Deinocerites*, *Mansonia* et *Wyeomyia*. Pub. Inst. Pasteur. Guy. Franc. Inini. 110:1-48.

FORATTINI, O. P. 1958. "Culicidae"' que se criam em buracos de carangueijos (Diptera). Rev. Brasil Biol. 18:175-179.

FORATTINI, O. P., E. X. RABELLO, and R. L. HEREDIA. 1956. Notas sobre Culicidae (Diptera). Arq. Fac. Hig. Saud. Pub. Univ. São Paulo 10:85-88.

FORATTINI, O. P., E. X. RABELLO, and D. PATTOLI. 1956. Nota sobre a larva e pupa de *Culicoides insignis* Lutz, 1913 (Diptera, Ceratopogonidae). Rev. Brasil Entomol. 4:195-198.

———. 1957. A brief note on breeding places of *Culicoides* in São Vicente, Brazil. Mosq. News 17:312-313.

———. 1958. *Culicoides* da região neotropical (Diptera, Ceratopogonidae). II—Observacões sobre biologia em condicões naturais. Arq. Fac. Hig. Saud. Pub. Univ. São Paulo 12:1-52.

FOREST, J., and D. GUINOT. 1961. "Crustaces decapodes brachyoures de Tahiti et des taumotu." Expedition francaise sur les recifs coralliens de la Nouvelle-Caledonie, Paris. xi, 195 p. + 18 pl.

FOX, I. and W. A. HOFFMAN. 1944. New neotropical biting sandflies of the genus *Culicoides* (Diptera: Ceratopogonidae). Puerto Rico J. Pub. Health Med. 20:108-111.

GALINDO, P. 1967. Preliminary observations on the colonization and bionomics of the crabhole breeding mosquito *Deinocerites pseudes* Dyar and Knab, 1909. Mosq. News 27:187-190.

GARTH, J. S. 1948. The brachyura of the "Askoy" expedition with remarks on carcinological collecting in the Panama Bight. Bull. Amer. Mus. Natur. Hist. 92:1-66.

________. 1960. Distribution and affinities of the brachyuran Crustacea. (Symposium: The biogeography of Baja California and adjacent seas. Part II. Marine biotas). Syst. Zool. 9:105-123.

GEORGE, R. W., and W. KNOTT. 1963. The ocypode ghost crabs of Western Australia (Crustacea, Brachypura). J. Roy. Soc. W. Aust. 46:15-21.

GIBSON-HILL, C. A. 1947. Field notes on the terrestrial crabs of Christmas Island. Bull. Raffles Mus. 18:43-52.

GIFFORD, C. A. 1963. Some observations on the general biology of the land crab, *Cardisoma guanhumi* (Latreille) in South Florida. Biol. Bull. 123:207-223.

GOINY, E. C. C. et al. 1957. The eggs of *Aedes* (*Skusea*) *pembaensis* Theobald discovered on crabs. East Afr. Med. J. 34:1-2.

GORDON, I. 1934. Resultats Scientifiques du Voyage aux Indes Orientales Neerlandaises, Crustacea brachyura. Mem. Musee Roy. Hist. Natur. Belg. Hors. Ser. 3, 15:1-78.

________. 1937. Notes on several Indo-Pacific species of *Sesarma* (Crustacea brachyura). Proc. Linn. Soc. London 149:150-156.

GORGAS Memorial Laboratory. 1970. Entomology, Blood meals of *Deinocerites* mosquitoes, p. 19-20. *in* Forty-first annual report of the work and operations of the Gorgas Memorial Laboratory, fiscal year 1969. Gorgas Memorial Laboratory, Panama City, Panama. 35 p.

GRABHAM, M. 1905. Notes on some Jamaican Culcidae. Can. Entomol. 37:401-411.

GRAYSON, M. A., S. SRIHONGSE, and P. GALINDO. 1967. Isolation of St. Louis encephalitis virus from *Deinocerites pseudes* in Panama. Mosq. News 27:204.

GREEN, J. P. 1964. Morphological color change in the Hawaiian ghost crab, *Ocypode ceratophthalma* (Pallas). Biol. Bull. 126:407-413.

GRESSITT, J. L. 1954. Introduction. Insects of Micronesia. 1:1-257.

HAEGER, J. S., and J. PHINIZEE. 1959. The biology of the crabhole mosquito *Deinocerites cancer*. (Typed report of Florida Antimosquito Assoc.).

HANNEY, P. W. 1960. Some notes on the insect fauna of crabholes in northern Nigeria. Entomologist 93:99-100.

HEDIGER, H. 1933. Beobachtungen an der marokkanischen winkerkrabbe, *Uca tangeri* (Eydoux). Verh. Schweiz. Naturforsch. Ges. 114:388-389.

________. 1934. Zur biologie und psychologie der flucht bei tieren. Biol. Zentralbl. Leipzig. 54:21-40.

HEISCH, R. B., H. H. GOINY, and M. IKATA. 1956. A new vector of filariasis in East Africa. Trans. Roy. Soc. Trop. Hyg. 50:421-422.

HERREID, C. F. 1963. Observations on the feeding behavior of *Cardisoma guanhumi* (Latreille) in Southern Florida. Crustaceana 5:176-180.

________. 1967. Skeletal measurements and growth of the land crab *Cardisoma guanhumi* Latreille. Crustaceana 13:39-44.

________, and C. A. GIFFORD. 1963. The burrow habitat of the land crab, *Cardisoma guanhumi* (Latreille). Ecology 44:773-775.

HILL, R. B., and C. D. 1948. The mosquitoes of Jamaica. Bull. Inst. Jamaica, Sci. Ser., No. 4. 60 p.

HOGUE, C. L., and D. B. BRIGHT. 1969. Study of the biologies of land crabs and their burrow associates. Assoc. Trop. Biol. Newsletter 18:9-11.

———. 1971. Observations on the biology of land crabs and their burrow associates on the Kenya coast. Los Angeles Co. Mus., Contrib. Sci. 210.

HOGUE, C. L. and W. W. WIRTH. 1968. A new Central American sand fly breeding in crabholes (Diptera, Ceratopogonidae). Los Angeles Co. Mus., Contrib. Sci. 152.

HOLTHUIS, L. B. 1953. Enumeration of the decapod and stomatopod Crustacea from Pacific Coral Islands. Atoll Res. Bull. 24:1-66.

———. 1959. The Crustacea decapoda of Suriname (Dutch Guiana). Zool. Verh. Leiden 44:1-296.

HOPKINS, G. H. E. 1952. Mosquitoes of the Ethiopian region I.—Larval bionomics of mosquitoes and taxonomy of culicine larvae, 2nd. ed. Trustees Brit. Mus. (Natur. Hist.), London. 355 p.

HOWARD, L. O., H. G. DYAR and F. KNAB. 1915. The mosquitoes of North and Central America and the West Indies. 3:1-523.

HUBBARD, W. G. 1894. Notes and exhibitions of specimens. Proc. Entomol. Soc. Wash. 3:184.

INGRAM, A., and J. W. S. MACFIE. 1917. The early stages of certain west African mosquitoes. Bull. Entomol. Res. 8:135-154.

INGRAM, A., and B. DE MEILLON. 1927. A mosquito survey of certain parts of South Africa, with special reference to the carriers of malaria and their control. (part 1). Pub. So. Africa Inst. Med. Res. 4:1-81, 15 pl.

KEILIN, D. 1921. On some dipterous larvae infesting the brachial chambers of land crabs. Ann. Mag. Natur. Hist., Ser. 9, 8:601-608.

KING, W. V., and H. HOOGSTRAAL. 1946a. Three new species of *Aedes* from Netherlands New Guinea. Proc. Entomol. Soc. Wash. 48:95-106.

———. 1946b. The New Guinea species of *Culex* (*Culiciomyia*), with descriptions of two new species. Proc. Biol. Soc. Wash. 59:143-154.

———. 1947. New Guinea species of mosquitoes of the genus *Aedes,* subgenus *Aedes*. J. Wash Acad. Sci. 37:113-134.

KNAB, F. 1910. Mosquito habits and mosquito control. Science 31:868-869.

KNIGHT, K. L., R. M. BOHART, and G. E. BOHART. 1944. Keys to the mosquitoes of the Australasian region, including a synopsis of their distribution and breeding habits. Nat. Res. Conn., Div. Med. Sci., Wash. 71 p.

KNIGHT, K. L., and W. B. HULL. 1953. The *Aedes* mosquitoes of the Philippine Islands. III. Subgenera *Aedimorphus*, *Banksinella*, *Aedes*, and *Cancraedes* (Diptera, Culicidae). Pacif. Sci. 7:453-481.

KOMP, W. H. W. 1956. Copulation in crabhole mosquitoes (Diptera, Culicidae). Proc. Entomol. Soc. Wash. 58:349-351.

KUMM, H. W. 1931. Studies on *Aedes* larvae in southwestern Nigeria and in the vicinity of Kano. Bull. Entomol. Res. 22:65-74.

LANE, J. 1942. Dixinae e Chaoborinae. Revisão das especies neotropicas (Diptera, Culicidae). Rev. Entomol. 13:81-148, 4 pl.

LEICESTER, G. F. 1908. The Culicidae of Malaya. Stud. Inst. Med. Res. F. M. S. 3(3):18-261.

LIEN, J. C. 1968. New species of mosquitoes from Taiwan (Diptera: Culicidae). Part III. Five new species of *Aedes*. Trop. Med. 10:95-115.

LUMSDEN, N. H. R. 1955. Entomological studies, relating to yellow fever epidemiology, at Gede and Taveta, Kenya. Bull. Entomol. Res. 446:149-183.

LUTZ, A. 1912. Contribuicão para o estudo ceratopogoninas hematofagas do Brasil. Parte geral primeira memoria. Mem. Inst. Oswaldo Cruz 4:1-33.

———. 1913. Contribuicão para o estudo ceratopogoninas hematofagas do Brasil. Parte sistematica segunda memoria. Mem. Inst. Oswaldo Cruz 5:45-73, 3 pl.

MACDONALD, W. W. 1957. Malaysian parasites—XVI An interim review of the nonanopheline mosquitoes of Malaya. Stud. Inst. Med. Res. Malaya No. 28. 34 p.

MACFIE, J. W. S. 1946. A new species of *Culicoides* (Diptera, Ceratopogonidae) from Fiji. Proc. Roy. Entomol. Soc. London, Ser. B, 15:15-16.

________, and A. INGRAM. 1916. New culicine larvae from the Gold Coast. Bull. Entomol. Res. 7:1-18.

MACNAE, W. 1963. Mangrove swamps in South Africa. J. Ecol. 51:1-25.

________. 1966. Mangroves in Eastern and Southern Australia. Aust. J. Bot. 14:67-104.

________, and M. KALK (Eds.). 1969. A natural history of Inhaca Island, Moçambique. Witwatersrand Univ. Press, Johannesburg. vi, 163 p.

MAN, J. G. de. 1879. On some new or imperfectly known Podophthalmous Crustacea of the Leyden Museum. Notes Leyden Mus. 1:1-61.

MANNING, R. B. and A. J. PROVENZANO. 1961. The occurrence of *Ucides cordatus* (Linnaeus, 1763) (Decapoda) in the United States. Crustaceana 2:158-159.

MARTINI, E. 1914. Some new American mosquitoes. Insecutor Inscitiae Menstruus 2:65-76.

MATTINGLY, P. F. 1958. The culicine mosquitoes of the Indomalayan area. Part III. Genus *Aedes* Meigen, subgenera *Paraedes* Edwards, *Rhinoskusea* Edwards and *Cancraedes* Edwards. Trustees Brit. Mus. (Natur. Hist.), London. 61 p.

________. 1959. The culicine mosquitoes of the Indomalayan area. Part IV. Genus *Aedes* Meigen subgenera *Skusea* Theobald, *Diceromyia* Theobald, *Geoskusea* Edwards, and *Christophersiomyia* Barraud. Trustees Brit. Mus. (Natur. Hist.), London. 61 p.

MELANDER, A. L. 1938. A new empidid fly in Hawaii. Proc. Hawaiian Entomol. Soc. 10:57.

MIERS, E. J. 1880. On a collection of Crustacea from the Malaysian region. Ann. Mag. Natur. Hist., Ser. 5, 5:226-239, 304-317.

MILLARD, N. A., and A. D. HARRISON. 1954. The ecology of South African estuaries. Part V. Richard's Bay. Trans. Roy. Soc. S. Afr. 34:157-179.

MILNE EDWARDS, A. 1879. Memoire sur les Crustaces decapodes du genre *Dynomene*. Ann. Sci. Nat. (VI), 8:1-11.

MILNE EDWARDS, H. 1834. Histoire naturelle des Crustacés, Paris, 1:1-360.

________. 1837. Historie naturelle des Crustacés, Paris, 2:1-531.

MIYAKE, S. 1939. Notes on Crustacea brachyura collected by Professor Teiso Esaki's Micronesia expeditions 1937-1938, together with a checklist of Micronesian brachyura. Rec. Oceanogr. Works, Japan, 10:168-247.

MONTCHADSKY, A. S., and I. GARCIA A. 1966. Las larvas de los mosquitos (Diptera: Culicidae) de Cuba. Su biología y determinación. Poeyana (A) 28:1-93.

MURPHY, R. C. 1944. Mountain and sea in the Choco (the sixth installment in the story of the "Askoy" expedition). Natur. Hist. 53:474-481.

DE OLIVEIRA, L. P. H. 1946. Estudos ecologicos dos Crustaceos comestiveis Uçá e Guaiamú, *Cardisoma guanhumi* Latreille e *Ucides cordatus* (L.). Mem. Inst. Oswaldo Cruz 44:295-322.

ORTMANN, A. E. 1894. Die Decapoden-Krebse des Strassburger Museum, 8. Zool. Jahrb., Syst. 7:683-772.

PEARSE, A. S. 1914a. On the habits of *Uca pugnax* (Smith) and *U. pugilator* (Bosc). Trans. Wisconsin Acad. Sci. 17:791-802.

__________. 1914b. Habits of fiddler crabs. 415-427. *in* Ann. Rep. Smith. Inst. for 1913.

__________. 1916. An account of the Crustacea collected by the Walker expedition to Santa Marta, Colombia. Proc. U.S. Nat. Mus. 49:531-556.

———. 1929. Two new mites from the gills of land crabs. Pap. Tortugas Lab. Carnegie Inst. Wash. 26:227-230.

———. 1932. Observations on the parasites and commensals found associated with crustaceans and fishes at Dry Tortugas, Florida. Pap. Tortugas Lab. Carnegie Inst. Wash. 28:107-115.

Pesta, M. 1931. Ergebnisse der Osterreichischen Biologischen Costa-Rica Expedition 1930. I. Teil. Crustacea decapoda aus Costa-Rica. Ann. Naturhist. Mus. Wien 45:173-181.

Peters, W. 1963. Mosquitoes of New Guinea (Diptera: Culicidae) IV.—Two new species, genera *Aedes* Meigen and *Armigeres* Theobald. Proc. Roy. Ent. Soc. Lond., Ser. B, 32:1-11.

Peyton, E. L. 1970. Studies on *Uranotaenia* at SEAMP A plea for further material. Mosq. Syst. Newsletter 2:2-5.

Peyton, E. L., J. F. Reinert, and N. E. Peterson. 1964. The occurrence of *Deinocerites pseudes* Dyar and Knab in the United States, with additional notes on the biology of *Deinocerites* species of Texas. Mosq. News 24:449-458.

Peyton, E. L., and T. M. Klein. 1970. Five new species of *Uranotaenia* from southeast Asia. Proc. Ent. Soc. Wash. 72:243-251.

Phillip, C. B. 1931. Two new species of *Uranotaenia* (Culicidae) from Nigeria, with notes on the genus in the Ethiopian Region. Bull. Entomol. Res. 22:183-193.

Pocock, R. I. 1888. On the Arachnida, Myriopoda and land-Crustacea of Christmas Island. Proc. Zool. Soc. London 1888:556-560.

Pratt, H. D., and E. L. Seabrook. 1952. The occurrence of *Culex iolambdis* Dyar in Florida and Puerto Rico, with a description of the larva (Diptera, Culicidae). Proc. Entomol. Soc. Wash. 54:27-32.

Pratt, H. D., W. W. Wirth, and D. G. Denning. 1945. The occurrence of *Culex opisthopus* Komp in Puerto Rico and Florida, with a description of the larva (Diptera, Culicidae). Proc. Entomol. Soc. Wash. 47:245-251.

Provost, M. W., and J. S. Haeger. 1967. Mating and pupal attendance in *Deinocerites cancer* and comparisons with *Opifex fuscus* (Diptera: Culicidae). Ann. Entomol. Soc. Amer. 60:565-574.

Qutubuddin, M. 1946(1947). A new species of *Uranotaenia*, Culicidae-Diptera from Hyderabad (Deccan). Indian J. Entomol. 8:117-118.

———. 1951. *Uranotaenia mattinglyi* sp. n., a new species of mosquito (Diptera, Culicidae) from Hyderabad (Deccan), India. Proc. Roy. Entomol. Soc. London, Ser. B, 20:107-109.

Rathbun, J. J. 1914. New species of crabs of the families Grapsidae and Ocypodidae. Proc. U. S. Nat. Mus. 47:69-85.

———. 1918. The Grapsoid crabs of America. Spec. Bull. U.S. Nat. Mus. 97:1-461.

———. 1921. The brachyuran crabs collected by the American Museum Congo expedition, 1909-1915. Bull. Amer. Mus. Natur. Hist. 43:379-474.

———. 1933. Brachyuran crabs of Puerto Rico and the Virgin Islands. *In* Scientific survey of Puerto Rico and the Virgin Islands, (New York Academy of Sciences). 15:1-121.

Ray, C. 1967. *Gecarcinus lateralis* Freminville in Texas. Texas J. Sci. 19:109.

Riqueau. 1929. Les trous de crabes, gites a larves. Bull. Soc. Pathol. Exot. 22:175-179.

Sakai, T. 1940. Bio-geographic review on the distribution of crabs in Japanese waters. Rec. Oceanogr. Works, Japan 11:27-63.

Salmon, M. 1965. Waving display and sound production in the courtship behavior of *Uca pugilator*, with comparisons to *U. minax* and *U. pugnax*. Zoologica 50:123-149.

———, and J. F. STOUT. 1962. Sexual discrimination and sound production in *Uca pugilator* Bosc. Zoologica 47:15-20.

SCANLON, J. E., and E. L. PEYTON. 1967. *Anopheles* (*Anopheles*) *tigertti*, a new species of the Aitkenii group from Thailand. Proc. Entomol. Soc. Wash. 69:18-23.

SCHARFF, J. W., and M. W. F. TWEEDIE. 1942. Malaria and the mud lobster. Trans. Roy. Soc. Trop. Med. Hyg. 36:41-44.

SCHMITT, W. L. 1921. The marine decapod Crustacea of California. Univ. Calif. Publ. Zool. 23:1-470.

SHROPSHIRE, J. B., and J. ZETEK. 1927. Unusual *Anopheles* habitats in the Canal Zone. Amer. J. Trop. Med. 7:331-338.

SILAS, E. G., and C. SANKARANKUTTY. 1960. On the castle building habit of the crab *Cardisoma carnifex* (Herbst) (Family Gecarcinidae) of the Andaman Islands. J. Mar. Biol. Assoc. India, 1960. 2:237-240.

SLOOF, R., and E. N. MARKS. 1965. Mosquitoes (Culicidae) biting a fish (Periophthalmidae). J. Med. Entomol. 2:16.

STEBBING, T. R. 1910. South African Crustacea (Part IV). Ann. S. Afr. Mus. 6:1-96.

STEFFAN, W. A. 1966. A checklist and review of the mosquitoes of the Papuan subregion (Diptera: Culicidae). J. Med. Entomol. 3:179-237.

STONE, A. 1950. The larva of *Culex foliaceus* Lane (Diptera, Culicidae). Rev. Entomol. 21:237-239.

———, and J. A. HAIR. 1968. A new *Culex* (*Melanoconion*) from Florida (Diptera, Culicidae). Mosq. News 28:39-41.

———, and P. BARRETO. 1969. A new genus and species of mosquito from Colombia, *Galindomyia leei* (Diptera, Culicidae, Culicini). J. Med. Entomol. 6:143-146.

SURTEES, G. 1958. Notes on the breeding habits of some culicine mosquitoes (Diptera: Culicidae) in southern Ghana. Proc. Roy. Entomol. Soc. London, Ser. A, 33:88-92.

SYMES, C. L. 1960. Observations on the epidemiology of filariasis in Fiji. J. Trop. Med. Hyg. 63:1-44.

TAMASHIRO, M. 1964. Observations on the larval ecology of *Aedes (Stegomyia) polynesiensis* Marks on Aitutaki, southern Cook Islands. WHO/EBL/22:1-29, 7 fig. (Mimeographed).

TEAL, J. M. 1958. Distribution of fiddler crabs in Georgia salt marshes. Ecology 39:185-193.

TEMPLIS, C. H., and P. GALINDO. 1970. Feeding habits of five species of *Deinocerites* mosquitoes collected in Panama. J. Med. Entomol. 7:175-179.

TESCH, J. J. 1917. Synopsis of the genera *Sesarma, Metasesarma, Sarmatium* and *Clistocoeloma*, with a key to the determination of the Indo-Pacific species. Zool. Meded. Rijks. Mus. Natur. Hist. Leyden 3:127-260.

———. 1918. The decapoda brachyura of the Siboga expedition. I. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae and Gecarcinidae. Siboga Exped. Monogr. 39c, (livre 82):1-148.

TWEEDIE, M. W. F. 1940. New and interesting Malaysian species of *Sesarma* and *Utica* (Crustacea, Brachyura). Bul.. Raffles Mus. 16:88-113.

———. 1947. On the brachyura of Christmas Island. Bull. Raffles Mus. 18:27-42.

———. 1950. Papers on the fauna of the Cocos-Keeling Islands. Bull. Raffles Mus. 22:105-148.

———. 1954. Notes on Grapsoid crabs from the Raffles Museum, Nos. 3, 4 and 5. Bull. Raffles Mus. 25:118-123.

VAN DEN ASSEM, J. 1961. Mosquitoes collected in the Hollandia area, Netherlands New Guinea, with notes on the ecology of larvae. Tijd. Entomol. 104:17-30.

van Someren, E. C. C., C. Teesdale, and M. Furlong. 1955. The mosquitoes of the Kenya Coast; Records of occurrence, behavior and habitat. Bull. Entomol. Res. 46:463-493.

Villalobos, A., and J. Cabrera. 1964. Los cangrejos del genero *Gecarcinus* como un peligro potencial para la agricultura de las zonas aledanas a nuestros litorales. Folia Entomol. Mexicana 7-8:27-29.

von Hagen, H. O. 1961. Nachtliche aktivitat von *Uca tangeri* in Sudspanien. Naturwissenschaften 48:1-140.

———. 1962. Frielandstudien zur Sexual-und fortplanzungsbiologie von *Uca tangeri* in Andulusien. Zeit. Morph. Okol. Tiere 51:611-725.

———. 1968. Studien an peruanischen winkerkrabben (*Uca*). Zool. Jaarb. Syst. 95:395-468.

Wanson, M. 1935. Note sur les trous de crabes, gites larvaires. Ann. Soc. Belg. Med. Trop. 15:575-585.

Ward, M. 1934. Notes on a collection of crabs from Christmas Island, Indian Ocean. Bull. Raffles Mus. 9:5-26.

Webb, G. E. 1922. Note on some young stages of *Gecarcoidea lalandii* Milne-Edwards. Ann. Mag. Natur. Hist. 10:530-534.

Wheeler, M. R. 1960. A new genus and two new species of neotropical flies (Diptera: Drosophilidae). Entomol. News 71:207-213.

Williams, F. X. 1938. *Asyndetus carcinophilus* Parent (Diptera, Dolichopodidae). Proc. Hawaiian Entomol. Soc. 10:126-129.

Wilson, C. B. 1913. Crustacean parasites of West Indian fishes and land crabs, with descriptions of new species. Proc. U. S. Nat. Mus. 44:189-277.

Wirth. W. W., and P. H. Arnaud. 1969. Polynesian biting midges of the genus *Culicoides* (Diptera: Ceratopogonidae). Pacific Insects 11:507-520.

Wood-Mason, J. 1873. On a new genus and species of land crabs from the Nicobar Islands. J. Asiat. Soc. Bengal 42:258-262.

Wright, H. O. 1966. Comparative studies of social behavior in Grapsoid crabs. Ph.D. Dissertation, Univ. California, Berkeley. 226 p.

Young, F. N. 1954. The water beetles of Florida. Univ. Florida Stud., Biol. Sci. Ser. 5(1):1-238.

Accepted for publication September 10, 1970

Printed in Los Angeles, California by Continental Graphics

NUMBER 221
FEBRUARY 16, 1972

FOSSIL MICROTINES FROM LATE CENOZOIC DEPOSITS IN THE ANZA-BORREGO DESERT, CALIFORNIA, WITH THE DESCRIPTION OF A NEW SUBGENUS OF *SYNAPTOMYS*

By RICHARD J. ZAKRZEWSKI

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1964 AIBS Style Manual for Biological Journals is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1964 AIBS Style Manual for Biological Journals in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Changes in the manuscript after galley proof will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

FOSSIL MICROTINES FROM LATE CENOZOIC DEPOSITS IN THE ANZA-BORREGO DESERT, CALIFORNIA, WITH THE DESCRIPTION OF A NEW SUBGENUS OF *SYNAPTOMYS*

By RICHARD J. ZAKRZEWSKI[1]

ABSTRACT: Remains of fossil microtines from the Late Cenozoic deposits of the Anza-Borrego desert are extremely rare. Microtines are found at only four out of 450 sites. The specimens found represent three genera: *Synaptomys, Microtus,* and an indeterminate one. The remains of *Synaptomys* when considered with similar forms described previously from Idaho and Kansas permit the naming of a new subgenus and species. The presence of the microtines adds credence to the suggestion of a more equable climate than at present in the area. The stage-of-evolution of the microtines confirms a Late Blancan to Irvingtonian time span for the deposits.

INTRODUCTION

Fossil-bearing deposits in the Anza-Borrego Desert of southern California have been recently described by Downs and White (1968). These deposits range in age from ?mid-Pliocene (Hemphillian) to mid-Pleistocene (Irvingtonian) and the fossils are arbitrarily placed into three local faunas. Over ninety vertebrate taxa have been reported, among which are three genera of microtine rodents.

The microtines are conspicuous in the deposits because of their extreme rarity. From 450 sites through 12,000 feet of beds, microtines are found at only four localities. This paucity may be ascribed to one or both of the following causes: 1. the southern location of the area; microtines are primarily boreal and temperate forms, and 2. the presence of the cricetine genera *Neotoma* and *Sigmodon,* which conservatively outnumber microtines in the deposits of this area some 100 to one and parallel them in dietary preferences. For example, Baker (1969) points out that *S. hispidus* is replacing *Pedomys ochrogaster* in the Recent fauna of the south-central states as the primary grass-eating rodent.

Unfortunately, not all the localities from which the microtines were obtained are in the type section, but rather from areas which have been subjected to an unknown amount of faulting. Consequently, exact stratigraphic relationships are difficult to determine. A detailed study of the geology of this region is presently underway. An attempt at correlation is based on the stage-of-evolution of the microtines. The nomenclature of the teeth follows Zakrzewski (1967).

---

[1] Department of Earth Sciences, and Sternberg Memorial Museum, Fort Hays Kansas State College, Hays, Kansas 67601.

SYSTEMATIC PALEONTOLOGY

Synaptomys Baird 1857

Metaxyomys, subgen. nov.

Holotype.—Synaptomys vetus Wilson, 1933, Carnegie Inst. Wash. Publ. 440: 124–126, fig. 3. Specimen 1364 C.I.T. now in LACM.

Referred species:

Synaptomys landesi Hibbard, 1954, Jour. Mammal. 35, (n. 2): 249–252, Fig. 1C.

Synaptomys anzaensis, n. sp.

*Subgeneric diagnosis.—*The subgenus *Metaxyomys* is distinguished by its M_1 (Fig. 1A, B, I), in which the first and second alternating triangles are confluent as in the subgenus *Mictomys* (Fig. 1C), while the external re-entrant angles are well developed as in the subgenus *Synaptomys* (Fig. 1D).

*Discussion and additional description.—*The decision to place the species listed above into a new subgenus was based on the fact that these forms possess a number of characters which are intermediate between those found in the two extant subgenera, *Synaptomys* and *Mictomys.* Likewise, the subgenus, *Metaxyomys* combines characters which are now found independently in the two extant subgenera, as shown by the morphology of the M_1.

Cement may be present or absent in the posterior-external re-entrant angle of the M_1 in *Metaxyomys.* In *Mictomys* cement is absent in all the external re-entrants of the M_1. In *Synaptomys* it is present. The anterior loop of the M_1 is more vole-like in *Metaxyomys* than it is in either of the other two subgenera.

The third and fourth alternating triangles in the M_2 and M_3 of *Metaxyomys* resemble *Synaptomys* while the first and second alternating triangles are confluent as in *Mictomys.*

The upper molar teeth of *Metaxyomys* tend to more closely resemble those of *Mictomys* because of the slight development of a third internal re-entrant which helps to better isolate the most posterior triangle or loop (Fig. 1E–H). However, even in this character, some *Metaxyomys* specimens show an intermediate development between that of the two extant subgenera.

The capsular process for the reception of the lower incisor is located at the very anterior end of the M_3 in *Metaxyomys.* In *Synaptomys,* although a partial north-south cline has been demonstrated (Hibbard, 1963), the incisor terminates more posteriorly in every case and usually behind the M_3. In Recent specimens of *Mictomys* the incisor ends at the posterior portion of the M_2. One fossil species of *Mictomys, M. kansasensis,* has the lower incisor terminate behind the M_3 (Hibbard, 1952). The grooves on the upper incisors are apparently also intermediate in position, but approach more closely the position observed in *Synaptomys* (Wilson, 1933).

*Etymology.—*The subgenus *Metaxyomys* takes its name from the Greek *metaxy* = between, in allusion to its intermediate nature and *mys* for mouse.

Synaptomys (Metaxyomys) vetus Wilson

(Figures 1A, E)

Synaptomys vetus Wilson, 1933, Carnegie Inst. Wash. Publ. 440: 124–126, Figs. 2–3.

Holotype.—Same as type of subgenus.

Horizon and type locality.—Upper part of the Glenns Ferry Formation, early Pleistocene, Grand View local fauna, Owyhee County, Idaho.

Emended diagnosis.—*Synaptomys vetus* is distinguished by its M_1, on

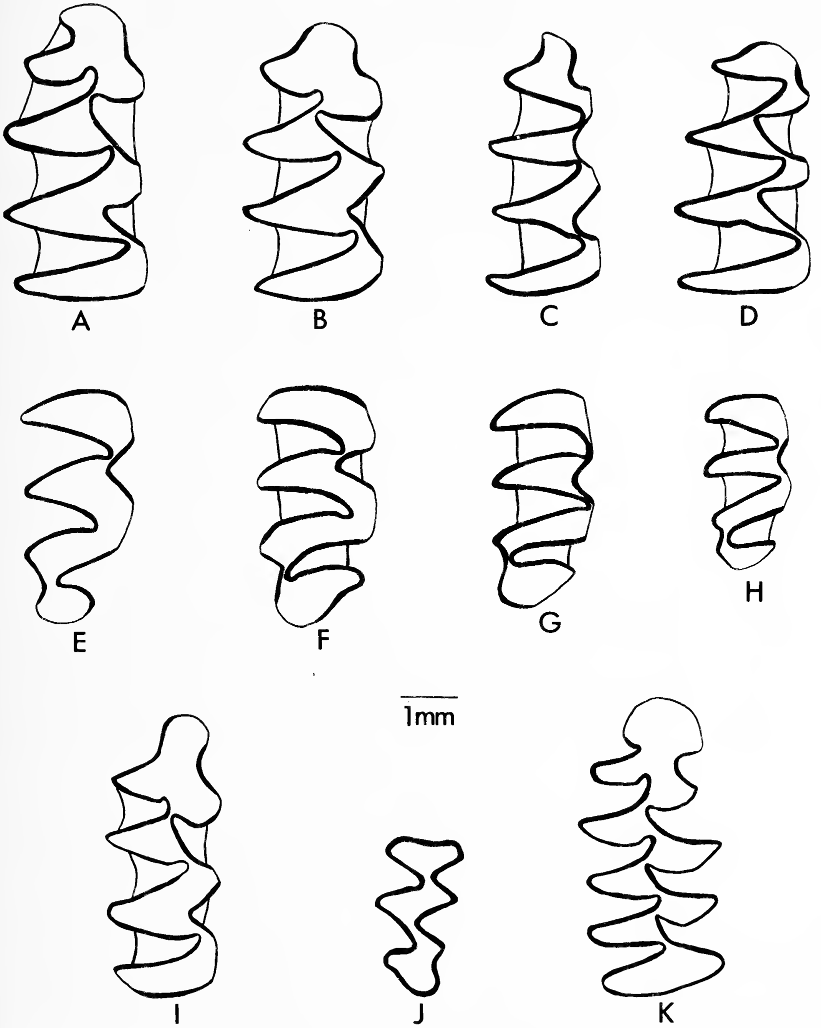


FIGURE 1. Occlusal views of microtine teeth. A-I, *Synaptomys*, A-D, RM$_1$s, E-H, RM^{3}s, A, *S.* (*Metaxomys*) *vetus*, UMMP V59973; B, *S.* (*M.*) *landesi*, UMMP V59982; C, *S.* (*Mictomys*) *borealis*, KU 43256; D, *S.* (*S.*) *cooperi*, KU 5041; E, *S.* (*Metaxomys*) *vetus*, UMMP V56322; F, *S.* (*M.*) *landesi*, UMMP V59972; G, *S.* (*Mictomys*) *borealis*, KU 43256; H, *S.* (*S.*) *cooperi*, KU 5041; I, *S.* (*Metaxomys*) *anzaensis*, *holotype*, LACM 19684; J, Microtine, *gen. et sp. indet.*, LACM 24647, LM^3; K, *Microtus californicus?*, LACM 24540, RM$_1$.

which the anterior loop generally possesses a deep, angular, internal re-entrant and a shallow, external re-entrant. The second alternating triangle of the M_1 is generally rounded in appearance. The M^3 has a posterior loop which is ellipsoidal in shape and lacks enamel along the entire posterior face.

Additional description.—Synaptomys vetus was chosen as the type of the subgenus because it is the best known member of the group. The M_1 is characterized by the first and second alternating triangles being confluent and having well-developed external re-entrant angles (Fig. 1A). The anterior loop appears to be generally smaller than those of other members of the subgenus. There is also a tendency for the internal re-entrant on the anterior loop of *S. vetus* to be more angular than in the other species and on occasion (5/22) this re-entrant is filled with cement. *S. vetus* is the only member of the subgenus in which this character has been found thus far. Cement is present in this re-entrant in the subgenus *Mictomys* but is lacking in the subgenus *Synaptomys.* The external re-entrant on the anterior loop of *S. vetus* is fairly shallow.

Generally the second alternating triangle appears rounded in outline (Fig. 1A) because of the flatness of the external surface due to the absence of enamel. On occasion (6/22), generally in ontogenetically younger specimens, the second alternating triangle is more triangular in nature. The triangularity of the second alternating triangle of M_1 is a character which predominates in *Synaptomys landesi* (Fig. 1B). Characters of the other lower molars will be considered under the discussion of *S. landesi.*

In the lower jaw of *Synaptomys vetus* and *S.* (S.) *cooperi* there is a ridge present between the tooth row and the ascending ramus. In *S. vetus,* a very shallow temporal fossa is found, exterior to this ridge on the ascending ramus, in a position approximate with the alveolar boundary between M_2 and M_3. An even less pronounced fossa occurs in *S. cooperi* in approximately the same position, while in *S. (Mictomys) borealis* the area between the tooth row and ascending ramus descends gradually to a deep point behind M_3. There is no obvious fossa or possibly the strengthening of the musculature, if any, occurs in the area behind the M_3. The condition which exists in the other species of the subgenus *Metaxyomys* is unknown. The ascending ramus of *S. vetus* thickens in the post-fossa area. The diastemal region appears to be more robust in the subgenus *Metaxyomys* than in either of the extant subgenera. The lower incisor of *S. vetus* terminates at the anterior edge of the M_3.

As mentioned above the posterior loop of the M^3 is very diagnostic in *Synaptomys vetus.* The loop is ellipsoidal in shape and enamel is absent from the entire posterior face (Fig. 1E). The first alternating and third alternating triangles open broadly into the second which is poorly developed to give a C-shaped pattern to the alternating triangles of the M^3. Characteristics of the other upper molars will be considered under the discussion of *S. landesi.*

Synaptomys (Metaxyomys) landesi Hibbard

(Figures 1B, F)

Synaptomys (Mictomys) cf. *S. (M.) vetus* Wilson. Hibbard, 1941, Kansas Geol. Surv Bull. 38, pt. 7: 213–214, pl. 2.

Synaptomys vetus Wilson. Hibbard, 1949, Bull. Geol. Soc. Amer. 60: 1424.

Synaptomys (*Synaptomys*) *landesi* Hibbard, 1954, Jour. Mammal. 35, (n. 2): 249–252, Fig. 1C.

Holotype.—UMMP V29961, fragmentary left ramus with M_1-M_3.

Horizon and type locality.—Type section of the Crooked Creek Formation, early Pleistocene, Borchers local fauna, Meade County, Kansas.

Emended diagnosis.—*Synaptomys landesi* is distinguished by its M_1, on which the anterior loop possesses a shallow internal and external re-entrant angle. The outline of the second alternating triangle of the M_1 is generally triangular in shape. The posterior loop of the M^3 is triangular in shape and the enamel is present along most of the posterior face. *S. landesi* appears to be slightly larger than the other members of the subgenus.

Additional description.—*Synaptomys landesi* has the first and second alternating triangles of the M_1 confluent, as do the other members of the subgenus. The second alternating triangle is closed off from the third. This closure was a character used by Hibbard (1954) to separate *S. landesi* from *S. vetus*. In the latter species the second triangle opened into the third. While this is true of some specimens, the majority of *S. vetus* specimens (19/22) also have these triangles closed. This variation in the degree of closure may be due to differences in the ontogenetic age of the individuals. The younger individuals show less closure. There is a tendency for the second alternating triangle of the M_1 in *S. landesi* to be more triangular in shape (Fig. 1B) than in the other species assigned to *Metaxyomys,* though there is some rounding exhibited in a few specimens (2/8).

Both of the re-entrants on the anterior loop are shallow. There is no evidence of cement in either of these re-entrants. From the sample on hand it appears that *Synaptomys landesi* is the largest of the three species (Fig. 2). This size difference is especially apparent in the height of the tooth.

The M_2 has the first and second alternating triangles confluent as in the subgenus *Mictomys.* The second triangle of *S. landesi* seems to be better developed, however. The third and fourth alternating triangles open broadly into each other, but the shape approaches more closely that of the subgenus *Synaptomys* for these triangles. The first external re-entrant of the M_2 in *S.*

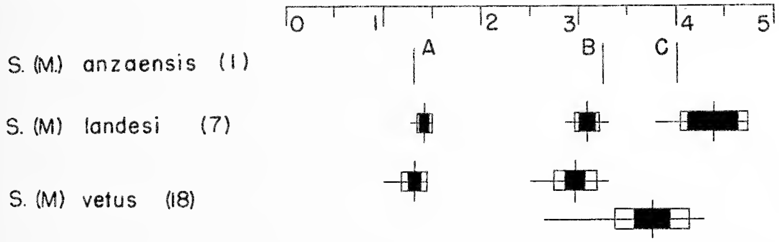


FIGURE 2. Bar diagrams showing variations in size parameters of *Synaptomys* (*Metaxomys*) M_1s. Vertical line represents the mean of the sample, the darkened area two standard errors of the mean, the white areas a standard deviation on either side of the mean, and the horizontal line the observed range. A, measurements (mm) of the width of the occlusal surface; B, length; and C, height of enamel crown. Size of sample is found in parentheses beside specific name.

landesi is short and broad as in *Mictomys.* The second external re-entrant is larger and more anteriorly directed than in either of the two Recent subgenera.

The M_3 of *Synaptomys landesi* resembles its M_2, in that the first and second alternating triangles resemble *Mictomys,* but are not as confluent, while the third and fourth alternating triangles more closely resemble *Synaptomys.* These M_2 and M_3 patterns do not differ significantly from those observed in *S. vetus.*

The characters of the lower jaw of *Synaptomys landesi* are largely unknown. The diastemal region is as robust and the incisor ends in the same position as in *S. vetus.*

The M^1 and M^2 of *Synaptomys landesi* resemble more closely those of the subgenus *Mictomys,* in that there is a slight development of an internal re-entrant angle near the posterior end of the teeth. The development of this re-entrant varies and in some cases is represented only by a shallow groove. These upper molars, likewise, do not differ significantly from those of the other two species of *Metaxyomys* except possibly in size.

Three M^3s of *Synaptomys landesi* are known. All three M^3s have the posterior loop shaped similarly to that of *Mictomys* but are not quite as angular (Fig. 1F). Enamel is absent from the posterior internal surface. The above two features readily distinguish *S. landesi* from *S. vetus.* In two of the M^3s, alternating triangles one and three open into two to give a C-shaped pattern. In the third tooth the middle external re-entrant nearly extends across the entire width of the tooth isolating the third alternating triangle. The first triangle still opens into the second.

Synaptomys (Metaxyomys) anzaensis, n. sp.

(Figure 1I)

Holotype.—LACM 19684, isolated RM_1.

Horizon and type locality.—Palm Springs Formation, probable middle Pleistocene, Vallecito Creek local fauna, San Diego County, California. loc. 6683.

Paratypes.—LACM 24539 RM^1, LACM 19071 $2RM^2$s.

Diagnosis.—*Synaptomys anzaensis* is distinguished from the other members of the genus by the shape of the anterior loop on the M_1, which is very vole-like and has deep internal and external re-entrant angles. The anterior loop is larger than that of other members of the genus examined.

Description of holotype.—The M_1 of *Synaptomys anzaensis* has the first and second alternating triangles confluent. The remaining connections between the loops and triangles are closed. The anterior loop is vole-like and relatively large when compared to other members of the genus. The re-entrant angles on the anterior loop are relatively deep but are rounded and lack cement. Cement is present in the remaining re-entrants of the tooth. The second and third internal re-entrants curve more forward than in *S. cooperi.* This feature appears to give the triangles a greater individuality than in the latter species. The external triangles of *S. anzaensis* are more rounded than those of *S. vetus* (Fig. 1I).

Etymology.—*Anza* from the Anza-Borrego Desert, *ensis* a suffix denoting a geographic location.

Description of paratypes.—These teeth have been characterized above in the discussions of the upper molars. They are not diagnostic enough, except possibly in size, to be separated from other members of the subgenus.

Discussion.—The lower jaw and M^3 of *Synaptomys anzaensis* are unknown at this time. I believe that if found their characteristics will be relatively close to those of the other members of the subgenus. To name a new species on the basis of so little material often presents problems, but the characteristics of the tooth, geographic separation of the localities, and the relatively large samples of the other members in the subgenus are sufficient to warrant this approach.

Relationships.—Because of the intermediate nature of the species which make up the *Metaxyomys* group it may appear that one or more could be ancestral to the extant subgenera of *Synaptomys.* The chief argument against this relationship is that good representatives of one extant subgenus are known from the fossil record prior to the first known appearance of *Metaxyomys.* This is *Synaptomys (Synaptomys) rinkeri* from the Dixon local fauna of Nebraskan age (Hibbard, 1956). The first known occurrence of the subgenus *Mictomys* is *Synaptomys* (M.) *meltoni* from the Cudahy fauna of Kansan age (Paulson, 1961). Faunas in which the subgenus *Metaxomys* is found are presently considered to be of Aftonian age (Hibbard, personal communication). If *Metaxyomys* types served as a common ancestor the divergence must have occurred some time in Pliocene time and the forms discussed above have carried on as a generalized type before becoming extinct.

Microtine, gen. and sp. indet.

(Figure 1J)

Material.—LACM 24647 RM^3; LACM 24648 $3M^1$s, $2M^2$s, 2 M_2s; loc. 1357.

Description.—The above specimens represent a small, primitive microtine with rooted teeth that lack cement in the re-entrant angles and have essentially no or only very slightly-developed dentine tracts. The M_2s possess the typical microtine pattern which consists of a posterior loop and four alternating triangles. The posterior loop is closed off from the alternating triangles. In one of the M_2s, considered to be a young adult individual, the first and second triangles open into each other, but are closed off from the third and fourth triangles which open into each other. These features impart a trilophed appearance to the tooth. The other M_2, in an adult stage of wear, shows a closure between the first and second alternating triangles. The enamel on the occlusal surface is very thick. There is no cement in the re-entrants and dentine tracts are essentially absent.

The M^1s of this species also possess the typical microtine pattern which consists of an anterior loop and four alternating triangles. The pattern most closely resembles that of *Pliophenacomys* from the Fox Canyon local fauna of Kansas (Hibbard, 1950). This similarity results from the development of a posterior internal re-entrant which isolates the fourth triangle from the third. An incipient "re-entrant pit" (Zakrzewski, 1969) is also present at the base of this re-entrant. There is also an incipient development of a re-entrant, or at least a slight depression, on the posterior external surface. There is a groove on the anterior face of the ontogenetically youngest specimen. The enamel is of equal thickness around the entire crown. Dentine tracts are incipient or very slight on the internal triangles and on the posterior face. Cement is absent from the re-entrants. The teeth are three rooted, with the medial-internal root being very reduced. The M^1s of this microtine approach *Ophiomys taylori* and the Fox Canyon *Pliophenacomys* in size. Microtine, gen. and sp. indet., differs from the former form because of the development of the posterior re-entrants, being slightly more hypsodont, having slightly better-developed dentine tracts, and a more reduced medial-internal root. It differs from the latter by the following characteristics: slightly more hypsodont; less-developed roots, especially the medial-internal; less-developed dentine tracts; and shallower internal re-entrants, with the exception of the most posterior one which is deeper.

The M^2s of Microtine, gen. and sp. indet., also resemble those of *Pliophenacomys* from the Fox Canyon local fauna. This similarity, again, results from the development of a posterior-internal re-entrant which tends to isolate the third alternating triangle. *Pliophenacomys* differs from the form under consideration in the following ways: *Pliophenacomys* is more robust for the size of the tooth; the enamel is thinner; the posterior-internal re-entrant is better developed which makes the third triangle more equilateral; it possesses a higher percentage of re-entrant pits; and the dentine tracts are slightly better developed. The M^2s of Microtine, gen. and sp. indet., also resemble that of a yet undescribed microtine in the collection of the University of Michigan Museum of Paleontology from the Sand Draw local fauna of Nebraska. The chief difference between the forms is that in the California specimens the posterior-internal re-entrant angle is deeper and the teeth have three roots, while the Nebraska specimen has only two roots.

In addition to the M_1, which is unfortunately missing in this case, the most diagnostic of the microtine teeth is the M^3. The M^3 of the microtine in question is characterized by an anterior loop, two alternating triangles and a posterior loop. The anterior loop opens slightly into the first triangle; the first triangle is confluent with the second; and the second triangle opens slightly into the posterior loop (Fig. 1J). The re-entrant angles are perpendicular except for the posterior-internal one which curves slightly back. The two anterior re-entrants are almost opposed. The enamel is very thick and equal around the entire tooth. Dentine tracts are absent. The tooth is two rooted. With the exception of the last character, the above description removes the California specimens from the genus *Pliophenacomys* which they resemble in the other upper molars. The M^3 of *Pliophenacomys* consists primarily of two lophs. The alternation of the triangles is not readily apparent. These features of the M^3 in *Pliophenacomys* were the chief reason why some microtines earlier placed in the genus were removed and the genus *Ophiomys* was erected for them (Hibbard and Zakrzewski, 1967). Though at about the same stage-of-evolution as some species of *Ophiomys*, the California specimens probably do not belong to that genus. The degree of confluency of the alternating triangles on the M^3 of the California specimen, along with the other characters of that tooth, suggests that another line of microtine is present. This line of reasoning is supported by the other molar teeth which morphologically appear closer to the *Pliophenacomys* line. The M^3 under discussion most closely resembles one belonging to a microtine from the Sand Draw local fauna. The Sand Draw M^3 was found at the locality mentioned above in the discussion of the M^2s. The two M^3s differ from each other only very slightly. Unfortunately for this study several genera and species of microtine are represented in the Sand Draw local fauna and not all of the specimens can be assigned properly because their remains are not associated. The two teeth from the Sand Draw discussed above are thought to be related to each other solely because of their morphological similarity to the Vallecito specimens, which by the laws of probability should represent one species. It might be mentioned here that the triangles on some young M^3 specimens of *Ophiomys taylori* approach the above teeth in degree of openness but are not as confluent, nor is the posterior internal re-entrant well developed. Possibly these microtines could have been derived from *Ophiomys* but they certainly represent a different line than the other species so far assigned to that genus. Only additional material will show the true relationship of this form.

Microtus californicus?

(Figure 1K)

Referred material.—LACM 24540 RM_1, loc. 6814; LACM 8252 RM_1, loc. 1942; LACM 24649 left edentulous lower jaw, loc. 6683.

Description of material.—LACM 24540 is an isolated RM_1 characterized by a posterior loop, five alternating triangles, and an anterior loop. The anterior loop can be considered to be composed of two additional alternating triangles and a small anterior loph (Fig. 1K). The posterior loop and the alternating triangles open very slightly into each other except on the anterior loop where the two triangles open broadly into the anterior loph. The enamel is differentiated into thin tracts on the posterior sides of the loops and triangles and thick tracts on the anterior edges, except on the anterior loop where the enamel is absent from the entire anterior face. Cement is present in all the re-entrants. The tooth is evergrowing. LACM 24540 measures 3.39 mm in length, 1.28 mm in width, and 4.72 mm in height.

The other M_1 (LACM 8252) is broken and still emplaced in a block of matrix. Only a portion of the anterior loop and 3 alternating triangles are visible. The tooth is assigned to *M. californicus?* for the following reasons: it is evergrowing, it has the enamel differentiated into thin and thick tracts, it has an anterior loop similar to LACM 24540, and it has cement in the re-entrants.

The lower jaw (LACM 24649) is assigned to *M. californicus?* because the alveolus for the M_1 shows that the tooth was evergrowing and of a type similar to LACM 24540 in terms of loops and alternating triangles. A relatively well-developed temporal fossa is also present. A similarly developed fossa is characteristic of the genus *Microtus* but is not found in *Synaptomys.* The latter genus is the only other microtine with evergrowing teeth present at this locality. However, it may be that the lower jaw represents another genus and/or species.

LACM 24540 in its stage of development, most closely resembles *Microtus californicus* among the Recent microtines. The fossil differs from the Recent forms chiefly in that the anterior loop is more rounded and the 6th alternating triangle is better developed. The fossil is larger than the specimens assigned to *M. californicus* in the collection of the Department of Biological Sciences, Fort Hays Kansas State College. The latter remains are thought to represent at least two and possibly three different subspecies on the basis of locality data with the specimens. The fossil is slightly smaller than the specimen of *M. c. aequivocatus* (UMMZ 79598) examined at the University of Michigan. It may be that the fossil represents a subspecies of *M. californicus*. It may also be that of a new species ancestral to extant *M. californicus*. But as the M_1 occlusal pattern of *Microtus* is highly variable it seems best to follow the above approach till more material becomes available.

PALEOECOLOGY AND AGE OF LOCALITIES

Microtines are generally found in boreal and/or relatively humid areas. This suggests that during the time the fossils lived the climate in the area of the Anza-Borrego Desert was more humid. Microtines are not found in this area at present. As the exact stratigraphic position of all the localities which contain microtines is not known (see discussion below), it cannot be stated with certainty whether the presence of the microtines coincides with an alternation of climate because of glaciation or whether other factors are involved.

All of the *Synaptomys* specimens and the edentulous *Microtus* lower jaw were found at loc. 6683. This might suggest that this locality was near a bog or marsh.

Downs and White (1968) compared the forms present in these deposits with the distribution in time of all known mammalian genera which have a fossil record in the late Pliocene and/or Pleistocene of North America. On the nature of the genera and their associations they arbitrarily divided the fossils in the superposed type section into three local faunas. The lowermost local fauna is the Layer Cake of early Blancan age, the middle local fauna is the Arroyo Seco of late Blancan age, and the uppermost local fauna is the Vallecito Creek of Irvingtonian age.

Loc. 1942, from which one of the RM_1s (LACM 8252) of *Microtus californicus?* is known, is the only locality of the four where microtines are found in the type section. Its position, 12,100 feet from the base of the section, places loc. 1942 in the Vallecito Creek local fauna. Savage (1951) assigned 2 RM_1s from the type Irvingtonian local fauna to *M. californicus*. This fact adds support for considering the Vallecito Creek l.f. to be of Irvingtonian age.

Loc. 6814 is not in the type section. A RM_1 of *Microtus californicus?* is found here. From the above discussion this locality is tentatively placed in the Vallecito Creek l.f.

Loc. 1357, where the remains of Microtine gen. and sp. indet. are found, is also not in the type section. The microtine from this locality appears to be most closely related to a species as yet undescribed from the Sand Draw local fauna of Nebraska. The Sand Draw l.f. is thought to be late Blancan in age. Hibbard (1970, footnote, p. 414) considers the Sand Draw l.f. to be Pleistocene, but to represent a time prior to continental glaciation. If a direct correlation can be assumed loc. 1357 would then be a part of the Arroyo Seco l.f. At present there is not enough evidence to substantiate whether or not this is indeed the case.

Loc. 6683, where the remains of *Synaptomys anzaensis* are found, is likewise not a part of the type section. The other species of *Synaptomys* assigned to the subgenus *Metaxyomys* are found in faunas considered Aftonian in age. The Borchers l.f. of Kansas is considered to represent an interglacial stage because of the nature of the fauna and was thought to be Yarmouthian because of its position above a volcanic ash (Hibbard, 1941). It has recently been suggested to Hibbard that the ash below the Borchers l.f. is not the Pearlette-like ash above the Cudahy l.f. He now considers the Borchers l.f. to be Aftonian in age (Hibbard, personal communication). Support for this thesis is the presence of some relict Pliocene species in the Borchers l.f. (*Sorex taylori, Perognathus pearlettensis, Etadonomys tiheni,* and *Hypolagus* sp.), and the better fit which would be obtained for the size chronocline in *Ondatra* demonstrated by Semken (1966). Hibbard is also working on a warm fauna from Ellsworth County, Kansas, which has an entirely different faunal complement from the Borchers, and is thought to be Yarmouthian on stratigraphic evidence. The Grand View l.f. of Idaho is correlated with the Borchers l.f. primarily on the stage-of-evolution of the *Synaptomys* and *Ondatra* which are known from both local faunas (Hibbard, 1959). Direct correlation on the basis of *Metaxyomys* would suggest an Aftonian age for loc. 6683. However, if the edentulous lower jaw of *Microtus californicus?* from loc. 6683 is correctly assigned, it may mean that *Metaxyomys* is a relict in California and this locality is of a younger age. Only more detailed work will enable us to know the true relationships of the deposits and contained faunas. The above discussion merely points out how scanty our information is and some of the possibilities one should be aware of.

ACKNOWLEDGMENTS

I am especially indebted to Theodore Downs, Chief Curator of Earth Sciences, Los Angeles County Museum of Natural History (LACM), Claude W. Hibbard, Museum of Paleontology, University of Michigan (UMMP), and John A. White, Idaho State University Museum, for the opportunity to study and report on the specimens under their care and for their critical reading of the manuscript.

I would also like to thank the following for the permission to examine specimens under their care: Eugene D. Fleharty, Department of Biological Sciences, Fort Hays Kansas State College; Emmet T. Hooper, Museum of Zoology, University of Michigan (UMMZ); and J. Knox Jones, Museum of Natural History, University of Kansas (KU).

Graduate Faculty Research Grants (5326 and 5409) from Fort Hays Kansas State College provided for the line drawings by Jerry L. Maxfield. This study began at Idaho State University while I was on a postdoctoral fellowship sponsored jointly by Idaho State University and the Los Angeles County Museum of Natural History (NSF-GB 5116).

LITERATURE CITED

BAKER, R. H. 1969. Cotton rats of the *Sigmodon fulviventer* group. Univ. Kans. Mus. Nat. Hist., Misc. Publ. 51: 177–232.

DOWNS, T., AND J. A. WHITE. 1968. A vertebrate faunal succession in superposed sediments from late Pliocene to middle Pleistocene in California. Inter. Geol. Cong. Report XXIII Session, Proc. Sec. 10: 41–47.

HIBBARD, C. W. 1941. The Borchers fauna, a new Pleistocene interglacial fauna from Meade County, Kansas. Kans. Geol. Surv. Bull. 38: 197–220.

———. 1950. Mammals of the Rexroad formation from Fox Canyon, Kansas. Contrib. Mus. Paleontol., Univ. Mich. 8: 113–192.

———. 1952. Vertebrate fossils from late Cenozoic deposits of central Kansas. Univ. Kans. Paleontol. Contrib. Vert. Art. 2: 1–14.

———. 1954. A new *Synaptomys,* an addition to the Borchers interglacial (Yarmouth?) fauna. Jour. Mammal. 35: 249–252.

———. 1956. Vertebrate fossils from the Meade formation of southwestern Kansas. Papers Mich. Acad. Sci. 41: 145–200.

———. 1959. Late Cenozoic microtine rodents from Wyoming and Idaho. Papers Mich. Acad. Sci. 44: 3–40.

———. 1963. A late Illinoian fauna from Kansas and its climatic significance. Papers Mich. Acad. Sci. 48: 187–221.

———. 1970. Pleistocene mammalian local faunas from the Great Plains and Central Lowland Provinces of the United States. p. 395–433. *in* Pleistocene and Recent environments of the Central Great Plains. Dept. Geology, Univ. Kans. Spec. Publ. 3. 433 p.

HIBBARD, C. W., AND R. J. ZAKRZEWSKI. 1967. Phyletic trends in the late Cenozoic microtine *Ophiomys* gen. nov., from Idaho. Contrib. Mus. Paleontol., Univ. Mich. 21: 255–271.

PAULSON, G. R. 1961. The mammals of the Cudahy fauna. Papers Mich. Acad. Sci. 46: 127–153.

SAVAGE, D. E. 1951. Late Cenozoic vertebrates of the San Francisco Bay Region. Univ. Calif. Publ., Bull. Dept. Geol. Sci. 24: 339–410.

SEMKEN, H. A. JR., 1966. Stratigraphy and paleontology of the McPherson *Equus* beds (Sandahl local fauna), McPherson County, Kansas. Contrib. Mus. Paleontol., Univ. Mich. 20: 121–178.

WILSON, R. W. 1933. A rodent fauna from later Cenozoic beds of southwestern Idaho. Carnegie Inst. Wash. Publ. 440: 117–135.

ZAKRZEWSKI, R. J. 1967. The primitive vole, *Ogmodontomys,* from the late Cenozoic of Kansas and Nebraska. Papers Mich. Acad. Sci. 52: 133–150.

———. 1969. The rodents from the Hagerman local fauna, Upper Pliocene of Idaho. Contrib. Mus. Paleontol., Univ. Mich. 23: 1–36.

Accepted for publication September 13, 1971

Printed in Los Angeles, California by Continental Graphic

NUMBER 222
FEBRUARY 22, 1972

A NEW NIGHT SNAKE FROM MEXICO (SERPENTES: COLUBRIDAE)

By James R. Dixon and Carl S. Lieb

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1964 AIBS Style Manual for Biological Journals is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1964 AIBS Style Manual for Biological Journals in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Changes in the manuscript after galley proof will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

VIRGINIA D. MILLER
Editor

A NEW NIGHT SNAKE FROM MEXICO (SERPENTES: COLUBRIDAE)

By JAMES R. DIXON[1] AND CARL S. LIEB[1]

ABSTRACT: A new species of *Hypsiglena* is described from eastern Querétaro, Mexico. Taken from the arid tropical scrub forest of the Jalpan Valley, the new species is distinguished from other *Hypsiglena* by having a longer tail and broader dorsal bands. The new species is morphologically distinct from the nearest population of *H. torquata jani.*

During the past 110 years, or since the original description of *Hypsiglena torquata* (Gunther), 1860 and *H. ochrorhyncha* Cope, 1860, the status of the two taxa has been a subject of much debate.

Cope (1860) proposed the genus *Hypsiglena* (type species: *ochrorhyncha*) from specimens collected at Cape San Lucas, Baja California. Ten months earlier, Gunther (1860) described a snake *(torquata)* from Nicaragua that he assigned to the genus *Leptodeira.* Later Gunther (1895) reassigned *torquata* to *Hypsiglena* and included *ochrorhyncha* as a synonym. He recognized the fact that two nape patterns existed: *torquata* with a cream-colored nuchal band followed by a single dark nuchal band, and *ochrorhyncha* which lacked the light band but possessed a dark nuchal band or spots.

Dunn (1936) placed the genus *Hypsiglena* in the synonymy of *Leptodeira,* asserting that the presence or absence of grooves in the posterior maxillary teeth was of no significant value. Taylor (1938) suggested retaining *Hypsiglena* and presented a redefinition of *Hypsiglena.* Tanner's (1944) systematic review of the genus *Hypsiglena* supported Taylor's views.

Three additional taxa of importance to this problem were named subsequent to Cope's description of the genus. Dugès (1866) described *Liophis jani* from Guanajuato, Mexico; Stejneger (1893) described *Hypsiglena texana* from near Laredo, Texas; and Taylor (1938) named a new race, *H. torquata dunklei,* from near Forlón, Tamaulipas, Mexico.

Boulenger (1894) placed *H. texana* Stejneger in the synonymy of *H. ochrorhyncha* Cope. Cope (1900) agreed with this, as did Taylor (1938). No mention was made by Boulenger or Cope of the status of *Liophis jani.* Even though *texana* was considered a race of *ochrorhyncha* by Stejneger and Barbour (1917), it was not generally recognized until Tanner's (1944) systematic review of the genus was published.

Taylor (1938) placed the species *Liophis jani* in the synonymy of *torquata.* However, Smith (1943) resurrected *jani* and gave it subspecific status

---

[1] Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843.

with *H. ochrorhyncha.* This arrangement was followed by Tanner (1944) and Smith and Taylor (1945). Dixon (1965) reviewed the status of *jani, texana,* and *ochrorhyncha,* and proposed relegating *H. o. texana* to synonymy of *H. o. jani.* Taylor's (1938) race, *Hypsiglena t. dunklei,* was elevated to a specific level by Tanner (1944). Dixon (1962) utilizing additional specimens, returned *dunklei* to a race of *torquata* based on the similarity of nuchal patterns.

Though *H. torquata* and *H. ochrorhyncha* were considered distinct species by earlier authors, Dunn (1936) suggested they were conspecific. Taylor (1938) and Tanner (1944) considered the possibility of combining the two forms, but favored retaining the two as separate species. Bogert and Oliver (1945) favored the arrangement of Dunn, based on similarities of squamation and habitat of snakes with both nuchal types from southern Sonora, Mexico. As a result, the races of *ochrorhyncha (texana, jani)* became races of *torquata.* This arrangement was maintained for the next 20 years until Dixon (1965) proposed the separation of *ochrorhyncha* from *torquata* at the specific level, based on the presence or absence of a light cream colored nuchal collar. Tanner (1966) and Hardy and McDiarmid (1969) suggested returning to Dunn's 1936 classification.

An attempt was made to solve the species problem by Mr. Ernest Tanzer, through the use of karyotyping, examination of all preserved material, and examination of hatchlings from clutches of eggs from areas of overlap between the two forms. Unfortunately, before the completion of his monograph of the genus, Ernest Tanzer died in January, 1971.

For the past three years we (Dixon, Ketchersid and Lieb) have undertaken a study of the herpetofauna of the Mexican state of Querétaro and recently discovered what we consider a new species of *Hypsiglena* in the isolated valley of the Rio Jalpan. In memory of Ernest Tanzer, a close friend and ardent field companion, we propose the new species be known as

Hypsiglena tanzeri, new species

Figure 1A, B

Holotype.—Texas Cooperative Wildlife Collection 34079, male, taken 5 km E. Jalpan, Querétaro, Mexico, 762 m, 99° 27′ W. 21° 13′ N., by Frank Guyer, 13 April 1971.

Paratype.—Los Angeles County Museum of Natural History (72068) male, taken 0.8 km W. Landa de Matamoros, 1067 m; Querétaro, Mexico, by Carl Lieb and Douglas Albaugh, 20 May 1971.

Diagnosis.—*Hypsiglena tanzeri* is readily distinguished from populations of snakes that have been referred to *H. ochrorhyncha* by possessing a broad nuchal collar. It most closely resembles *H. torquata* from which it is readily distinguished by the presence of wider (usually reaching the second dorsal scale row) and longer (usually 3 to 4 scales long) brown to black bands on the anterior two-thirds of the body. *H. torquata* has dorsal blotches reaching the sixth or seventh scale row and 2 to 3 scales long. Additionally *H. tanzeri* has the following characters: tail length, 22.5 per cent of the total length; postocular stripe not continuous with nape blotch, and 7 supralabials; whereas, *H. torquata* has a tail length 19.5 per cent or less of the total length; a postocular stripe that may or may not join the nuchal blotch; usually (99 per cent of specimens examined) 8 or more supralabials.

Description of the Holotype.—Head and body proporations normal for *Hypsiglena;* total length 328 mm, tail 73 mm, ratio of tail to total length .225; dorsal scale formula 21-21-17; 2 pair of chin shields of about equal length; ventrals 175; caudals 69, including tip; supralabials 7-7; infralabials 10-10, preoculars 2-2, postoculars 2-2, loreal single; temporals 1+2+3; third and fourth supralabials entering eye; fifth and sixth supralabials and sixth infralabials largest of series; first five infralabials contact first pair chin shields, primary temporal contacts parietal, both secondary temporals, fifth and sixth supralabials; maxillary teeth 9-9, followed by a distema and two large ungrooved teeth.

Color pattern consists of 37 black bands and spots on body; anterior 26 bands 16 to 17 scale rows wide, reducing the intercalary spots to narrow brownish black lines on scale rows one and two on most of the body; dorsal color pattern above the last 26 ventrals consists of three rows of spots, the outer rows alternating with the middle row; interspaces between major bands one to two scales in length, grayish white with dark pigment in the center of each scale; nape band ten scales in length, 15 scales if the median anterior projection of the nape band (Fig. 1A) is included in the count; dorsal surface of head heavily pigmented with brownish black spots on a ground color of dark gray; nasal-prefrontal area heavily pigmented, less so from frontal to posterior edge of parietal; postocular stripe reaching one scale row beyond last supralabial on left side, terminating on last supralabial on right side, not connected to nape blotch; two coalesced black spots on medial edge of center of parietals; labials dirty white with scattered marks of brownish black; mental and anterior two infralabials heavily pigmented with brownish black; center of each scale between parietals and anterior edge of nuchal blotch densely pigmented with brownish black; venter cream white.

Variation.—The single paratype (Fig. 1B) differs from the type in having the band color dark brown rather than black; 21 large anterior bands; posterior bands small, forming an alternating series of smaller spots above the last 58 ventrals. The paratype lacks an anterior median projection of the nuchal blotch. Otherwise, the general color pattern is similar to the type. Unfortunately, the paratype is missing about one-third of its tail, and tail/total length ratio could not be determined. The only scale difference between the paratype and the type is 178 ventrals in the former.

Remarks.—Data from 315 specimens of *Hypsiglena* were made available to us by Mrs. Glenda Tanzer and 200 additional specimens were examined

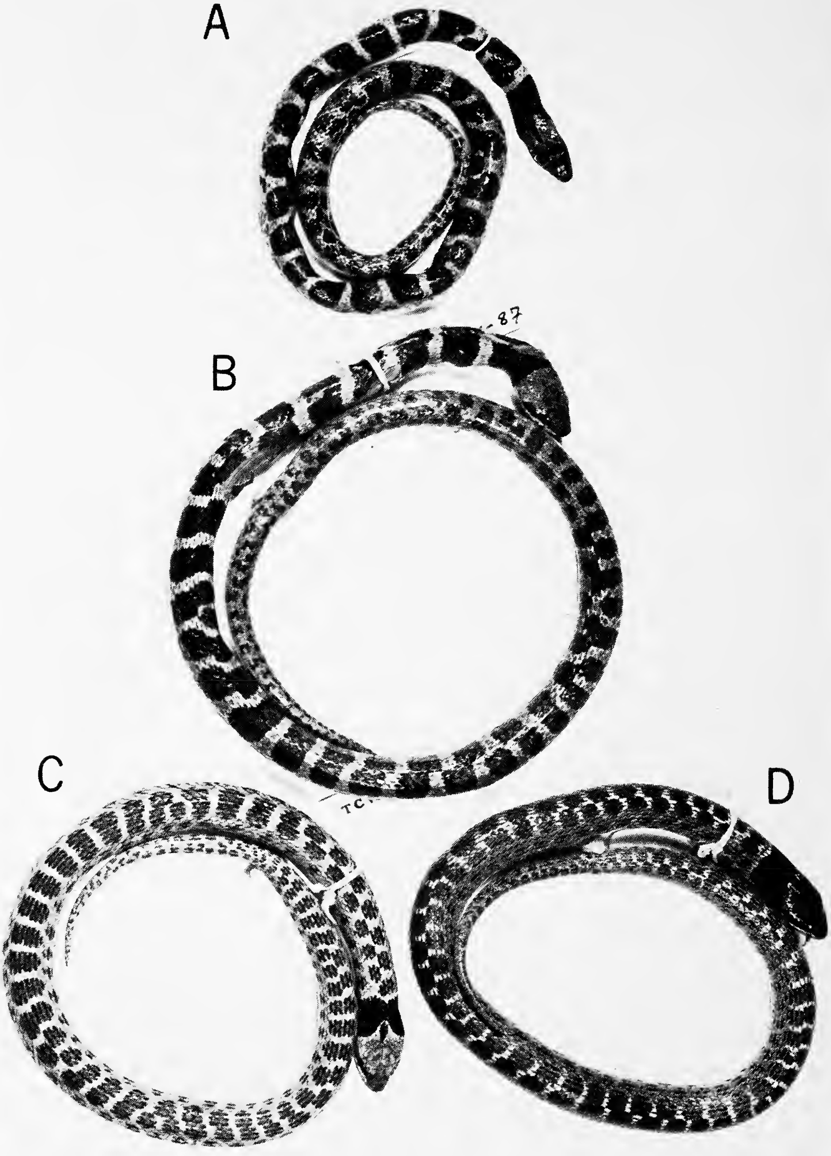
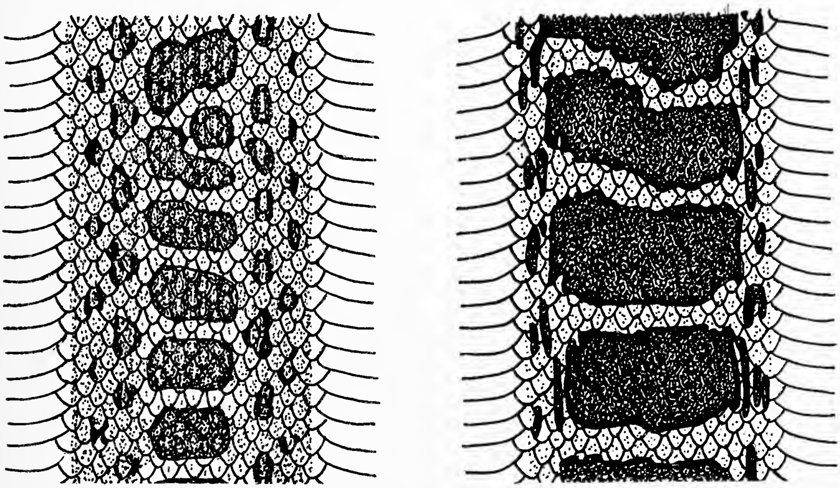


FIGURE 1. Dorsal view of the holotype (A) and paratype (B) of *Hypsiglena tanzeri*, and two male specimens (C and D) of *H. torquata* from Querétaro.

by Dixon. The 515 specimens represent at least three distinct geographic populations; (A) northern Sinaloa, Sonora, and Arizona; (B) the remainder of Sinaloa, Nayarit, Jalisco, Michoacan, Guerrero, and Morelos; (C) all of the Mexican Plateau, the lowlands of northeastern Mexico, Texas, New Mexico, Oklahoma, and Kansas. These will be discussed in greater detail elsewhere. Population "(C)" is of special interest since it is geographically closest to the locality of *H. tanzeri.* The general variation of the former population is as follows: Counts of ventrals plus caudals of 206 male specimens range from 200 to 232 (x = 215.0), in 177 females, 200 to 231 (x = 214.4); midbody scale rows of both sexes generally 21 (in 373 specimens), with 23 rows occurring three times, 20 (4), and 19 (5); scale rows just anterior to the vent are highly variable, with 19 occurring in one specimen; 18 in 4, 17 in 275, 16 in 76, and 15 in 27. Preoculars usually two with a 1-1 combination occurring in ten specimens, 1-2 in 8, 2-2 in 358, 2-3 in 5, 3-3 in 2; postoculars usually two, with 1-1 occurring in eight specimens, 1-2 in 11, 2-2 in 358, 2-3 in 5, and 3-3 in 1; supralabials usually eight, with 7-7 occurring in five specimens, 7-8 in 8, 8-8 in 359, and 8-9 in 11; infralabials usually ten, with 9-9 in 20 specimens, 9-10 in 31, 10-10 in 296, 10-11 in 20, 11-11 in 13, 11-12 in 2, and 12-12 in 1; loreals usually one, with 1-2 in 3 specimens, and 2-2 in 1. Body blotches vary from 41 to 72 (x=51.8) in 186 females, and 36 to 69 (x=49.3) in 215 males.

From the large series available, only 10 male specimens of *H. torquata*



TCWC 34082 TCWC 34079

Figure 2. Midbody color patterns of *H. torquata* (left) and *H. tanzeri* (right) from Querétaro, Mexico.

jani were found that represented the nearest geographic localities to the area where *H. tanzeri* has been taken. The comparative material is represented by one specimen from the Mexican state of Hidalgo, four from San Luis Potosi, two from Querétaro (Fig. 1, C and D), and three from Guanajuato. Their characteristics are: ventrals, 153-166 (x=159.3); caudals, 48-55 (x=50.2); ventrals + caudals, 201 to 219 (x=210.4); supralabials, 8 in eight specimens, 7 in two; infralabials, 9 in two, and 10 in eight; preoculars, 1 in two, 2 in eight; postoculars, 2 in all, third and fourth supralabials entering orbit in two, fourth and fifth in eight; tail length ranges from 15.8 to 18.8 (x=17.5) per cent of total length; body blotches vary from 39 to 53 (x=44.9); width of fifteenth dorsal blotch ranges from 7 to 8 scale rows wide; all specimens with two to three rows of intercalary spots.

Three specimens of *H. torquata jani* were taken 18 and 19 May, 1971, in the Rio Extoraz Valley in Querétaro, some 58 airline kilometers from the type locality of *H. tanzeri.* Their color pattern is typical of nearly all races of *H. torquata* and show no approach to the condition found in *H. tanzeri* (Fig. 2).

The differences presently used to separate the currently recognized races of *H. torquata* are comparatively small. Most are based on the number of ventrals and caudals, subtle differences in color pattern, and reduction in the number of midbody scale rows. When these "racial" criteria are considered with respect to the characters of *H. tanzeri* and adjacent populations of *H. torquata,* additional support is gained for recognition of *H. tanzeri* at the specific level.

Specimens of *H. torquata jani* have been taken from the desert in the states of Querétaro and San Luis Potosí, Guanajuato, and Hidalgo, from tropical deciduous forest in southern Tamaulipas and eastern San Luis Potosí, and from arid scrub in southern San Luis Potosí. Although none have yet come from the arid tropical scrub in the Jalpan Valley, they may someday be taken there.

The soils in the vicinity of the type locality consist of Karst Limestone on the slopes, with alluvial top soil on the valley floor. Dense thickets of cacti and non-thorny shrubs cover the limestone hillsides and cultivated crops are grown on the valley floor. The other nocturnal snakes which have been taken from the same general area are *Elaphe guttata, Lampropeltis triangulum, Leptoderia septentrionalis,* and *Trimorphodon tau.*

ACKNOWLEDGMENTS

We wish to thank Juan Cifentes L., Biologist in the Department de Estudios Biologicos Pesqueros de la Direccion General de Pesca e. Indus. Conexas. for granting us a permit for our studies in Mexico. We would also like to thank Douglas Albaugh, Frank Guyer, and James C. Kroll for their assistance in the field.

RESUMEN

Se describe una nueva especie de *Hypsiglena* de la parte occidental de Querétaro, Mexico. Colectada en la zona de mezquital (árido tropical) del valle de Jalpan. La nueva especie se distingue de las otras *Hypsiglena* por tener la cola más larga y bandas dorsales más anchas. La nueva especie es morfológicamente diferente de las poblaciones más cercanas de *H. torquata jani.*

LITERATURE CITED

BOGERT, C. AND J. A. OLIVER. 1945. A preliminary analysis of the herpetofauna of Sonora. Amer. Mus. Nat. Hist. Bull. 83:301-425.

BOULENGER, G. A. 1894. Catalogue of the Snakes in the British Museum (Natural History). London. Vol. 2, 382 p.

COPE, E. D. 1860. Catalogue of the Colubridae in the Museum of the Academy of Natural Sciences of Philadelphia, with notes and descriptions of new species. Part 2, Proc.. Acad. Nat. Sci. Phila. 12:241-266.

———. 1900. The Crocodilians, Lizards, and Snakes of North America. U.S. Natl. Mus. Rep. 1898:153-1270.

DIXON, J. R. 1962. Three additional specimens of the night snake, *Hypsiglena dunklei.* Herpetologica 8(2):134-135.

———. 1965. A taxonomic reevaluation of the night snake *Hypsiglena ochrorhyncha* and relatives. Southwest Nat. 10(2):125-131.

DUNN, E. R. 1936. Notes on North American *Leptodeira.* Proc. Nat. Acad. Sci. 22:106-119.

DUGES, A. 1865. Du *Liophis janii.* Mem. Acad. Sci. Lett. Montpellier, 6:32-33.

GUNTHER, A. 1860. Description of *Leptoderia torquata,* a new snake from Central America. Ann. Mag. Nat. Hist. Ser. 3, 5:169-171.

———. 1895. Biologia Centrali-Americana. Reptilia and Batrachia. 1885-1902. London. 326 p.

HARDY, L. M., AND R. W. MC DIARMID. 1969. The amphibians and reptiles of Sinaloa, Mexico. Univ. Kans. Publ., Mus. Nat. Hist. 18:39-252.

STEJNEGER, L. 1893. The Death Valley Expedition. A biological survey of parts of California, Nevada, Arizona, and Utah. Part II: 2. Reptiles and Batrachians. North American Fauna 7:159-234.

STEJNEGER, L., AND T. BARBOUR. 1917. A checklist of North American amphibians and reptiles. Harvard Univ. Press, Cambridge. 125 p.

SMITH, H. M. 1943. Summary of the collection of snakes and crocodilians made in Mexico under the Walther Rathbone Bacon Traveling Scholarship. Proc. U.S. Nat. Mus. 93:393-504.

SMITH, H. M., AND E. H. TAYLOR. 1945. An annotated checklist and key to the snakes of Mexico. U.S. Nat. Mus. Bull. 187:1-239.

TANNER, W. W. 1944. A taxonomic study of the genus *Hypsiglena.* Great Basin Nat., 5(3-4):25-92.

———. 1966. The night snakes of Baja California. Trans. San Diego Soc. Nat. Hist. 14(15):189-196.

TAYLOR, E. H. 1938. On Mexican snakes of the genera *Trimorphoden* and *Hypsiglena.* Univ. Kans. Sci. Bull. 25(16):357-383.

Accepted for publication October 11, 1971

Printed in Los Angeles, California by Continental Graphi

NUMBER 223
FEBRUARY 23, 1972

MORE VERTEBRATES, INCLUDING A NEW MICROSAUR, FROM THE UPPER PENNSYLVANIAN OF CENTRAL COLORADO

By PETER PAUL VAUGHN

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1964 AIBS Style Manual for Biological Journals is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1964 AIBS Style Manual for Biological Journals in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Changes in the manuscript after galley proof will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

MORE VERTEBRATES, INCLUDING A NEW MICROSAUR, FROM THE UPPER PENNSYLVANIAN OF CENTRAL COLORADO

By PETER PAUL VAUGHN[1]

ABSTRACT: More fossils, mostly vertebrate, have been collected from a black shale low in the Sangre de Cristo Formation in the Arkansas River valley of central Colorado. Some of the fossils probably represent "residents" in the pond, but most of the bones seem to have been washed in from nearby. None of the recently found specimens conflicts with the estimate of Late Pennsylvanian, probably Missourian, age based on the previously reported fossils (Vaughn, 1969); and recognition of the pelycosaur *Edaphosaurus* cf. *E. ecordi* corroborates this estimate. The presence of bisaccate gymnosperm pollen is attributed to proximity of the area to elements of the Ancestral Rocky Mountains. An almost complete, articulated skeleton of a new kind of microsaur requires the naming of a new genus and species, *Trihecaton howardinus.* This form is clearly a microsaur, as shown by the structure of the first vertebra and the character of the scales; but it is remarkable in the infolding of the enamel of the marginal teeth, and in the possession of large presacral intercentra with capitular facets. There are also large intercentral haemal arches. A new family, Trihecatontidae, is based on the genus, but the position of this family within the Microsauria is obscure. *T. howardinus* seems primitive in a number of respects, but it occurs too high in the stratigraphic column to be regarded as an actual "urmicrosaur." More materials of the diadectid *Desmatodon hesperis* are now on hand. A braincase and connected parts of the dermal roof of an apparently immature specimen show essential similarity to the Early Permian *Diadectes,* but the basipterygoid joint was mobile, and, as rarely seen in *Diadectes,* there are narrow fenestrae between the postparietal and tabular regions. The teeth of a juvenile maxilla contrast with those of the holotypic maxilla in several ways: smaller number, much greater relative length and more incisiform aspect of the first two, separation by longer spaces, and lack of wear facets. An analysis of the replacement cycle of the teeth in the holotypic maxilla of *Desmatodon hesperis* shows a much longer replacement wave than in *Diadectes,* and also reveals the existence of a "gap" between the second and third teeth. In its longer replacement wave, *Desmatodon hesperis* may also differ from the type species, *Desmatodon hollandi,* and it may become necessary to set up a new genus. The problems of the origin and affinities of the diadectids remain unsolved.

---

[1] Research Associate in Vertebrate Paleontology, Natural History Museum of Los Angeles County; and Department of Zoology, University of California, Los Angeles, California 90024.

INTRODUCTION

I have recently published on vertebrate fossils found low in the Sangre de Cristo Formation of central Colorado (Vaughn, 1969). These fossils, which seem to be of Late Pennsylvanian, more specifically Missourian, age represent the only sizable North American tetrapod fauna of that age known from west of the Garnett quarry of eastern Kansas (see Peabody, 1952), although tetrapod trackways are known from elsewhere in the Pennsylvanian of Colorado. They are of special interest in that they occur in the region of the Ancestral Rocky Mountains of late Paleozoic time. The present paper is a report on additional materials recently recovered from the same site; these include remains of new faunal elements, an almost complete skeleton of a new kind of microsaur, and materials that contribute significantly to our understanding of the only known Pennsylvanian diadectid, *Desmatodon.*

The quarry is near the town of Howard in the valley of the Arkansas River, in NW¼ NE¼ SW¼ sec. 22, T 49 N, R 10 E, Fremont County, Colorado. It is about 1450 feet above the base of the Sangre de Cristo Formation as defined by Brill (1952) in a two- to three-foot thick black shale that he designated as part of "Interval 300"; the total thickness of the formation in this region is about 8800 feet. The steeply dipping attitude of the beds has made quarrying difficult, and the shale is not yet completely exposed, but it may be said in general that it is a lens-shaped deposit that probably represents a pond, perhaps an oxbow within the general system of stream channels indicated in this part of the formation. The presently exposed face is about 70 feet in length, from where it is cut by a small stream that flows close to a soil-covered bank, to where it pinches out to the northwest. A study of the layering of the shale and the pattern of distribution of the fossils within the shale is in progress and will be reported at a later date.

I have been fortunate to have had access to Mr. Walter Pierce's manuscript on the stratigraphy of the Howard area (unpublished master's thesis, Colorado School of Mines, 1969), which has assisted greatly in my field work. The Interval 300 quarry is in the upper part of Pierce's "Unit V"; within the lower part of this unit, which has a maximum thickness of about 3700 feet, lies the limestone that Brill (1952) correlated with the Whiskey Creek Pass Limestone to the south and with the Jacque Mountain Limestone to the north. The Sangre de Cristo Formation as defined by Brill begins directly above this limestone. Pierce demonstrates an angular unconformity between Unit V and the overlying Unit VI, but it is not yet known how much time is represented in this break. Pierce also shows that the dominant sedimentary pattern of Unit V is the point-bar type, with streams that flowed generally toward the northwest.

The Sangre de Cristo Formation was deposited in the southern half of the trough that lay between the Late Pennsylvanian and Early Permian Front Range to the east and the Uncompahgre Highland to the west. Mallory (1958, 1960) has presented paleogeographic reconstructions of the trough and surrounding highlands. There is some debate as to the proper name of the formation; Brill (1952) extended the name Sangre de Cristo northward from New Mexico and southern Colorado, but Chronic (1958) has recommended that this name not be used in central Colorado and that instead the older term, Maroon, be retained to emphasize the essential continuity of the beds with the Maroon Formation deposited in the northern half of the trough. Geologists at the Colorado School of Mines are currently engaged in studies of the general region around the Interval 300 quarry, and more detailed stratigraphic analyses will soon appear, but for the present we may rely on Brill's terminology. It must also be noted that the lower parts of the Sangre de Cristo Formation, in Brill's usage of the term, are not everywhere of the same age; in central Colorado the lower part, which includes Interval 300, is apparently Late Pennsylvanian, but the equivalent strata in northern New Mexico are marine and are assigned to the Madera Formation whereas the terrestrial Sangre de Cristo Formation as mapped there is probably entirely of Early Permian age (see Brill, 1952; Vaughn, 1969).

ADDITIONS TO THE FLORA AND FAUNA

Most plant remains from the Interval 300 quarry are very poorly preserved, but there are carbonized bits of wood, and *Calamites* impressions are recognizable. Stratigraphically somewhat lower, but still within Pierce's Unit V and above the limestone correlated with the Whiskey Creek Pass Limestone by Brill, better preserved plants are found in SW¼ SW¼ NW¼ sec. 22. These include *Calamites* pith casts, carbonized impressions of *Walchia* fronds, and impressions of fernlike plants. Below this, in Pierce's Unit IV—roughly equivalent to the upper part of the Minturn Formation of Brill's usage—are found more *Calamites* remains and also bisaccate gymnosperm pollen, which latter Scott (1967) takes as an indication of Permian rather than Pennsylvanian age. Microscopic examination of the black shale of Interval 300 also reveals bisaccate gymnosperm pollen. This may seem to conflict with the evidence presented earlier (Vaughn, 1969) and below for Late Pennsylvanian age of Interval 300, but not necessarily. Clapham (1970), in a study of Permian pollen from Oklahoma, came to the conclusion that gymnosperms producing bisaccate pollen were upland forms. Langenheim (1959:569) has pointed out that our picture of late Paleozoic plant successions is based largely on the record from farther east, where extensive uplands did not exist in the Pennsylvanian, and that, therefore, "lowland plants became known as Pennsylvanian indices and upland plants as Permian indices in the mid-western and eastern United States. . . however, the upland environments of the Ancestral Rockies were close to the marginal swamp and marine environments early in the Pennsylvanian. The result is the presence of 'Permian' plants in intimate association with 'Pennsylvanian' plants and marine invertebrates." Elias (1970:696) accounts in much the same way for recent discoveries of *Walchia*, previously not known to occur below the Upper Pennsylvanian, in the Middle Pennsylvanian of Oklahoma; he feels that "*Walchia* undoubtedly existed . . . in the ancient highlands which rose in conjunction with the very early Pennslyvanian orogenies in the areas of the Arbuckle and Ouachita uplifts." The principle is similar to that expressed by Axelrod (1952) when he suggested that angiosperms may have been present in the Permian and Triassic, but "hidden" in uplands remote from the lowland areas of deposition. It seems probable that the presence of bisaccate gymnosperm pollen in and even below Interval 300 is only a matter of ecological difference, that is, a reflection of the upland conditions of the nearby Ancestral Rocky Mountains and not really inconsistent with the more compelling evidence of Late Pennsylvanian age presented by the vertebrates.

Shells of small pelecypods were noted in my earlier paper; the only other invertebrate remains that have been recognized in Interval 300 are parts of carapaces of the branchiopod *Cyzicus.*

The vertebrates known to date from Interval 300 are:

- Elasmobranch fishes
  - A xenacanth
- Palaeoniscoid fishes
  - One or more kinds
- Labyrinthodont amphibians
  - ?Anthracosaurs
    - A large ?embolomere
  - Temnospondyls
    - Several small rhachitomes including the dissorophid ?*Amphibamus*
- Lepospondyl amphibians
  - Aistopods
    - *Coloraderpeton brilli* Vaughn, 1969
  - Microsaurs
    - *Trihecaton howardinus*, new genus and species
- ?Cotylosaurs
  - *Desmatodon hesperis* Vaughn, 1969
- Pelycosaurian reptiles
  - A "medium-sized" ophiacodont
  - A small sphenacodont
  - *Edaphosaurus* aff. *E. raymondi* (Case, 1908)
  - *Edaphosaurus* cf. *E. ecordi* Peabody, 1957

The additions to my earlier list are: the xenacanth, the dissorophid labyrinthodont, the new microsaur, and *Edaphosaurus* cf. *E. ecordi*; it is also now clear that I am dealing with more kinds of small rhachitomes than I previously recognized. The great difficulty is in the disarticulated nature of almost all the materials, which occur mostly as isolated bones. It is obvious that more faunal elements are represented than can be identified.

The xenacanth "shark" is represented by only one spine (UCLA VP

1736[1]), but this, with its two rows of recurved denticles, is sufficient for identification. The presence of this freshwater form at this site is no surprise.

The remains of palaeoniscoid fishes are frustrating. Mostly, the scales are isolated, but they also occur in articulated patches, and sometimes small parts of skulls and fins are found in association with these patches. The scales are almost all small, smooth and shiny, with diamond-shaped outlines and with the peg-and-socket articulation common among palaeoniscoids, but rare signs of different scales indicate the presence of more than one kind of palaeoniscoid. That these thin scales are found in patches as often as they are would seem to indicate that palaeoniscoids, at least, were "resident" in the pond. Perhaps also to be counted as a resident is the aistopod, *Coloraderpeton brilli*, vertebrae and osteoderms of which are frequently found in articulation or very close association. It may even be that trails of tiny pellets found in a number of places in the quarry are the result of burrowing activity of this aistopod. The presence of coprolites, some containing palaeoniscoid scales, also points to a resident fauna. The scattered remains of almost all the other faunal elements seem to indicate that they were washed in from elsewhere, but parts of what was apparently a single individual of *Desmatodon hesperis* were found not far removed from one another on the same plane, and the specimen of the microsaur described below is almost complete and in nearly perfect articulation. There are no signs of wear on the bones that would indicate transportation from a distant source. It is possible, of course, that some of the scattering of the bones may be due to predatory activity of the xenacanths, but the lack of any discernible bite marks makes it seem more likely that the specimens were washed in from the immediately surrounding area, perhaps during periods of flooding of the adjacent streams.

In my earlier paper, I illustrated premaxillary and palatine bones (UCLA VP 1700 and 1699) of what I took to be a large rhachitomous labyrinthodont. More cranial parts of this form (UCLA VP 1737) are now at hand, including another premaxilla and an associated large part of a dentary bone with small teeth that are slightly recurved at their tips. The premaxilla has a formidable tusk of about 25 mm length, with an oval base 10 mm long but only 6 mm wide. All the teeth show deep infolding of the enamel and dentine in their basal portions. The general shape of the preserved part of the dentary and the traces of the meckelian fenestrae cause me to think that, contrary to my earlier identification, this form may be an anthracosaur, perhaps an embolomere similar to the large *Neopteroplax conemaughensis* described by Romer (1963) from the Conemaugh Group of Ohio. Other elements, including a squamosal bone (UCLA VP 1701), seem to support this. Better materials must be found before a positive identification can be made, but it is clear that a labyrinthodont amphibian of crocodilelike proportions was present in the area.

---

[1] The designation UCLA VP refers to the vertebrate paleontological collection of the University of California, Los Angeles.

Many parts of small to "medium-sized" rhachitomes are represented in the collection from Interval 300. Some of these, as a fairly well-preserved dentary bone with slim, conical teeth (UCLA VP 1738), are of trimerorhachoid aspect; but most are indeterminate. One small, slender dentary with numerous, tiny teeth (UCLA VP 1739) seems clearly to be of a dissorophid. It falls within the size range of dentaries of *Amphibamus lyelli* from the uppermost part of the Allegheny Group of Ohio (Carroll, 1964), which it closely resembles, and it may represent a species of that genus.

Descriptions of remains of a number of pelycosaurian reptiles including a "medium-sized" ophiacodont and a small sphenacodont were given in my earlier paper. More materials of these forms continue to appear. These include: the basi-parasphenoid part of a braincase of the ophiacodont (UCLA VP 1740), with a distance of 26 mm between the lateralmost points of the basipterygoid processes; and a vertebra of the small sphenacodont (UCLA VP 1741), with a centrum about 11 mm long and a neural arch that shows the characteristic excavations on its lateral surfaces. These finds help to demonstrate the taxonomic diversity of the fauna and also reinforce the developing picture of a variety of pelycosaurs in the Late Pennsylvanian (see DeMar, 1970).

My earlier paper also recorded the presence of the little edaphosaurian pelycosaur *Edaphosaurus* aff. *E. raymondi.* It is now evident that there was also another small edaphosaur. UCLA VP 1742 is a partial neural spine that is strikingly similar in both shape and size to the spine of *Edaphosaurus ecordi* Peabody, 1957. As in that species, the spine is laterally flattened but flares distally within the anteroposterior plane and has only incipiently developed tubercles along the sides. The holotype of *E. ecordi* was found near Garnett in eastern Kansas, in a shale that forms part of a lagoonal deposit within the Stanton Formation, Missourian Stage, Upper Pennsylvanian (see Peabody, 1952). The general nature and fauna of the Garnett quarry, from which come the only known specimens of the reptile *Petrolacosaurus kansensis,* are quite different from the Interval 300 quarry, but Peabody (1957:949) points out that the holotype of *E. ecordi* was found near the bottom of the lagoonal deposit, "in heavily carbonaceous shale containing a more typical, coalswamp flora than higher and off-shore deposits in the lagoon."

The new specimens of *Desmatodon hesperis* and the holotype of the new microsaur are described in detailed fashion below. There remain, of course, many skeletal elements that defy taxonomic identification at this time, but they do indicate the presence of a diverse fauna and hold out the promise of further interesting finds.

I have already shown that the vertebrates previously reported indicate Late Pennsylvanian, probably Missourian, age (Vaughn, 1969). This is based largely on the essential similarity of *Desmatodon hesperis* to *D. hollandi* known from the middle part of the Conemaugh Group west of Pittsburgh, Pennsylvania. The association of remains of *Edaphosaurus raymondi* with the holotype of *D. hollandi* supports this estimate of approximate time-equivalence. The primitive nature of the aistopod from Interval 300, *Coloraderpeton brilli*, may perhaps also be cited as evidence for Pennsylvanian, rather than Permian, age.

There is nothing among the recently found vertebrate materials from Interval 300 that would contradict Missourian age; rather, *Edaphosaurus* cf. *E. ecordi* provides corroboration. Sturgeon and Hoare (1968) place the Stanton Formation, from which comes the holotype of *E. ecordi*, at about the same level as the Ames Limestone of the Conemaugh Group. The Round Knob Formation, from which comes the holotype of *Desmatodon hollandi*, lies shortly below the Ames. The Stanton Formation is near the top of the Missourian Stage and thus a closer, but not necessarily more accurate, estimate of the age of Interval 300 might be late Missourian. Nor does an estimate of Missourian age conflict with any other data—excepting perhaps the bisaccate gymnosperm pollen which, as I have said, may merely reflect environmental difference; according to Brill (1952), the Sangre de Cristo Formation in the area of Interval 300 rests conformably on rocks of Desmoinesian (Middle Pennsylvanian) age.

A NEW MICROSAUR

A well-preserved, articulated skeleton of a hitherto unknown kind of microsaurian amphibian is remarkable in a number of features that make it important in consideration of the origin and relationships of the Microsauria. Its distinctness from all previously known microsaurs requires the naming of a new family.

Order MICROSAURIA Dawson, 1863

TRIHECATONTIDAE, new family

This family is based on the new genus *Trihecaton*, described below. Because this is the only known genus, definition of the family is tentative: microsaurs with infolded enamel on the marginal teeth, and with large presacral intercentra with capitular facets for the ribs.

Trihecaton, new genus

*Type species: **Trihecaton howardinus**,* new species.

Diagnosis: Marginal teeth simple cones with shallow infolding of enamel. Prominent coronoid process on lower jaw. Thirty-six presacral vertebrae—as nearly as can be determined. First vertebra of characteristic microsaurian structure, with forward-facing articular facet on either side of short "odontoid" process on anterior face of centrum, and deep notochordal pit on posterior face; two costal facets on either side of first centrum; first neural arch incomplete dorsally. Pleurocentra the dominant central elements, but large intercentra, with capitular facets, in presacral vertebral column. Intercentral haemal arches in tail. Almost regular alternation in shape of presacral neural spines. Presacral ribs articulate with transverse processes low on anterior parts of neural arches and also with intercentra. Stem of interclavicle very short, with abrupt termination. Well-developed limbs. Entepicondylar foramen in humerus. Scales of characteristic microsaurian pattern, with radiate striae.

Etymology: Named for the Interval 300 quarry. From the Greek *treis,* three, and *hekaton*, hundred.

Trihecaton howardinus, new species

Holotype: UCLA VP 1743 (Figs. 1; 2; 3, A-C), an articulated skeleton that lacks most of the skull although a maxilla and a mandible are present. The entire presacral vertebral column and most of the ribs are preserved. There are large parts of the left pectoral girdle and the interclavicle, and most of the left front limb, as well as parts of the right front limb. The pelvic girdle is poorly preserved, but the left femur is complete, and the distal half of the right femur is also preserved. Scales are present throughout the region of the vertebral column.

Referred specimen: UCLA VP 1744 (Fig. 3, D), a partially articulated series of twelve caudal vertebrae with haemal arches. Same kind of scales present as in holotype. Found immediately adjacent to the plastered-out block of matrix that contained the holotype, and probably part of the same individual.

Horizon and locality: Collected by a field party from the University of California, Los Angeles, in the summer of 1970, from Interval 300 of the section of the Sangre de Cristo Formation measured by Brill (1952:870), about 1450 feet above the base of the formation, in NW¼ NE¼ SW¼ sec. 22, T 49 N, R 10 E, Fremont County, Colorado. The age is Late Pennsylvanian, probably Missourian. In European terms, the horizon would be within the lower part of the Stephanian Series. The species is named after the nearby town of Howard.

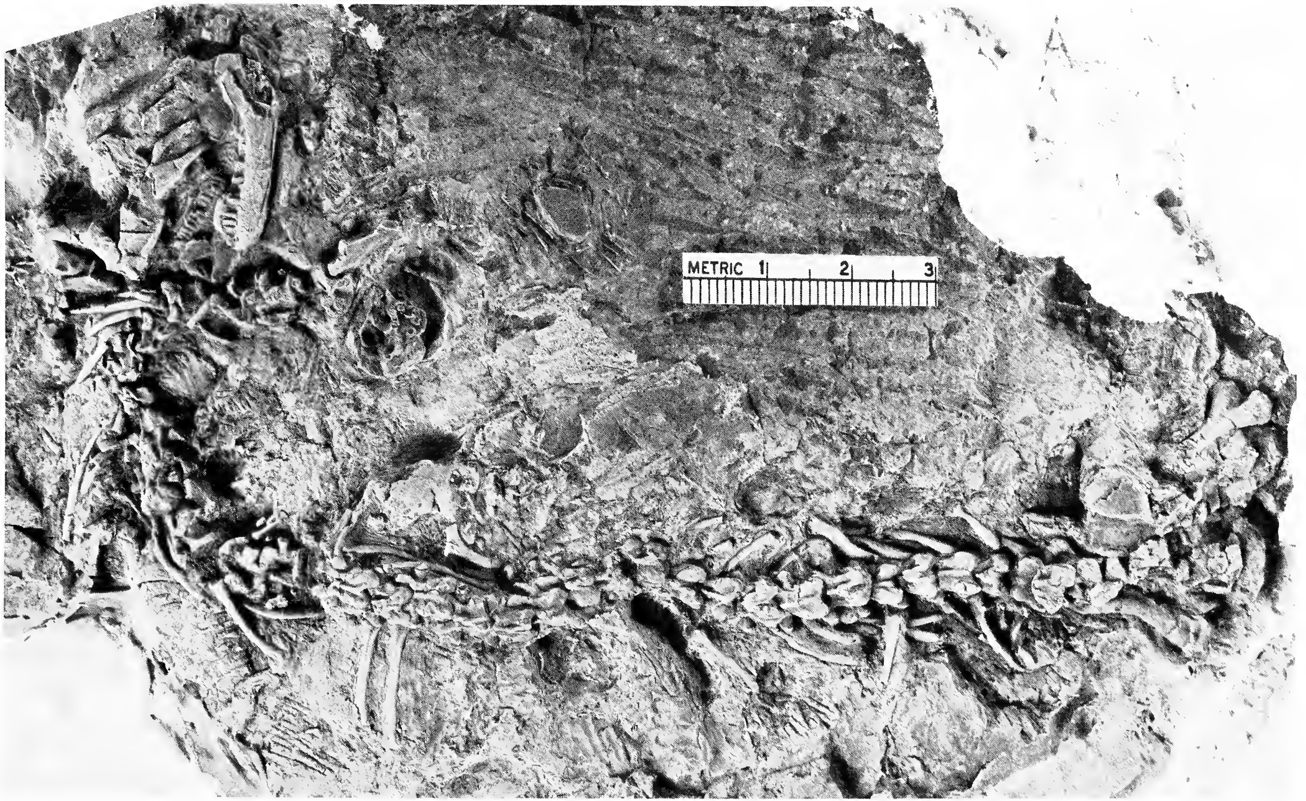
Diagnosis: The same as for the genus as this is the only known species, but a note on size may be appropriate. The length of the skull, as known from the lower jaw, is about 2.5 cm, and the length of the presacral vertebral column is about 16 cm.

Description: Most of the features of the holotype and the referred specimen can be readily seen in the illustrations (Figs. 1, 2, 3). The anterior quarter of the presacral vertebral column is bent to the right and backward. The girdles and limbs are in their proper places relative to the column, but the maxilla, mandible and the few other preserved cranial fragments are displaced and lie adjacent to the interclavicle.

The left maxilla lies directly behind the interclavicle. It seems to be nearly

⟶

FIGURE 1. *Trihecaton howardinus,* new genus and species: photograph of the holotypic specimen, UCLA VP 1743. Dusted with white powder to bring out details. White material surrounding the matrix is plaster. Smallest divisions on the scale are millimeters.


METRIC 1 2 3

complete except for the lack of a small posteriormost part. As preserved, it is 14 mm long; its greatest depth, about 2 mm, occurs about a third way back in its length, and posterior to this it tapers gradually to a depth of less than 0.5 mm. Nineteen slender, conical teeth are present, and there are spaces for three more. The anteriormost two are very slightly recurved, but the rest are straight. The longest, about 1.8 mm, are in the region of greatest depth of the maxilla; anterior to this they become slightly shorter, and posteriorly they

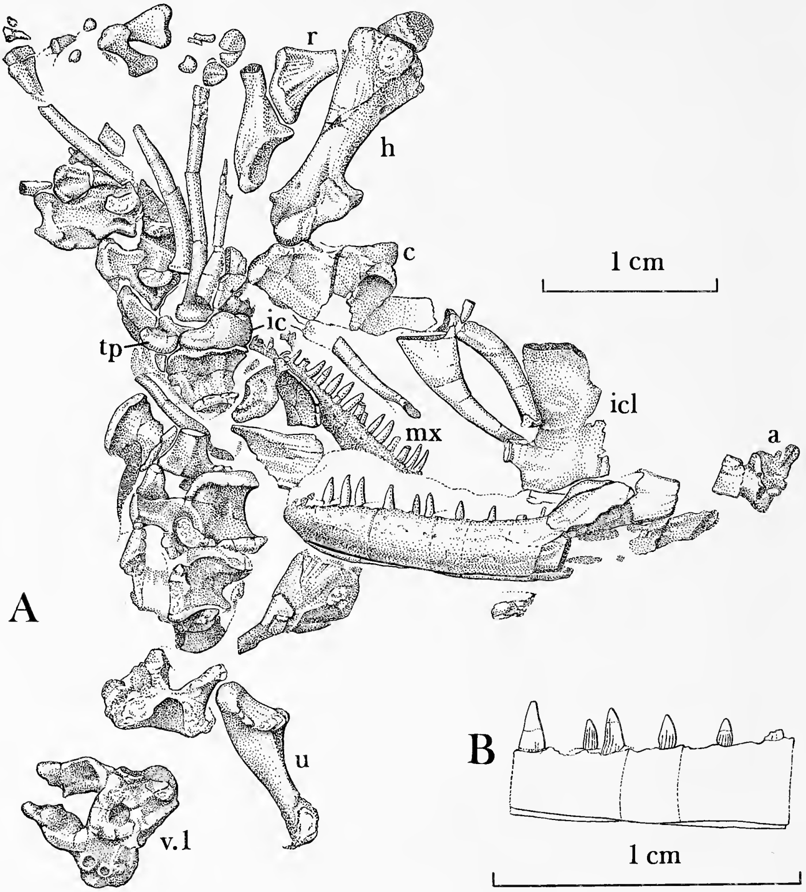


FIGURE 2. *Trihecaton howardinus*, new genus and species: details of holotypic specimen, UCLA VP 1743. A, anterior part of holotype, with mandible in lateral view, elements of pectoral girdle in internal view, and vertebrae in various views—first vertebra seen from behind; B, mandibular teeth at greater magnification. Abbreviations: a, articular region of mandible; c, coracoid plate; h, left humerus; ic, intercentrum following vertebra 6; icl, interclavicle; mx, maxilla; r, left radius; tp, transverse process of vertebra 7; u, right ulna; v. 1, first vertebra. Size indicated by the 1 cm scales.

decrease gradually to very small size—the exact length of the posteriormost teeth cannot be determined, due to breakage. A number of the teeth clearly show infolding of the enamel, expressed externally by fine grooves that are especially obvious in the basal portions; that the infolding is shallow is evident from the fact that those teeth that were worn, either prior to or during preparation, lack the grooves.

Almost all of the left mandible is preserved, exposed in lateral view. Although the posterior portion of the surangular, to which is attached an articular bone that projects mediad as a long spur, is broken and slightly displaced from the rest of this element, the clean fracture premits confident measurement of the total length of the mandible, 26 mm; this provides, of course, an excellent index to length of skull. The lateral surface of the mandible, especially the dentary, is irregularly pockmarked by small, subcircular pits; this is also true of the maxilla. The mandible is slender in most of its length, with a depth of only 3 mm midway along the tooth row, but posteriorly it rises in a prominent coronoid process, 6 mm deep, in which region the dentary overlaps the anterior part of the surangular and is capped by a conspicuous coronoid bone. The dentary meets a long splenial along the ventral border of the mandible. The angular bone is badly fractured, but it seems to have extended about as far posteriorly as did the surangular. Nine teeth are preserved in their entirety, stumps of three others are present, and there are spaces for about seven more. As in the maxilla, the teeth are slender cones, with the more anterior ones slightly recurved. Five of the teeth clearly show the grooves related to the infolding of the enamel; these grooves are more

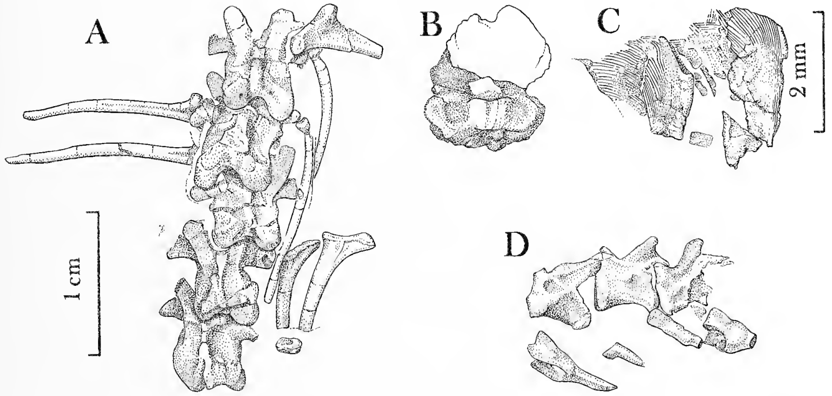


FIGURE 3. *Trihecaton howardinus*, new genus and species: details of holotypic specimen, UCLA VP 1743, and referred specimen, UCLA VP 1744. A, vertebrae 17-21 of holotype in dorsal view, and associated ribs; B, first vertebra of holotype in anterior view, some matrix left adherent to permit reunion with rest of specimen; C, fragmentary scales taken from near vertebra 17 of holotype; D, caudals from posterior portion of vertebral string of referred specimen. Size of A, B and D indicated by the 1 cm scale; size of C indicated by the 2 mm scale.

prominent at the bases but extend about three-quarters of the way up the teeth. In the rest of the teeth, which are worn, the grooves are not apparent. As in the maxilla, the longest teeth, about 1.8 mm, lie a short distance back in the jaw; anteriorly and posteriorly the teeth become shorter, with the shortest lying just in front of the root of the coronoid process. The anteriormost teeth are preserved only as stumps, and their exact lengths cannot be ascertained.

A few scraps of other cranial elements lie near the maxilla and mandible, but they cannot be identified with confidence.

As nearly as can be determined, there are 36 presacral vertebrae, in a column that was about 16 cm long. What I count as the last presacral has been pushed upward to partially override the poorly preserved, but obviously more massive, remains of what I judge to be a sacral, closely appressed to the pelvic girdle. The first vertebra is displaced from the second by several millimeters, but there is no evidence of an intervening vertebra. It is conceivable that there may have been 37 presacrals, but I am fairly confident that 36 is the correct number. There seems to have been only one sacral, but this cannot be stated positively. Scraps of caudals are present in the holotype, but the nature of the caudals is evident only in the referred specimen, and their number is unknown. Slight rotation and displacement of various vertebrae in the anterior part of the column display some in lateral, some in ventral, and some in dorsal view. Farther posteriorly, most of the vertebrae are seen in dorsal view, but rotation of vertebra 14 and loss of the neural arches of 15 and 16 allow intercentra to be seen in that region—as well as in the anteriormost parts of the column. These circumstances are fortunate, because the highly fissured nature of the matrix would make it hazardous to attempt to display the column from below.

Wherever in the column a series of well-preserved vertebrae is exposed in dorsal view, there can be seen an almost regular alternation in the shape of the neural spines. This is especially clear in vertebrae 17-21 and 26-35. The alternation is not quite as marked as in *Pantylus* (Carroll, 1968) but is pronounced nevertheless. In the "low" type (e.g., vertebrae 27 and 29), the spine runs the entire length of the neural arch as a low, rounded ridge. In the "high" type (e.g., vertebrae 28 and 30), the low ridge occupies only the anterior half of the arch; posteriorly, the spine broadens abruptly, rises slightly higher, and sends a short process forward. In the more anterior portions of the column this process is generally single, but posteriorly it is divided into a side-by-side pair of processes. That the alternation is not completely regular is shown by vertebrae 17-21, where the sequence is low-high-low-high-high. The significance of this alternation, which occurs also in other late Paleozoic tetrapods, is obscure. I have attempted an analysis of a similar pattern in the Early Permian reptile *Captorhinus* in terms of the system of interspinous ligaments, with particular regard to an "extended nuchal ligament" (Vaughn, 1970), but the presence of this pattern in the long-trunked *Trihecaton* casts doubt on such an explanation.

The first vertebra fits so well into the general microsaurian pattern (see Carroll and Baird, 1968) that only its salient features need description. Its length, from the tip of the "odontoid" process to the posterior edge of the centrum, is 4 mm. The "odontoid" process, on the anterior face of the centrum, is short, is rounded on its anteroventral surface, and is channeled by the neural canal on its dorsal surface. On either side of this process is a large, subcircular, slightly concave articular facet for the occiput; these facets face directly anteriad. The distance between the tips of the winglike buttresses for these facets is 7.5 mm. Each of these wings has on its posterolateral surface two small, slightly raised and centrally dimpled facets, one above the other; these are obviously for the first rib. The posterior face of the centrum, with a deep notochordal pit, has a width of only 3.5 mm. The greatest height of the centrum is 4 mm; the highest points of the neural arch are 8 mm above the bottom of the centrum. The lateral halves of the neural arch almost meet at a point anteriorly, but posteriorly they diverge widely. A short, blunt spine rises above each posterior zygapophysis. The lack of junction of the halves of the neural arch is not unique; Miss Eleanor Daly (personal communication, 1971) has shown me a similar condition in certain microsaurs from the Lower Permian of Oklahoma.

The shape of the centra (pleurocentra) can be easily made out in several of the anterior vertebrae and also in the region of vertebrae 14-16. In general, the centra are like those of the microsaur *Tuditanus* (see Peabody, 1959; Carroll and Baird, 1968). They are notochordal, are excavated on their lateral surfaces in such a way that they appear pinched, and a rounded ridge forms the concave ventral border. They are different from those of *Tuditanus* in that the ventral portions of both the anterior and posterior lips of the centra are bevelled for the reception of the large intercentra. The centra that can be measured are each somewhat more than 4 mm long, and are about 5 mm wide and 3.5 mm high at the posterior end. Vertebrae 15 and 16 show that the floor of the neural canal paralleled the hourglass-shaped notochordal canal.

The neural arches are not swollen. They are firmly joined to the centra, but the lines of the neurocentral sutures are evident as curved ridges. The neural spines have already been described. The zygapophyses are oval with long anteroposterior axes, with their articular surfaces in the horizontal plane. Stout transverse processes about 1.5 mm long occur near the junctions of the neural arches and centra on all the presacral vertebrae excepting the first, and possibly the second, which is poorly preserved. They are kidney-shaped in cross-section, concave side to the rear, with the upper end lying approximately midway in the length of the vertebra and the lower end near the front edge of the centrum, apparently in contact with the apex of the intercentrum. The costal facets of the transverse processes face forward, laterally and ventrally.

An intercentral scrap is visible in front of the second vertebra, large parts of the intercentra are exposed in front of vertebrae 3 and 6, and a complete one lies in apparently its life position against the posterior rim of the centrum of vertebra 6. Parts of intercentra may also be seen in front of vertebrae 14, 15 and 17. The intercentrum in front of vertebra 14 seems to have been as large as the one behind vertebra 6; this, plus the presence of large haemal arches in the caudal series, makes it seem likely that intercentra were present throughout the entire presacral column.

As shown by the one behind vertebra 6, the intercentrum is a large crescent that extends halfway up along the bevelled lip of the centrum. The ventral portion is much swollen toward the sides, almost bulbous, and has an anteroposterior length of 2 mm, almost half as long as the centrum. On either side, the wedge-shaped ascending part of the intercentrum bears a large, concave articular facet that faces posteriorly as much as it does laterally. This ascending part is abruptly truncated where it meets—actually lies against —the ventral end of the transverse process. This proximity of capitular and tubercular facets is consonant with the structure of the ribs described below. The intercentrum in front of vertebra 14 also shows the capitular facet.

The first several ribs are not preserved, but the costal facets on the first vertebra show that ribs must have been present in this region. Indeed, the well-developed transverse processes back to and on the last presacral, plus ribs either articulated or in close association with almost all the vertebrae, show that there were ribs throughout the presacral column. The ribs articulated on the left sides of vertebrae 18 and 19 have gradually tapered shafts about 14 mm long. Ribs farther forward in the column have expanded distal ends. The structure of the head is best seen in partial ribs lying to the right of vertebrae 17 and 19. The dorsoventral length of the head is about 4 mm. The strongly convex capitulum is separated by only 0.5 mm from the slightly concave tuberculum; the connecting web is much thinner than either the capitulum or tuberculum, but its margin is not incised. Distal to the head the shaft narrows rapidly. Wherever else the heads of ribs can be seen, including the anterior part of the column, the pattern is similar, and what can be seen of the ribs immediately anterior to the pelvic girdle indicates that articulation was with both transverse process and intercentrum throughout the presacral column, excepting of course the first rib.

The referred specimen contains parts of twelve caudal vertebrae. Two of these, in articulation but displaced from the rest, have transverse processes that are fairly well developed but without the ventrad prolongations seen in the presacral vertebrae. Intercentral elements are not attached to these two vertebrae, but the bilaterally bevelled surfaces of the posteroventral parts of the centra indicate that haemal arches were present. The other ten vertebrae, of which the most anterior is represented by only a fragmentary haemal arch, are in one string, but two vertebrae midway in this string have undergone rotation in the vertical plane. This displacement of parts is in accord with the jumbled nature of the pelvic bones of the holotype. A vertebra toward the anterior end of the string has a small transverse process, but only small nubbins are present in the same positions on the more posterior vertebrae. The neural spines are thin, short, and inclined somewhat posteriad; there is no sign of alternation in shape. Posteroventrally directed haemal arches are present throughout the string; they are clearly separate from the centra, between which their proximal ends are wedged. A well-preserved haemal arch toward the posterior end of the string is 7 mm long. Part way along the length of each haemal arch, coinciding with the ventral limit of the haemal canal, there is a bulbous swelling; distal to this the arch tapers, ending in a slight dilatation in the more anterior ones, in a point in the more posterior ones. The swollen portion comes to lie more proximally farther back in the string. A bridge of bone completes the haemal canal dorsally. As previously mentioned, the referred specimen also includes scales identical to those of the holotype. There is also a metatarsal or phalangeal element.

Although the pectoral girdle of the holotype is not entirely preserved, it is clear that in most features it resembles that of *Pantylus* (see Carroll, 1968). A fragmentary element on the left side of the interclavicle may be part of a cleithrum or clavicle, but this is not certain; an adjacent element seems to be a displaced anterior rib with expanded distal end. The interclavicle is seen in internal view. It is T-shaped, with an expanded bowl that must have been about 15 mm in width but, quite unlike *Pantylus*, the stem is very narrow and remarkably short, only about 1 mm. This shortness does not appear to be due to fracture; at its termination the stem dilates slightly and ends abruptly in a rugose surface. It would almost seem that it was continued in cartilage, but this is highly unlikely in a dermal element. The coracoid plate of the left scapulocoracoid, which lies in the region of vertebrae 4-6, is exposed in internal view. Most of the scapular blade is missing, but it is clear that, as in *Pantylus*, it joined the coracoid plate anterior to the glenoid fossa. Also as in *Pantylus*, the glenoid fossa is buttressed anteriorly by a ventrad projection along which the articular surface is continued, and the part of the coracoid plate posterior to the fossa is short and narrow. There is a coracoid foramen medial to the junction of the scapular blade and coracoid plate. The greatest anteroposterior length of the scapulocoracoid seems to have been about 13 mm.

Only the proximal portion of the right humerus is preserved, but the left is complete and is nearly in articulation with the glenoid fossa. As in both *Tuditanus* (Carroll and Baird, 1968) and *Pantylus*, there is an entepicondylar foramen about three-fifths of the way from the head to the distal end of the humerus, but the overall resemblance is closer to *Tuditanus*, in which the entepicondyle is more widely flared than the ectepicondyle. In *Pantylus* (Carroll, 1968, fig. 5), the capitellum lies on a prominently produced ectepicondyle, quite unlike the general tetrapod pattern. The distal and proximal planes of the humerus are twisted at almost a right angle to one another as in *Pantylus* (this feature is obscure in *Tuditanus*), but the shaft is somewhat more distinct. The articular ends are rugose, but there is no indication of immaturity; all the usual processes of the head are present, and the capitellum is a well-developed hemisphere. The humerus is 15 mm long, 6 mm wide across the head, slightly wider across the distal end, and has a minimum thickness of about 2 mm in the shaft.

Only the left radius is present; this has a semicircular head, narrow shaft —which is broken—and dilated distal end, much as in *Pantylus*. Only the right ulna is complete. It is 10 mm long, has a prominent olecranon, and is much narrower distally than proximally. There are closely associated but disarranged carpal elements and two metacarpals near the epipodials on the left side, but nothing can be confidently said of their original organization, nor of the number of digits.

The broken bones of the pelvic girdle overlap one another; while it is possible to recognize the individual elements, distinctive features cannot be discerned. The femur of the left side is complete, and the distal half of the right one is also present. The femur is gently sigmoidal, about 17 mm long, with a moderately developed adductor ridge and well-separated tibial condyles. The shaft has a diameter of about 2 mm in its narrowest portion; the distance across the distal condyles is 7.3 mm. A proximal fragment of an epipodial is present, but there is nothing more distal. The nature of the remains and the matrix demands "blind" removal of most of the blocks at the quarry, and in this process the holotype was truncated just behind the pelvis, probably separated from the referred specimen as mentioned earlier.

Imbricated scales may be seen alongside almost all the skeletal elements. Their fragility makes them extremely difficult to remove and prepare satisfactorily, but it has been possible to study the surface details of a number of them. They resemble very closely those of Pennsylvanian microsaurs illustrated by Carroll and Baird (1968, fig. 20). They are oblong, have a ridge along one border, and have radiate striae. The striae are especially well displayed on some of the scales of the referred specimen. A scale taken from the region of vertebra 17 of the holotype is about 1 mm wide by 3 mm long.

It is possible that other parts already collected from Interval 300 will eventually prove to be referable to *Trihecaton howardinus*. A specimen that consists mostly of finely denticulate palatal elements but also includes a partial maxilla with small, conical teeth (UCLA VP 1698) was identified in my earlier paper as a labyrinthodont amphibian, because of the infolded enamel (Vaughn, 1969). It may be of *T. howardinus*, but the specimen does not include the characteristic scales that would make this clear. Further excavation at Interval 300 is planned, and hopefully, better cranial materials may soon be found.

Discussion: Trihecaton must be regarded as a microsaur. Among Paleozoic tetrapods, the kind of first vertebra seen in *T. howardinus* is found only among the lepospondyl amphibians; and the combination of pleurocentral-intercentral construction of the vertebrae, well-developed limbs, and characteristically microsaurian scales—plus the fact that the neural arches are not, with the exception of the first vertebra, divided dorsally—rules out all lepospondyls but microsaurs. It is also clear that *Trihecaton* differs greatly from all previously described microsaurs. No others have infolded enamel (Carroll and Baird, 1968), although the bases of the teeth in *Trachystegos* do show a coarse fluting (Carroll, 1966). Although haemal arches have been found in several microsaurs including *Pantylus* (Carroll, 1968; Carroll and Baird, 1968), and small presacral intercentra have been reported in *Microbrachis* (Brough and Brough, 1967), none of the known microsaurs approaches *Trihecaton* in its large presacral intercentra with capitular facets for the ribs; and it must be remembered that *Trihecaton* also has well-developed haemal arches. The recently described lepospondyl *Acherontiscus* (Carroll, 1969) does have large intercentra, but the vertebral construction is so similar to that of the embolomerous labyrinthodonts that Carroll hesitated to assign *Acherontiscus* to any recognized order. The enamel in *Acherontiscus* is not infolded. It is difficult to escape the impression that *Trihecaton* is very primitive, despite its occurrence fairly high within the stratigraphic range of known microsaurs.

Two groups usually included in the Microsauria, the Adelogyrinidae and the Lysorophidae, are now considered by Carroll and Baird (1968) to be somewhat separate stocks; this is also the view of Thomson and Bossy (1970), who distinguish these two families from what they call "eumicrosaurs," a convenient term for present purposes. There does seem, however, to be general agreement that the adelogyrinids, lysorophids and eumicrosaurs are much more closely related to one another than any of these are to the remaining lepospondyls of traditional classification, the Nectridea and Aistopoda. Thomson and Bossy are of the opinion that the trend toward a holospondylous vertebral condition seen among the lepospondyls is not a reliable indicator of relationship but is, instead, a parallel tendency somehow correlated with small size. They conclude that the "Lepospondyli" are not a natural assemblage and suggest that the term be abandoned; with this I heartily concur.

Trihecaton would seem to be allied with the eumicrosaurs. The lysorophids are so different that they need hardly be considered, and no evidence of pleurocentral-intercentral construction of adelogyrinid vertebrae has ever been presented. Nevertheless, *Trihecaton* may represent something of a bridge between adelogyrinids and eumicrosaurs. Thomson and Bossy point out that the adelogyrinid jaw system was probably of the kinetic-inertial kind (see Olson, 1961), whereas the small coronoid process and other cranial features in the eumicrosaurs indicate a predominantly static-pressure system. *Trihecaton* has a prominent coronoid process. It is unfortunate that more of the skull is not known in *Trihecaton*, but in this seemingly annectent feature we may have reason to regard this genus as primitive.

It is certainly unwise to assume that all amphibians were derived from the Late Devonian ichthyostegalians—the variety of Mississippian forms is too great—but perhaps we may assume, in conservative style and for the time being, that the microsaurs and the labyrinthodont amphibians did have a common origin. If we do, we may perhaps regard the infolded enamel and the large intercentra in *Trihecaton* as additional marks of primitiveness. This suggestion invites dispute. Thomson and Bossy (1970) give reason to believe that such characters of tooth and vertebral structure may not be the reliable indices to relationship that they were once thought to be. However, their argument that infolding of the enamel is merely a function of large tooth size is considerably weakened by the occurrence of this character in such a small form as *Trihecaton*, even granted that the infolding is shallow. With regard to the vertebrae, Thomson and Bossy agree with Panchen (1967) that the structure of the centrum is extremely plastic. Differential composition of the centrum–multipartite versus unitary, differential emphasis on the parts when multipartite—may merely reflect different responses to problems of support and locomotion. Carroll (1969) regards the "embolomerous" construction of the vertebrae in *Acherontiscus* as probably associated with lengthening of the segments to assist in sinuous swimming movements. As Thomson and Bossy say (1970:14), "the combined centrum (divided or whole) is homologous in all amphibians," that is, not too much stress should be laid on the pleurocentrum and intercentrum in terms of strict homology. Despite these cautions, it does still seem that a combination of features in *Trihecaton*—infolding of the enamel, large presacral intercentra, prominent coronoid process—give this genus an overall aspect of primitiveness.

Trihecaton, at a Stephanian horizon, is of course too late in time to be considered as an actual "urmicrosaur." Adelogyrinids are known from the Lower Carboniferous (see Carroll, 1967); the problematic *Acherontiscus*, with a skull similar to that of eumicrosaurs, probably occurs in the lowest Upper Carboniferous (Carroll, 1969); and eumicrosaurs are known as low as the Westphalian B level, in the Joggins Formation of Nova Scotia (Carroll, 1966). Perhaps we may regard *Trihecaton* as a relict.

Of the eumicrosaurs, Carroll and Baird (1968) tentatively recognize the families Gymarthridae, Tuditanidae, Hyloplesionidae and Microbrachidae; and Carroll (1968) suggests that we consider the pantylids as a separate family. It is difficult to select from among these the family closest to the Trihecatontidae. For example, *Trihecaton* resembles the microbrachids in having a large number of presacral vertebrae (38-40 in *Microbrachis*) and in the presence of presacral intercentra (see Brough and Brough, 1967); but in its well-developed limbs and in the presence of an entepicondylar foramen in the humerus, *Trihecaton* resembles the shorter-trunked tuditanids (29 presacrals in *Tuditanus*) and pantylids (24 presacrals in *Pantylus*), with the resemblance to *Pantylus* extending to details of the pectoral girdle (see Carroll and Baird, 1968; Carroll, 1968). Aside, it may be noted that a long trunk in microsaurs is usually thought to be a sign of aquatic habits, and the feeble limbs in *Microbrachis* do seem to corroborate this, but *Trihecaton* has fairly sturdy limbs. Because of the incomplete nature of most microsaurian remains, there is at present little ground for decision as to whether an elongate column is primitive or advanced in this group. It may be of functional significance that the two microsaurs known to have presacral intercentra, *Trihecaton* and *Microbrachis*, also have long trunks. Perhaps the larger intercentra in *Trihecaton* are correlated with the sturdier limbs; Parrington (1967) has shown how the large intercentra in rhachitomous labyrinthodonts helped strengthen the column in terrestrial locomotion while still allowing flexibility, but rhachitomes are short-trunked. The alternation in shape of the neural spines may at first glance seem to be a special resemblance to *Pantylus* (see Carroll, 1968), but this phenomenon was apparently of widespread occurrence among late Paleozoic tetrapods and may be seen also in the Pennsylvanian lysorophid *Molgophis* (Dr. Donald Baird, personal communication, 1971) and even in the Early Permian reptile *Captorhinus* (Vaughn, 1970). *Trihecaton* stands alone among known microsaurs in its infolded enamel and its large presacral intercentra with capitular facets. It seems best, for now, not to pursue the placement of the Trihecatontidae within the Microsauria, but to leave this for later studies against, hopefully, a larger background of known forms.

Present knowledge of *Trihecaton* does not help solve the question of possible affinities of the microsaurs and the captorhinomorph reptiles. Romer (1969), in a recent and thorough study of the cranial anatomy of the Early Permian *Pantylus*, has demonstrated that the braincase and branchial arches of this form have a definitely amphibian cast, and comes to the conclusion that microsaurs and captorhinomorphs cannot have any antecedent-descendent relationship. Nevertheless, distinctions between microsaurs and captorhinomorphs continue to disappear; for examples, Carroll and Baird (1968) have demonstrated that the microsaurian first vertebra is a compound of elements probably homologous to the reptilian atlas and axis, and knowledge of *Trihecaton* adds to the growing list of microsaurs that have pleurocentral-intercentral vertebrae. Possibly this points to some remote community of origin of captorhinomorphs and microsaurs, but this is far from clear.

NEW INFORMATION ON *Desmatodon hesperis*

The genus *Desmatodon* was based by Case (1908) on *Desmatodon hollandi*, the holotype of which is a fragment of maxilla with four complete teeth and the root of a fifth (CM 1938, Carnegie Museum, Pittsburgh); the holotype was collected from the Round Knob Formation, Conemaugh Group, western Pennsylvania. I have named the species *Desmatodon hesperis* on the basis of a complete left maxilla with twelve teeth (UCLA VP 1706) taken from the Interval 300 quarry, and to this species I have already referred other materials: more teeth including "incisors," vertebrae, a humerus, and other elements (Vaughn, 1969). I have also pointed out that, while *D. hesperis* and *D. hollandi* are essentially similar as far as comparisons can be made, the tendency toward more conical shape of the teeth in *D. hesperis* gives this species a somewhat more primitive aspect. More materials referable to *D. hesperis* are now on hand from Interval 300, and these provide welcome additional information on the nature of *Desmatodon*, the only known Pennsylvanian member of that odd group of primitive reptiles—or seymouriamorph labyrinthodonts—called the diadectids.

UCLA VP 1745 (Fig. 4, A-C) consists of a braincase and firmly joined fragments of the posterior elements of the dermal skull roof. It was found on a plane that yielded various closely associated parts referable to *Desmatodon hesperis*, including teeth and vertebrae, but even without this association the diadectid nature of the specimen would be immediately obvious. It resembles in almost all ways the corresponding portion of the skull in the Early Permian *Diadectes*, and it may be safely assumed that the specimen is of *Desmatodon hesperis*. It has been distorted in such a way that the angle between the occipital surface and the dermal roof has been decreased, and parts of the braincase on the left side have been moved forward to leave a large gap between the ventral portions of the proötic and opisthotic. This distortion makes it difficult to take accurate measurements, but the original distance between the facets for the quadrate bones may be estimated at about 43 mm, and the distance between the lateralmost points of the paroccipital processes was about 48 mm. The specimen is very probably of an immature individual, to judge from the almost complete lack of ossification in the region of the otic labyrinth and by its close association with the juvenile maxilla described below. Because of the essential resemblance to *Diadectes*, for which excellent illustrations are available (Olson, 1947, 1966; Watson, 1954), description may be limited to salient features.

As in *Diadectes,* the opisthotic, supraoccipital, postparietal and tabular bones are indistinguishably fused; but the exoccipitals are separate, and the line of junction between the proötic and opisthotic can be easily discerned on either side. It is impossible to trace the suture between the parietal and postparietal bones with any confidence although it does seem clear that, again as in *Diadectes*, the postparietal has both occipital and roofing components. A symmetrically curved line across the postparietal area separates the rugose surface of the roof from the smoother occipital surface. A median ridge running ventrad from the postparietal, and a transverse ridge across the supraoccipital region mark out areas for attachment of occipital muscles. The parietal foramen is enormous, with almost the same diameter as the foramen magnum (about 12 mm), although distortion in both regions makes this only a rough comparison; the proportions in *Diadectes* are similar. The suture between the parietals can be followed for a short distance behind the foramen. About 1.5 cm to the left of the parietal foramen there is a deep longitudinal groove on the dorsal surface; this is seen also in certain *Diadectes* specimens (Watson, 1954, fig. 22), in which the groove partially demarcates the lateral parietal lappet from the main body of the parietal. A faint suture can be traced along the floor of the posterior part of this groove; this supports

Olson's (1950) arguments that an intertemporal bone was present in diadectids and that the parietal lappet is formed by this element. The nature of the groove, showing incomplete ossification between two dermal elements, is in accord with the pattern in *Diadectes*, of which Olson (1950:63) says, "Fusion of adjacent elements in the occipital and temporal regions appears to have been initiated at an early stage and to have progressed from the inner to the outer surface of the skull"; and it is also additional evidence of the immaturity of the specimen. Fractures and displacements in the region of the supratemporal make it impossible to delimit this bone satisfactorily, but an undulating longitudinal furrow probably marks its contact with the tabular.

One of the most interesting features of the specimen is the presence, on either side, of a fenestra between the postparietal and tabular regions. The thin, finished borders leave no doubt that these openings actually existed. The bone along the lateral border of the right fenestra is lacking, but the left fenestra is completely bounded. It is about 14 mm long; toward its posterior end it is about 8 mm wide as preserved but was probably narrower in life—the fragment of the tabular in this region is displaced slightly to the left, overriding the most posterior part of the facet for the supratemporal. *Desmatodon hesperis* is not really different from *Diadectes* in this feature. Although the fenestrae are rarely seen in *Diadectes*, they do occur in certain specimens (Case, 1911; Huene, 1913). Olson (1947) has commented on these openings in *Diadectes* and has pointed out that they do not lie in the position of "normal" reptilian temporal fenestrae. In view of the sporadic appearance of the fenestrae in *Diadectes*, and the indications that UCLA VP 1745 is immature, it certainly would be unwise to consider the fenestrae as diagnostic of *Desmatodon hesperis*, let alone the genus.

As in *Diadectes*, the supraoccipital sends a process under the postparietal, terminating abruptly at a line that corresponds to the separation dorsally between the roof and occipital surfaces. Despite the distortion that has driven the left proötic forward, both proötics are well preserved and resemble the same elements in *Diadectes*, extending upward and backward to their broad junctions with the opisthotics. The foramina for the abducent nerves penetrate the dorsum sellae, and a deep incisure that is more evident on the anterior margin of the right proötic presumably marks the place of exit of the trigeminal nerve. Jutting forward from just above the dorsum sellae are bilaterally placed plates that must represent the pilae antoticae; it is not clear that their lack of actual connection with the dorsum sellae might not be due to fracture and slight displacement, but they do seem to be separate elements, and perhaps this is another sign of immaturity. Olson (1966) has illustrated broad pleurosphenoids in this region in *Diadectes*, coösified with the dorsum sellae. Above and partly behind the upper end of the proötic, there is on the lateral surface of each opisthotic a deeply concave, elongate facet; this is the socket for the quadrate bone. This unusual mode of articulation of quadrate and braincase is known also in *Diadectes.* This specimen helps show that Olson (1966) has correctly interpreted the socket as occurring on the opisthotic in *Diadectes,* not on the proötic as was stated by Watson (1954).

The parasphenoidal rostrum is incomplete, but enough is left to show that it flared dorsad in front of the sella turcica. Only the left basipterygoid process of the basisphenoid is preserved. This has smooth anterodorsal and

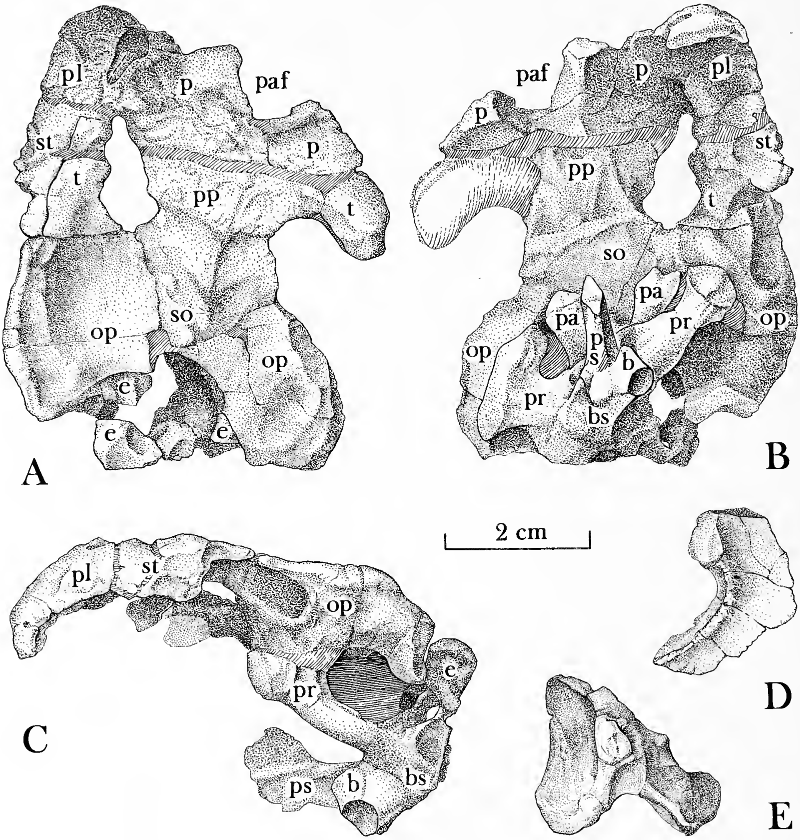


FIGURE 4. *Desmatodon hesperis:* A, dorsal, B, ventral, and C, left lateral views of braincase and connected dermal roofing elements (UCLA VP 1745); D, upper part of a right quadrate (UCLA VP 1746) in posterolateral view; E, lower part of another, larger right quadrate (UCLA VP 1747) in posterior view. Abbreviations: b, basipterygoid process; bs, basisphenoid; e, exoccipital; op, opisthotic; p, parietal; pa, pila antotica; paf, parietal foramen; pl, parietal lappet (=intertemporal?); pp, postparietal; pr, proötic; ps, parasphenoid; st, supratemporal; t, tabular. Because of fusion in the temporal region, some of the abbreviations mark general areas rather than distinctly demarcated elements. Line shading indicates matrix. Size indicated by the 2 cm scale.

anteroventral articular surfaces that are directed anteriorly and laterally. It is obvious that the joint between braincase and palate was mobile, unlike the condition in *Diadectes* where, despite an illustration by Watson (1954, fig. 18) that may give the opposite impression, the basisphenoid and pterygoid were firmly joined (see Olson, 1947). This feature could be interpreted as a mark of primitiveness of *Desmatodon hesperis*, but it could also be argued that it is merely another sign of immaturity of the specimen.

An upper part of a right quadrate bone (UCLA VP 1746, Fig. 4, D) was found near the braincase, to which it is appropriate in size. It has a well-defined condyle for articulation with the facet on the opisthotic bone. A lower part of another right quadrate (UCLA VP 1747, Fig. 4, E) found elsewhere in the quarry is obviously of a more mature individual, with a width of 25 mm across the articular end. The articular surface is divided into medial and lateral facets by a deep notch, and there is a large, rugose tubercle on the posterior surface above the notch, indicating a stapedial apparatus similar to that in *Diadectes* (see Olson, 1966). The resemblance of these specimens to *Diadectes* is very close (see Watson, 1954, fig. 24), and there can be little doubt that they are of *Desmatodon hesperis.*

A toothed right maxillary bone (UCLA VP 1748, Fig. 5, A, B) was found only a few inches away from the above-described braincase. The transversely widened, cusped teeth show that this specimen is of a diadectid, surely *Desmatodon hesperis.* The thin anteriormost part, where it overlapped the premaxilla, and the upper parts of the lateral wall have been broken away, but it is otherwise complete. Except for size and for certain features of the teeth, it is so similar to the holotypic maxilla that the description of the latter (Vaughn, 1969) suffices for both. A small projection on the medial side behind the last tooth is similar to one in the same position on the holotype, making it clear that the specimen is complete posteriorly and that no teeth have been lost. The new maxilla is 53 mm long as preserved, considerably shorter than the 77 mm long holotypic maxilla, and it is apparent that it is of a juvenile individual.

Whereas there are twelve teeth in the holotypic maxilla (Fig. 5, C), the juvenile maxilla has only eight, which seem to correspond to the first eight of the holotype. This correspondence is evident not only from the positions of the teeth with respect to the anterior end of the maxilla, but also from the fact that a narrow channel crossing the thickened medial surface of the maxilla ends ventrally at the plane between the third and fourth teeth in both specimens. Furthermore, the total length of the dental row in the juvenile is only slightly less than the length occupied by the first eight teeth of the holotype, 42 mm and 47 mm respectively. The juvenile teeth are all much shorter from front to back than the corresponding teeth of the holotype—for tooth 7 the respective dimensions are 2.6 mm and 5.2 mm—but they are separated by much longer spaces. It is obvious that with growth, the teeth of *D. hesperis* came to be replaced by more robust ones, and it is almost as obvious that the dental lamina must have become extended backward. These are common phenomena that may be observed also in living lizards (Edmund, 1969), but the elongation of the lamina in *D. hesperis* is striking when it is remembered that the transition from the juvenile dentition to that represented in the holotype involved the addition of four teeth, one-third of what is presumably the adult dentition. This is in sharp contrast to what is seen in the Early Permian *Diadectes*. For example, an immature specimen of *Diadectes san-*

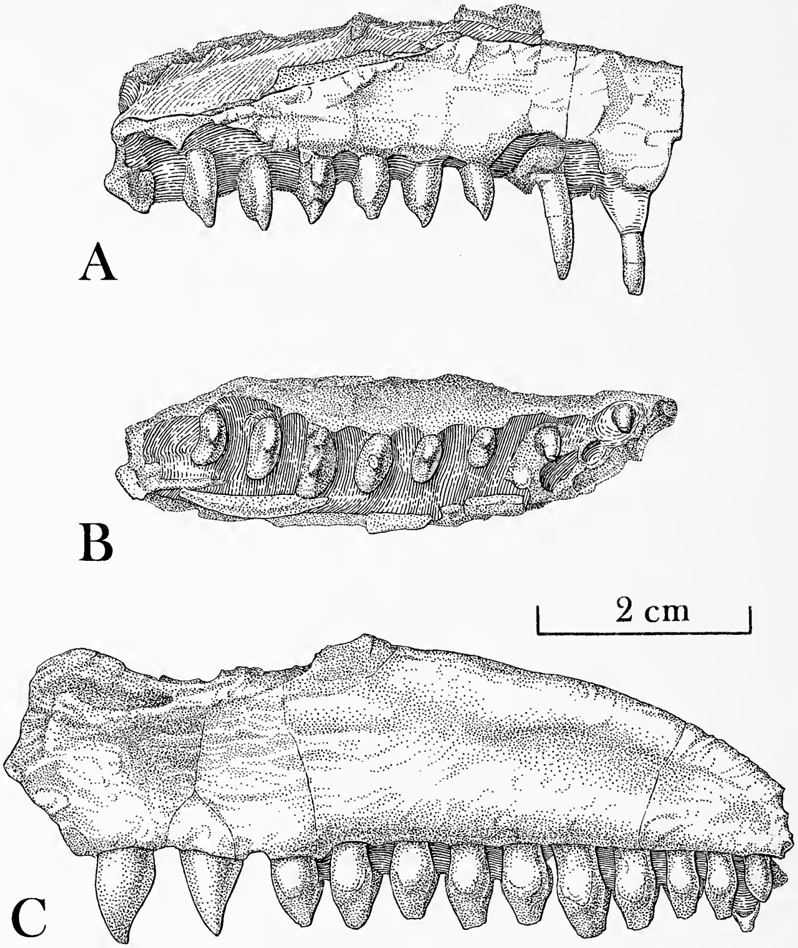


FIGURE 5. *Desmatodon hesperis:* A, lateral, and B, occlusal views of juvenile right maxilla (UCLA VP 1748); C, lateral view of holotypic left maxilla (UCLA VP 1706). Line shading indicates matrix and, in A and B, epoxy resin used to repair the specimen. Size indicated by the 2 cm scale.

miguelensis has a total of eleven teeth and empty alveoli in a maxilla only about 42 mm long (Lewis and Vaughn, 1965), and the number of maxillary teeth is hardly greater in adults of the various species of *Diadectes*, ranging from eleven to thirteen with eleven the usual number, as far as I have been able to determine from specimens and the literature. A specimen of *Diadectes lentus* at hand has a total of eleven teeth in a maxilla about 68 mm long. It is interesting to note that Romer (1952) has described a battery of eight small, diadectid-like cheek teeth contained in a length of only 11 mm, from the Conemaugh Group, and that Langston (1963) has described six diadectid-like teeth in a length of 10.5 mm, from the Lower Permian of Prince Edward Island; these specimens are, however, very poorly preserved, and their significance is difficult to assess.

Another notable contrast between the juvenile and holotypic dentitions is the much greater relative length of the first two teeth in the juvenile. In the holotype, the first two teeth are somewhat more acuminate than the succeeding, and they jut out slightly beyond the general tooth row. The difference is greatly accentuated in the juvenile, where the first two teeth are markedly incisiform, bowed with concave lingual sides, and twice as long as the succeeding teeth; the first and second teeth are each about 10 mm long, but the third is only about 5 mm long. It must be noted that the base of tooth 1 was lost during removal of the juvenile maxilla from the matrix, but this part was cast in epoxy resin from the impression, and the restored length is quite accurate. The teeth in the juvenile are, as might be expected, narrower from side to side than the corresponding teeth of the holotype—for tooth 7 the respective dimensions are 6 mm and 7.8 mm—but their lesser anteroposterior length makes them more bladelike. Labial, central and lingual cusps are present on teeth 5-8, but the lingual cusp is indistinct on teeth 3 and 4; all three cusps are distinct on teeth 3-8 of the holotype (actually, for the labial "cusp" the word "shoulder" would be more appropriate, this structure not being as well set off as in *Diadectes*). There are no signs of attrition on any of the teeth in the juvenile; this is remarkably different from the holotype, in which there are distinct wear facets on most of the teeth.

A combination of ways in which the juvenile maxillary dentition differs from that of the adult, much greater relative length and more incisiform aspect of the first two teeth, smaller number of teeth, teeth more bladelike and separated by longer spaces, lack of wear facets, fosters the suspicion that the change from juvenile to adult may have included a shift in dietary habit. *Diadectes* has been variously interpreted as herbivorous or molluscivorous; small pelecypods frequently found in association would seem to support the latter view, and it seems significant that small pelecypods are also known alongside the remains of *Desmatodon hesperis* in the Interval 300 quarry. It is hard to guess as to the diet of young *D. hesperis*. It is, of course, conceivable that the lack of wear facets on the juvenile teeth could be a result of more rapid replacement—it is known in crocodilians, for example, that the replacement rhythm becomes slower with age (Edmund, 1969)—but this would not account for the other juvenile-adult differences. Whatever further indications of a dietary shift may appear, it is at least clear that the transition from juvenile to adult in *Desmatodon hesperis* included much more pronounced dental changes than in *Diadectes*; in the immature specimen of *Diadectes sanmiguelensis* previously mentioned there is no great disparity between the first two maxillary teeth and those that follow.

Despite the above differences, the actual replacement of individual teeth in *Desmatodon hesperis* seems to have occurred in essentially the same manner as in *Diadectes* (see Edmund, 1960). A lingual pit was developed alongside each tooth, the base of the tooth became eroded, and the replacing tooth must have been ready for use soon after the overlying older tooth was shed, as shown by the lack of empty alveoli in both the juvenile and holotypic maxillae. Nevertheless, it will be shown that the cycle of tooth replacement in *Desmatodon hesperis* was different from what is known in *Diadectes.*

A diagrammatic analysis of the tooth-replacement cycle in *Desmatodon hesperis,* as inferred from the teeth of the holotypic maxilla, is presented in Figure 6. On the basis of intactness or attrition of the crown, and the degree of development of the lingual pit, five stages are arbitrarily delimited: newly erupted, not yet ankylosed (tooth 2); unworn but ankylosed (teeth 10, 12); worn, small lingual pit (teeth 1, 3, 5, 7); worn, large lingual pit (tooth 9); worn, base eroded (teeth 4, 6, 8, 11). If we assume that a "gap" exists between teeth 2 and 3, it will be seen that the teeth

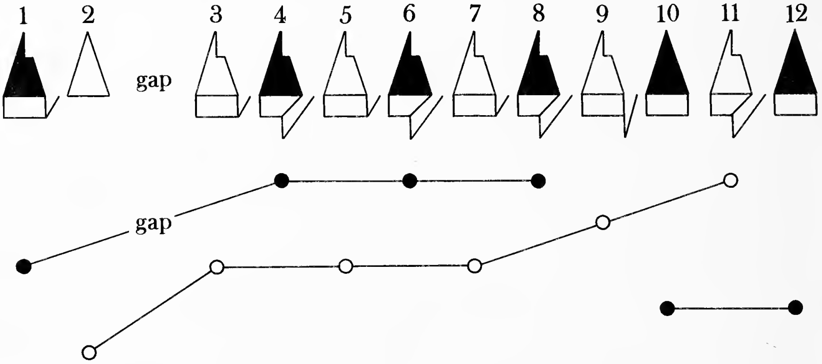


FIGURE 6. Analysis of tooth-replacement cycle based on the holotypic maxilla of *Desmatodon hesperis* (UCLA VP 1706). Filled-in and open symbols represent members of the two alternating replacement series. The symbols also indicate presence or absence of wear facets and the condition of the base, as: tooth 2, newly erupted, not yet ankylosed; tooth 10, unworn but ankylosed; tooth 1, worn, small lingual pit; tooth 9, worn, large lingual pit; tooth 4, worn, base eroded. The graph represents the partial waves of replacement, with the lowest level corresponding to newly erupted, not yet ankylosed, and the highest level corresponding to worn, base eroded.

can be arranged into two alternating replacement series, 1-gap-4-6-8-10-12 and 2-3-5-7-9-11, and it will also be seen that the cephalad waves of replacement overlap one another in an orderly manner, in accord with the usual tetrapod pattern (see Edmund, 1960). In the graphic representation of the waves, the five levels from lowest to highest correspond to the arbitrarily delimited stages described above, in the same order. Only if we assume the existence of the gap can the teeth be brought into such a pattern and, indeed, there is evidence for the reality of this gap, as will be brought out below. It is evident that the waves of replacement were long. Through graphic analysis in "Edmundian" style, it can be shown that a complete replacement wave included about seventeen teeth, from initial erosion of the old tooth to destruction and loss of the new, from birth to death of a tooth so to speak. This is considerably longer than replacement waves that have been analyzed in *Diadectes*, where a complete wave apparently included only about seven teeth (Edmund, 1960). The difference seems all the more profound when it is appreciated that a complete replacement wave can be seen within a jaw containing fourteen teeth in *Diadectes*, whereas it would take a jaw of at least thirty-three teeth to show a complete wave in *Desmatodon hesperis*.

Because of damage suffered by the juvenile maxilla when it was discovered through splitting of the enclosing matrix, most of the lingual pits cannot be studied, but those alongside the first two teeth are plainly evident, and these show that the second tooth has undergone some posteriorward displacement; this is also indicated by fragmentation of the bone at the base of the tooth. Thus it seems that there was originally an appreciable gap between the second and third teeth. In the holotypic maxilla there are short diastemata between the first and second and the second and third teeth, in marked contrast to the close packing in the rest of the row. However, a remnant of the base of an older tooth at the second position shows that the present tooth, newly erupted, and not yet ankylosed, must have moved posteriorward as it came in, creating the diastema between itself and the first tooth and reducing the gap between itself and the third. It is difficult to say whether or not this gap, which "shows up" in the replacement pattern as outlined above, was a constant feature in *Desmatodon hesperis*, but the condition is reminiscent of that noted by Edmund (1969:134) in certain of the teiid lizards where "Segments of the dentition may show regular rhythms, but these are not continuous along the entire jaw. The explanation may lie in the suppression of one or two adjacent tooth matrices to accommodate a single larger tooth." In the holotypic maxilla of *Desmatodon hesperis*, the disruption of regularity seems to be associated with development of the two short diastemata.

The fragmentary holotypic maxilla of *Desmatodon hollandi* has only four complete teeth and the root of a fifth; the represented stages are, from anterior to posterior: unworn but ankylosed; worn, base eroded; worn, small lingual pit; unworn but ankylosed; ?, large lingual pit. There are, of course, too few teeth to permit a definite statement, but it would seem that the replacement wave in *D. hollandi* was much shorter, and thus nearer to the condition in *Diadectes*, than in *D. hesperis*. As indicated in the initial description of *D. hesperis* (Vaughn, 1969), this species seems on other bases to be somewhat more primitive than *D. hollandi*, and it is conceivable that the longer replacement wave may present further grounds for differentiation, but nothing is known of the ranges of variation within the two species.

Even if it may eventually become necessary to set up a new genus based on *D. hesperis*, close relationship to *D. hollandi* would still be obvious; and the cranial parts described above should allay any doubts as to the diadectid affinities of *Desmatodon*. Although *Desmatodon* is more primitive in certain features than *Diadectes*, the two genera are nevertheless essentially similar; and it may be said definitely that the diadectid organization was well established in the Late Pennsylvanian. The known Early Permian diadectids form a closely knit group. Olson (1947) has summarized the various North American species, recognizing two genera, *Diadectes* and *Diasparactus*. *Phanerosaurus* and *Stephanospondylus* (probably synonyms) of the European Lower Permian are basically like *Diadectes* but, like *Desmatodon*, appear more primitive, having somewhat more acuminate teeth (Geinitz and Deichmüller, 1882, pl. 4) and, apparently, a mobile basipterygoid joint (Stappenbeck, 1905, fig. 4).

The phylogenetic origin of the diadectids remains obscure although *Tseajaia* from the Lower Permian of Utah does seem to provide a morphological link to seymouriamorph labyrinthodont amphibians (Vaughn, 1964). The recently described Late Mississippian anthracosaur *Mauchchunkia* may, as Hotton (1970) thinks, represent the ancestry of all "reptiliomorphs" including diadectids, but intermediate forms are still unknown. Romer (1964) has proposed that we consider *Diadectes* as a seymouriamorph rather than as a cotylosaur. This is consonant with the recent suggestion by Carroll (1970) that we exclude from definition as true reptiles all those forms that achieved reptilian morphological characteristics independently of the line that passed through romeriid captorhinomorphs; it would certainly be difficult to argue for romeriid-diadectid affinities. Perhaps we should follow the advice of Olson (1947) and think of diadectids as "parareptiles," but in an informal sense only, without intending the term as a taxonomic category.

ACKNOWLEDGMENTS

I thank my hard-working field assistants, Messrs. Kerry Clegg, Marc Gallup, Michael Novacek, and David Vaughn. Mr. Thurston Phetteplace, of the Bureau of Land Management, helped smooth the way for quarrying operations. Mr. Herbert Klug's skill has been valuable in removal of the difficult matrix. The drawings are the work of Mrs. Hermine Kavanau, and the photograph of the microsaur was taken by Mr. Takeo Susuki. I am grateful to the National Science Foundation for continued support of this study through grant GB-19971.

LITERATURE CITED

AXELROD, D. I. 1952. A theory of angiosperm evolution. Evolution 6:29-60.

BRILL, K. G., JR., 1952. Stratigraphy in the Permo-Pennsylvanian zeugogeosyncline of Colorado and northern New Mexico. Geol. Soc. Amer., Bull. 63:809-880.

BROUGH, M. C., AND J. BROUGH. 1967. Studies on early tetrapods. II. *Microbrachis*, the type microsaur. Roy. Soc. London, Philos. Trans., ser. B, 252:131-146.

CARROLL, R. L. 1964. Early evolution of the dissorophid amphibians. Harvard Univ., Mus. Comp. Zool., Bull. 131:161-250.

———. 1966. Microsaurs from the Westphalian B of Joggins, Nova Scotia. Linn. Soc. London, Proc. 177:63-97.

———. 1967. An adelogyrinid lepospondyl amphibian from the Upper Carboniferous. Canadian Jour. Zool. 45:1-16.

———. 1968. The postcranial skeleton of the Permian microsaur *Pantylus*. Canadian Jour. Zool. 46:1175-1192.

———. 1969. A new family of Carboniferous amphibians. Paleontology 12:537-548.

———. 1970. The ancestry of reptiles. Roy. Soc. London, Philos. Trans., ser. B, 257:267-308.

———, AND DONALD BAIRD. 1968. The Carboniferous amphibian *Tuditanus* [*Eosauravus*] and the distinction between microsaurs and reptiles. Amer. Mus. Nat. Hist., Novitates 2337:1-50.

CASE, E. C. 1908. Description of vertebrate fossils from the vicinity of Pittsburgh, Pennsylvania. Carnegie Mus., Ann. 4:234-241.

———. 1911. A revision of the Cotylosauria of North America. Carnegie Inst. Washington, Publ. 145:1-122.

CHRONIC, JOHN. 1958. Pennsylvanian rocks in central Colorado. Rocky Mountain Assoc. Geol., Symposium on Pennsylvanian Rocks of Colorado and Adjacent Areas, p. 59-63.

CLAPHAM, W. B. 1970. Nature and paleogeography of Middle Permian floras of Oklahoma as inferred from their pollen record. Jour. Geol. 78:153-171.

DEMAR, ROBERT. 1970. A primitive pelycosaur from the Pennsylvanian of Illinois. Jour. Paleont. 44:154-163.

EDMUND, A. G. 1960. Tooth replacement phenomena in the lower vertebrates. Roy. Ontario Mus., Life Sci. Div., Contrib. 52:1-190.

———. 1969. Dentition. *In* Biology of the Reptilia, Carl Gans, A. d'A. Bellairs and T. S. Parsons, eds., London and New York, Academic Press, p. 117-200.

ELIAS, M. K. 1970. Progress in correlation of Carboniferous rocks. Compte Rendu 6e Congrès Internat. Strat. Géol. Carbonif., Sheffield, 1967, vol. 2:695-714.

GEINITZ, H. B., AND J. V. DEICHMULLER. 1882. Die Saurier der unteren Dyas von Sachsen. Paleontographica 29:1-46.

HOTTON, NICHOLAS, III. 1970. *Mauchchunkia bassa,* gen. et sp. nov., an anthracosaur (Amphibia, Labyrinthodontia) from the Upper Mississippian. Cleveland Mus. Nat. Hist., Kirtlandia 12:1-38.

HUENE, FRIEDRICH VON. 1913. The skull elements of the Permian Tetrapoda in the American Museum of Natural History, New York. Amer. Mus. Nat. Hist., Bull. 23:315-386.

LANGENHEIM, R. L. 1952. Pennsylvanian and Permian stratigraphy of the Crested Butte Quadrangle, Gunnison County, Colorado. Amer. Assoc. Petrol. Geol., Bull. 36:543-574.

LANGSTON, WANN, JR. 1963. Fossil vertebrates and the late Paleozoic red beds of Prince Edward Island. Nat. Mus. Canada, Bull. 187:1-36.

Lewis, G. E., and P. P. Vaughn. 1965. Early Permian vertebrates from the Cutler Formation of the Placerville area, Colorado, *with a section on* Footprints from the Cutler Formation *by* Donald Baird. U. S. Geol. Survey, Prof. Paper 503-C:1-50.

Mallory, W.W. 1958. Pennsylvanian coarse arkosic redbeds and associated mountains in Colorado. Rocky Mountain Assoc. Geol., Symposium on Pennsylvanian Rocks of Colorado and Adjacent Areas, p. 17-20.

———. 1960. Outline of Pennsylvanian stratigraphy of Colorado. Geol. Soc. Amer. and Rocky Mountain Assoc. Geol., Guide to the Geology of Colorado, p. 23-33.

Olson, E. C. 1947. The family Diadectidae and its bearing on the classification of reptiles. Fieldiana: Geol. 11:1-53.

———. 1950. The temporal region of the Permian reptile *Diadectes*. Fieldiana: Geol. 10:63-77.

———. 1961. Jaw mechanisms: rhipidistians, amphibians, reptiles. Amer. Zoologist 1:205-215.

———. 1966. Relationships of *Diadectes*. Fieldiana: Geol. 14:199-227.

Panchen, A. L. 1967. The homologies of the labyrinthodont centrum. Evolution 21:24-33.

Parrington, F. R. 1967. The vertebrae of early tetrapods. Colloq. Internat. Cent. National Recherche Sci. 163:269-279.

Peabody, F. E. 1952. *Petrolacosaurus kansensis* Lane, a Pennsylvanian reptile from Kansas. Univ. Kansas Paleont. Contrib., Vertebrata 1:1-41.

———. 1957. Pennsylvanian reptiles of Garnett, Kansas: edaphosaurs. J. Paleontol. 31:947-949.

———. 1959. The oldest known reptile, *Eosauravus copei* Williston. Smithsonian Misc. Collec. 139:1-14.

Romer, A. S. 1952. Late Pennsylvanian and Early Permian vertebrates of the Pittsburgh-West Virginia region. Carnegie Mus., Ann. 33:47-113.

———. 1963. The larger embolomerous amphibians of the American Carboniferous. Harvard Univ., Mus. Comp. Zool., Bull. 128:415–454.

———. 1964. *Diadectes* an amphibian? Copeia 1964:718-719.

———. 1969. The cranial anatomy of the Permian amphibian *Pantylus*. Harvard Univ., Mus. Comp. Zool., Breviora 314:1-37.

Scott, G.R. 1967. Upper part of Minturn Formation possibly of Permian age. U. S. Geol. Survey, Prof. Paper 575-A:82.

Stappenbeck, Richard. 1905. Über *Stephanospondylus* n. g. und *Phanerosaurus* H. v. Meyer. Deutsch. geol. Ges., Zeitschr. 57:380-437.

Sturgeon, M. T., and R. D. Hoare. 1968. Pennsylvanian brachiopods of Ohio. Ohio Dept. Nat. Resources, Div. Geol. Survey, Bull. 63:1-95.

Thomson, K. S., and K. H. Bossy. 1970. Adaptive trends and relationships in early Amphibia. Forma et Functio 3:7-31.

Vaughn, P. P. 1964. Vertebrates from the Organ Rock Shale of the Cutler Group, Permian of Monument Valley and vicinity, Utah and Arizona. J. Paleontol. 38:567-583

———. 1969. Upper Pennsylvanian vertebrates from the Sangre de Cristo Formation of central Colorado. Los Angeles Co. Mus., Contrib. Sci. 164:1-28.

———. 1970. Alternation of neural spine height in certain Early Permian tetrapods. So. Calif. Acad. Sci., Bull. 69:80-86.

Watson, D. M. S. 1954. On *Bolosaurus* and the origin and classification of reptiles. Harvard Univ., Mus. Comp. Zool., Bull. 111:295-449.

Accepted for publication December 20, 1971

NUMBER 224
FEBRUARY 28, 1972

TWO NEW *MICROVELIA* FROM CRABHOLES IN COSTA RICA

(Hemiptera: Veliidae)

By John T. Polhemus and Charles L. Hogue

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1964 AIBS Style Manual for Biological Journals is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1964 AIBS Style Manual for Biological Journals in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Changes in the manuscript after galley proof will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

TWO NEW *MICROVELIA* FROM CRABHOLES IN COSTA RICA (Hemiptera: Veliidae)

By John T. Polhemus[1] and Charles L. Hogue[2]

Abstract: *Microvelia inquilina,* n. sp. and *Microvelia chanita,* n. sp. are described from the Pacific Coast of Costa Rica. These two species, along with another Costa Rican species, *M. oraria* Drake (crab unrecorded), are found inhabiting land crab burrows made by *Cardisoma crassum* and *Ucides occidentalis* respectively, but the nature of the association is unknown.

The two *Microvelia* described below were found inhabiting crabholes on the Pacific Coast of Costa Rica. Previously, *Microvelia oraria* was the only veliid known from crabholes and was described from an Atlantic Coast locality in Costa Rica by Drake (1952).

Because veliids are poorly known in the Neotropical region, it is hazardous to surmise that crabholes are the sole habitat of these new species. Yet one of them, *inquilina,* has reduced eyes similar to the bromeliad-inhabiting species *laesslei* Drake and Hussey. Compared to normal pond and stream species, the ommatidia are larger but with only about half as many. For example, *Microvelia pulchella* Westwood (a pond dweller) has an interocular space to eye width ratio (I/W) of 2.43, whereas in *inquilina* and *laesslei* I/W is 3.40 and 3.34 respectively. Small eyes may be an adaptation to specialized container habitats such as bromeliads and crabholes offer.

The material upon which these species are based was made available by the junior author and Dr. Donald B. Bright, California State College, Fullerton, from their collections in connection with a general study of the biology of land crabs and their burrow associates (LCBA), a project conducted with the support of grants from the American Philosophical Society.

All specimens were taken from samples of water extracted from deep within land crab burrows with a simple bottle pump fixed with an intake hose of one-half inch inside diameter. The bugs are hygrophobic and readily come to the surface of water taken with the pump. The construction and use of the device itself (small type mosquito pump) is described by Belkin et al. (1965:70-71).

Both species were taken in the same locality and general habitat. However, their specific microhabitats are very different. *Microvelia chanita* was found in only a single burrow, that of a full-grown crab, *Cardisoma crassum.* The collectors observed that this crab typically constructs its burrows just above the highest high tide line where they are never (or rarely) flooded but receive ground water most of the year directly from the sea or from some

---

[1] 3115 South York, Englewood, Colorado 80110

[2] Entomology Section, Natural History Museum of Los Angeles County, Los Angeles, California 90007

other proximate water body. In the present case the burrow was located only a few feet from a fresh water seepage pond which was separated from the sea by a slight rise and a distance of approximately 100 meters. At the time of the collection the level of free water was depressed below the burrow mouth, and the water was brackish (NaCl 2020 ppm). The bugs were observed in and about the crabhole but most were collected with the mosquito pump. None were seen on the surface of the nearby pond, but they might have occurred there also. It is possible that the presence of these water bugs at this site was simply accidental, the species being normally adapted to living on open pools as is true of most of its relatives.

From the reduced eyes of *inquilina*, which may be a morphological trait associated with life in a container habitat (see above), behavior, and that it was collected repeatedly from crabholes (LCBA 526 represents a pooled sample of 25 burrows of the crab, *Ucides occidentalis*, all siphoned with the bottle pump), this species is more likely than *chanita* to be a normal inhabitant of this specialized microhabitat. *Ucides occidentalis*, unlike *C. crassum*, constructs its burrows at a low elevation where they are partially or completely flooded by daily high tides or at least annual spring tides. This poses the additional question: if its niche is destroyed for a portion of the day or year, does this species become a littoral dweller, invade the burrows of other crabs, or utilize a resistant stage (egg?) to pass this critical period? Extensive collecting in the type locality of *inquilina* in the season of high tides has yielded no specimens from *C. crassum* holes.

Microvelia inquilina Polhemus and Hogue, new species

DESCRIPTION

Apterous male, adult:

Size.—Very small, short, broad; length 1.15 mm; width 0.44 mm.

Coloration and vestiture.—Ground color black to blackish brown. Grey pruinose on areas as follows: fore part of head; connexivum, and much of abdominal dorsum, lateral portions of tergite 2; all but median area on tergite 3; median third of tergite 6; broad triangular area of tergite 7; all of genital segment 1 dorsally. Pronotum broadly testaceous, blackish brown laterally beyond middle of eyes. Apex of abdominal tergite 6 and genital segments brown, latter lighter ventrally; underparts of head and rostrum testaceous. Legs and antenna yellowish to yellow brown. Entire body covered with short, semi-erect pubescence.

Head.—Length .28 mm; width (including eyes) .40 mm; interocular space .25 mm. Vertex strongly convex; eyes small, with about 50 ommatidia. Antennal formula; segments I-IV, 8:7:16:18; segments 1 stout, segment 2 less stout, segments 3 and 4 slender; all segments clothed with long hairs. Rostrum reaching past front coxae.

Thorax.—Proportional lengths, pronotum/mesonotum: 6/4. Width across humeri .57 mm. Posterior margins of pronotum, mesonotum straight; metanotum with angles broadly exposed, length .13 mm; mesonotum with small pits behind posterolateral angles of pronotum, widely separated (.35 mm); dorsal surface of thorax feebly convex.

Legs short, stout, covered with pale hairs, longer on tibia; fore tibia with short comb. Measurements of legs as follows:

	Femur	Tibia	Tarsal 1	Tarsal 2
Anterior	.37 mm	.27	.17	–
Middle	.42	.33	.07	.13
Posterior	.42	.45	.08	.13

Abdomen.—Proportional lengths, abdominal tergites I-VII, 7:5:5:3:3:5:9; first genital segment protruding from tergite 7 by .10 mm, rounded apically; connexiva moderately broad (.10 mm), slightly raised; entire abdomen broad, tapering slightly posteriorly, lateral margins of connexiva more sharply rounded along tergites 6-7. Venter of abdomen broadly raised medially, extending onto ventrite 5, which is produced slightly medio-caudad and emarginate; ventrite 6 similarly but more strongly produced and emarginate, excavate on midline; ventrite 7 not raised medially; broadly, roundly and deeply excavate medially forming a semicircular depression opening caudad. Genital segment 1 roundly emarginate ventrally; segment 2 swollen, not extending beyond tip of segment 1; parameres visible, hooklike, extending caudad and upward along grooves on the posterolateral margins of genital segment 1 (Fig. 1 F).

Apterous female, adult:

Very similar to male, except connexivum almost vertical, abdominal venter unmodified, body somewhat more robust; length 1.33 mm; width 0.65 mm.

MATERIAL

Holotype ♂, Allotype ♀, and Paratypes 6 ♂♂, 7 ♀♀, Costa Rica, Puntarenas Province, Boca de Barranca, 9-11 Feb. 1969, Hogue and Bright, LCBA 526, ex. crabhole *Ucides occidentalis.* The holotype, allotype and seven paratypes are deposited in the collections of the Natural History Museum of Los Angeles County. Six paratypes are in the Polhemus collection.

DIAGNOSIS

The color, extremely small size, larger proportional length of head vs. remainder of body (17/52 = .328), small eyes, long antenna and modification of the male venter distinguish this species from all other *Microvelia. Microvelia laesslei* Drake and Hussey and *Microvelia distanti* Lundblad, with which *inquilina* would most likely be confused, are both larger (*laesslei* ♂ 2.28 mm, ♀ 2.3 mm; *distanti* ♂ 1.9 mm, ♀ 2.3 mm). Neither of them has ventrite 5 produced or ventrite 6 excavated medially, and their heads are proportionally smaller than *inquilina* (length of head/remainder of body: *distanti,* 35/155 = .226; *laesslei,* 45/185 = .243). Additionally, the colora-

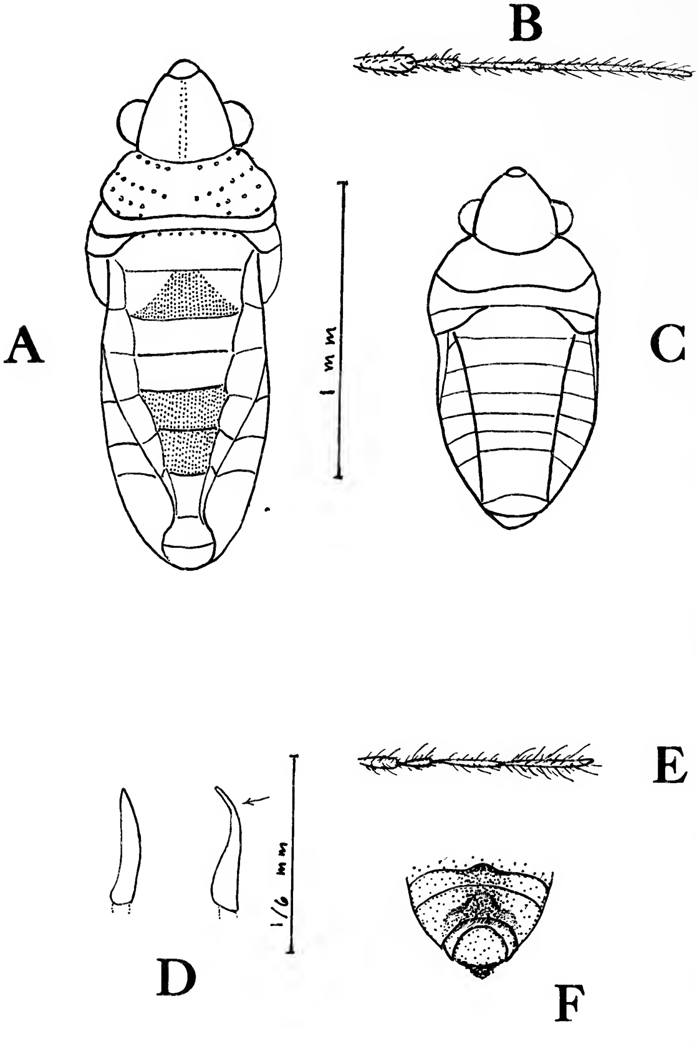


FIGURE 1. A-B: *Microvelia chanita*, new species. A, female, dorsal view; B, antenna. C-F: *Microvelia inquilina*, new species. C, male, dorsal view; D, male paramere, dorsal (left) and lateral (right) views; E, antenna; F, male, apical abdominal segments, ventral view.

tion is different, *distanti* being deep brown with the first two tergites pruinose and the first three connexiva flavous forming a light transverse band, and *laesslei* being deep brown with a rufous pronotum and white wing pads in the micropterous form (apterous form not known). In both of these species the pronotum covers the mesonotum, whereas in *inquilina* the mesonotum is broadly exposed. The eyes in *distanti* are not reduced significantly in relation to the head as in *inquilina.*

Microvelia chanita Polhemus and Hogue, new species

DESCRIPTION

Apterous female, adult:

Size.—Small, subfusiform. Length, 1.77 mm; width, 0.72 mm.

Coloration and vestiture.—Ground color brown; grey pruinose on fore part of head, collar, median wedge on abdominal tergite 2, all of tergites 5 and 6; anterior lobe of pronotum white pruinose; median area of head and pronotum, most of mesonotum and tergite 1, posterior part of each connexival segment yellowish; venter ochraceous, midventral areas, midlateral spots brownish; antenna ochraceous to brownish; legs leucine to ochraceous, dorsally and apically brownish; underparts of head and rostrum ochraceous.

Head.—Length .37 mm, width (including eyes) .43 mm, interocular space .28 mm. Vertex strongly convex; eyes of moderate size; antennal formula I-IV, 13:10:16:29; segment 1 stout, 2 less stout, 3-4 slender; all segments clothed with recumbent hairs of length equal to diameter of segment 2, and scattered longer hairs. Rostrum reaching beyond fore coxae.

Thorax.—Proportional lengths, pronotum/mesonotum: 11/3; midline lengths, anterior pronotal lobe/posterior pronotal lobe: 5/6. Width across metanotal angles .72 mm; collar marked by a row of widely spaced pits; lobes of pronotum separated by a row of deep pits, interrupted medially, as is transverse row of pits on caudal lobe; caudal margins of pronotum and mesonotum slightly concave; metanotal angles narrowly exposed, length .83 mm (from postero-lateral angle of mesonotum); mesonotum broadly excavate under posterolateral margins of pronotum; lateral margins of thorax set with semi-long, curved, bristly hairs; dorsal surface slightly convex, pronotum depressed below level of mesonotum; propleura depressed along caudal margin.

Legs of moderate length, covered with short pale hairs, longer on under surface of femora; measurements of legs as follows:

	Femur	Tibia	Tarsal 1	Tarsal 2
Anterior	.47 mm	.40	.23	—
Middle	.52	.43	.12	.15
Posterior	.52	.62	.13	.17

Fore tibia slightly flattened and widened apically, narrowing abruptly just before apex.

Abdomen.—Proportional lengths of abdominal tergites I-VIII, 9:8:8:8:9:9:8:6. Connexiva moderately broad, semi-erect along tergite 1 to vertical at apex; set with bristly hairs at apex. Venter broadly rounded, feebly flattened medially, clothed with decumbent hairs visible from above. Shape as in figure 1 A.

Male: Unknown.

MATERIAL

Holotype ♀ and 8 ♀♀ Paratypes, Costa Rica, Puntarenas Prov., Boca de Barranca, 8 August 1967, Hogue and Bright, LCBA 158, ex. crabhole *Cardisoma crassum.* Deposited in the collection of the Natural History Museum of Los Angeles County. Three paratypes are in the Polhemus collection.

DIAGNOSIS

Microvelia chanita belongs to the *albonotata* group including *albonotata* Champion, *mimula* White, *tateiana* Drake, *quieta* Drake, *novana* Drake, *cubana* Drake and *portoricensis* Drake. This group, not previously recognized, is comprised of those small species (circa 2 mm) which have the pronotum of medium length, having two distinct lobes separated by a depressed transverse line of pits, but leaving much of the mesonotum exposed. The ratio of midline length of pronotum/mesonotum in this group varies from 12/7 = 1.73 (*tateiana*) to 11/3 = 3.67 (*chanita*).

The primary distinguishing characteristics of *chanita* are extremely long fourth antennal segment combined with a relatively short thorax (measured on dorsal midline, thorax/head: 15/25). *M. albonotata*, the only other species with very long fourth antennal segments, has thorax/head: 25/28. Additionally, *chanita* has narrow apical abdominal tergites, a character state shared within the *albonotata* group only by *M. portoricensis.*

RESUMEN

Microvelia inquilina, sp. nov., y *Microvelia chanita*, sp. nov., de la costa pacifica de Costa Rica son descritos. Estas dos especies, con otra de Costa Rica, *M. oraria* Drake (cangrejo no conocido), se encuentran habitando las cuevas de cangrejos terestres construidas por *Cardisoma crassum* y *Ucides occidentalis*, respectivamente, pero la naturaleza de la asociación no es conocida.

LITERATURE CITED

DRAKE, C. J. 1952. Two new *Microvelia* Westwood (Hemiptera: Veliidae). Bull. Brooklyn Ent. Soc. 47(1):13-15.

BELKIN, J. N., C. L. HOGUE, P. GALINDO, T. H. G. AITKEN, R. X. SCHICK AND W. A. POWDER. 1965. Mosquito studies (Diptera, Culicidae) II. Methods for the collection, rearing and preservation of mosquitoes. Contrib. Amer. Entomol. Inst. 1(2):19-78.

Accepted for publication January 18, 1972

NUMBER 225
MARCH 2, 1972

DORSADENA YAQUINAE, A NEW GENUS AND SPECIES OF MYCTOPHID FISH FROM THE EASTERN NORTH PACIFIC OCEAN

By LEONARD R. COLEMAN
AND BASIL G. NAFPAKTITIS

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1964 AIBS Style Manual for Biological Journals is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1964 AIBS Style Manual for Biological Journals in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Changes in the manuscript after galley proof will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

DORSADENA YAQUINAE, A NEW GENUS AND SPECIES OF MYCTOPHID FISH FROM THE EASTERN NORTH PACIFIC OCEAN

By Leonard R. Coleman[1] and Basil G. Nafpaktitis[2]

Abstract: A new genus and species of myctophid fish, *Dorsadena yaquinae,* from the eastern north Pacific Ocean is described. Relationship between the new form and *Lampadena* Goode and Bean is suggested by similarities in the structure, size and position of the supra- and infracaudal luminous glands, in the arrangement of the body photophores and in otolith morphology. *Dorsadena yaquinae,* like *Lampadena* and *Taaningichthys,* seems to be one of the deepest dwelling myctophids. Its isolated occurrence off Oregon may be attributed to inadequate sampling of depths exceeding 1500 meters in the central and western north Pacific. On the other hand, the eastern north Pacific specimens may represent an expatriate population.

Recent collections of oceanic fishes by the Department of Oceanography, Oregon State University, have yielded specimens of an undescribed lanternfish. This fish is so distinct from any other myctophid as to preclude its placement in any of the approximately thirty genera of the family.

The new species is represented by five specimens, 58.0–101.5 mm in standard length, collected between latitudes 44°N and 45°N, and longitudes 134°W and about 139°W where subarctic water predominates in at least the upper 300 meters.

Counts and measurements were taken according to Nafpaktitis (1968). Photophore and otolith terminologies follow those of Bolin (1939) and Frizzell and Dante (1965), respectively. The otoliths are deposited in the collections of John E. Fitch of the California Department of Fish and Game.

Dorsadena, new genus

Diagnosis: A large, elongate luminous gland immediately in front of adipose fin. Large, undivided supra- and infracaudal luminous glands. Four to five Prc, in three groups: first two close together and about at level of dorsal margin of infracaudal luminous gland, third at midlateral line, fourth posterior to, and about at level of ventral margin of, supracaudal luminous gland; often a fifth Prc develops close to, and at level of, fourth Prc. Numerous minute secondary photophores on head, trunk and base of caudal fin.

The name *Dorsadena* [dorsal and adena, from the Greek $\alpha\delta\eta\nu$ (aden) = gland] refers to the unique preadipose gland. Type species:

---

[1] Department of Oceanography, Oregon State University, Corvallis, Oregon 97331.

[2] Department of Biological Sciences, University of Southern California, Los Angeles, Calif. 90007; and Research Associate in Ichthyology, Natural History Museum of Los Angeles County, Los Angeles, Calif. 90007.

Dorsadena yaquinae, new species

Figures 1–4

Holotype: Los Angeles County Museum of Natural History (LACM) 30841-1; 77.0 mm, R/V YAQUINA, haul MT-866, between 45°05′N, 138°33′W and 44°44′N, 138°32′W, 0453-1205 hrs, 25 July 1966; 10′ Isaacs-Kidd Midwater Trawl, depth of haul 0-2700 m, 8000 m of wire out; bottom depth approximately 4207 m.

Paratypes: Oregon State University Department of Oceanography (OSUDO) 1226, 101.5 mm, and 1227, 58.0 mm. Collection data for both are the same as for the holotype. U.S. National Museum (USNM) 204869; 87.0 mm, R/V YAQUINA, station NH-450, haul OTB-163, between 44°39′N, 134°34′W and 44°45′N, 134°46′W, 1835-0400 hrs, 1-2 March 1967; 22′ shrimp-type otter trawl, depth of haul 0-3860 m, 6000 m of wire out. Museum of Comparative Zoology (MCZ) 46681; 62.0 mm, R/V YAQUINA, station NH-450, haul MT-1040, between 44°45′N, 134°46′W and 44°43′N, 134°42′W, 0223-0305 hrs, 2 March 1967; 6′ Isaacs-Kidd Midwater Trawl, depth of haul 0-180 m, 800 m of wire out; bottom depth approximately 3800 m.

Diagnosis: As for genus.

Description: D. 14-15; A. 12-14; P. 15-16; V. 8 (9 on one side of one specimen); gill rakers (4)5+1+11, plus 1-3 rudiments on the upper limb and 3-4 rudiments on the lower limb of the first (right) gill arch; PO 6-8; VO 3-5; SAO 3; AO 5-7+3-5, total 9-11; Prc 2+1+1-2.

A moderately large myctophid fish. Head large, about 3.3 in standard length (SL). Eye large, 12.3 (11.6-13.5) in SL, 3.8 (3.7-4.1) in length of head and 2.5 (2.3-2.8) in length of upper jaw. Mouth large, terminal, somewhat oblique; length of upper jaw about 5 in SL, 1.5 in length of head, extending 1.0 to 1.3 times the diameter of eye behind vertical through posterior margin of orbit. Length of snout 1.4 (1.2-1.5) in diameter of eye. Posterior opercular margin forming a blunt point somewhat above base of pectoral fin. Pterotic spine well developed. Caudal peduncle 10.0 (9.0-11.0) in SL.

Origin of dorsal fin over base of ventral fin. Origin of anal fin on, or slightly in advance of, vertical through end of base of dorsal fin. Pectoral fin short, its delicate, fragile rays about as long as diameter of eye. Ventral fins extending to anus. Base of adipose fin over end of base of anal fin.

Dn absent. A very small, poorly developed Vn immediately above, or in contact with, dorsal margin of CO1 (lacrimal) bone. Op_1 poorly defined, about at level of angle of mouth and close behind preopercular margin. Op_2 twice as large as general body photophores, at least twice its own diameter above and behind Op_1.

Body photophores generally small and ill defined, at least in preserved specimens. PLO slightly in advance of vertical through upper end of base of pectoral fin and about its own diameter below lateral line. PVO_1 under, or slightly in advance of, PVO_2, which is located about its own diameter in front

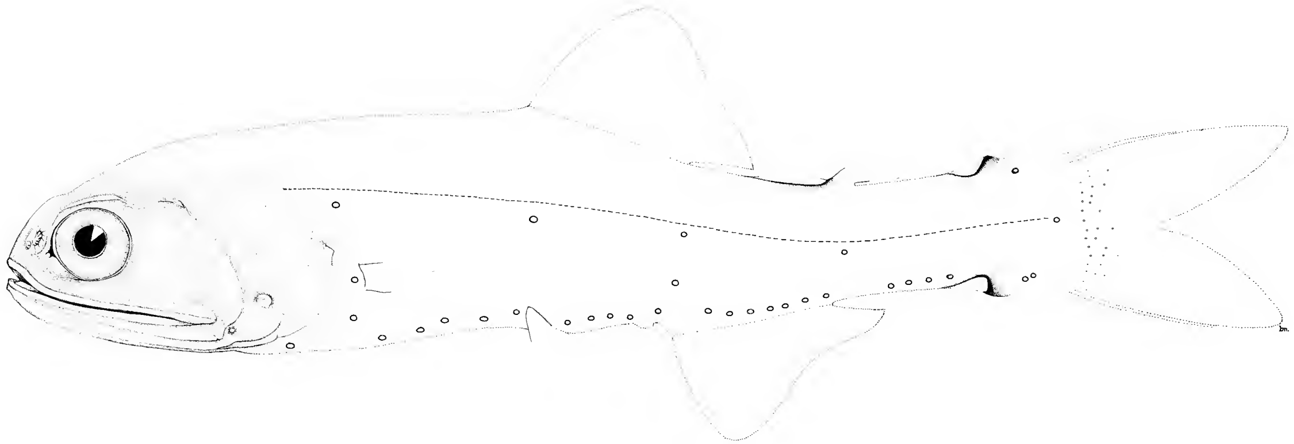


FIGURE 1. *Dorsadena yaquinae;* holotype, 77.0 mm in SL; LACM 30841-1.

TABLE 1. Measurements of *Dorsadena yaquinae*

	OSUDO 1226 101.5 mm	MCZ 46681 62.0 mm	OSUDO 1227 58.0 mm	LACM 30841-1* 77.0 mm	USNM 204869 87.0 mm	
Character	*Measurements in percent of standard length*					*Mean*
Diameter of eye	7.4	8.4	8.6	8.2	8.0	8.1
Length of upper jaw	20.7	19.8	19.8	20.6	19.5	20.1
Length of head	30.5	30.6	31.6	31.2	30.5	30.9
Depth of caudal peduncle	11.0	11.3	9.7	10.4	9.2	10.3
From tip of snout to base of pectoral fin	33.5	33.1	33.6	33.0	32.2	33.1
From tip of snout to base of ventral fin	48.3	48.4	46.9	50.6	47.7	48.4
From tip of snout to origin of dorsal fin	48.3	48.4	46.6	50.6	48.3	48.4
From tip of snout to origin of anal fin	63.1	64.5	63.8	63.6	64.4	63.9
From tip of snout to base of adipose fin	77.8	79.0	75.0	77.9	75.6	77.1
Length of caudal glands	5.4	4.8	5.2	4.2	4.6	4.8
Length of preadipose gland	8.4	8.1	6.2	7.8	7.8	7.7
Character	*Measurements in percent of head length*					*Mean*
Length of upper jaw	67.7	64.7	62.8	66.3	64.2	65.1
Diameter of eye	24.2	27.4	27.3	26.3	26.4	26.3
Length of snout	21.0	18.4	19.1	18.8	18.9	19.2

*Holotype

of middle of base of pectoral fin. Six to eight PO, variably spaced on a wavy line. VLO about 1.5 times its own diameter below lateral line. Three to five, usually four, VO, level. SAO forming an obtuse angle; SAO$_1$ over anus and slightly raised above level of last VO; distance between SAO$_2$ and SAO$_3$ 1.5 to 2.0 times as large as that between SAO$_1$ and SAO$_2$; SAO$_3$ somewhat in advance of, or behind, vertical through center of SAO$_2$ and about its own diameter below lateral line. First and last AOa interspaces sometimes distinctly enlarged; first AOa, or last, or both slightly raised. Pol behind last AOa, under base of adipose fin and about its own diameter below lateral line. AOp evenly spaced, level; last AOp over anterior portion of infracaudal luminous gland. Prc$_1$-Prc$_2$ interspace less than one photophore diameter; Prc$_2$ slightly higher than Prc$_1$; Prc$_3$ well behind Prc$_2$ and at level of lateral line; one or two additional Prc organs posterior to supracaudal luminous gland and under dorsal procurrent caudal rays.

Supra- and infracaudal luminous glands undivided, of equal size, their length 1.6-2.0 times in diameter of eye, directly apposed to each other, and framed by darkly pigmented tissue; most luminous tissue found within a darkly pigmented "hood" at posterior part of each organ.

An undivided luminous gland, about as long as eye diameter, extending from anterior end of base of adipose fin to about midway between end of base of dorsal fin and adipose fin; gland outlined by black pigment, with luminous tissue bulging dorsally.

Large numbers of minute secondary photophores present on head, trunk and proximal part of caudal fin. Along the lateral line, they appear to be arranged in a rather regular pattern (Fig. 2).

Jaws with needlelike teeth, inner ones longer than outer; 5 to 8 broad-based, hook-like, forward-inclined teeth on posterior part of dentary; a long, narrow band of slender teeth on each palatine; mesopterygoids with minute, widely scattered teeth and enlarged, widely spaced ones along periphery and posterior part of each mesopterygoid; vomer toothless.

The gonads of all five specimens are either poorly developed or regressed.

Circumorbital bones

The circumorbital bones (Fig. 3) show some interesting features. In the following discussion the terminology is that used by Paxton (in press).

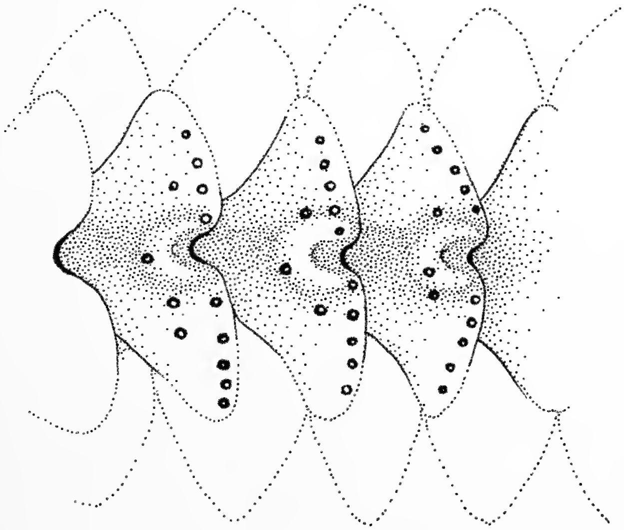


FIGURE 2. *Dorsadena yaquinae;* distribution of secondary photophores on lateral line scales.

The anterodorsal part of the first circumorbital, CO1 (lacrimal of some authors), is folded over to form a large, lateral flap anteroventrad to the eye. This flap is clearly visible on intact specimens. Paxton (in press) found that in myctophids "The anterodorsal margin is folded ventrally, so that the anterior end of the CO1 approaches a closed tube in some forms. In a number of species, the Vn orbital organ lies on top of the folded edge of the CO1." However, with the exception of those members of the genus *Diaphus* with a well developed Vn (ventronasal) and those of the genus *Gymnoscopelus*, e. g., *G.* (*Gymnoscopelus*) *opisthopterus, G.* (*Nasolychnus*) *piabilis*, with extensive luminous tissue along the anterior and anteroventral orbital margin, in no other myctophid form is this flap so extensively developed. It is conceivable that the ancestral stock from which *Dorsadena* evolved had a well-developed Vn. Interestingly, the CO1 lateral flap appears relatively well developed in *Lampadena anomala*, the Vn of which is very small, poorly developed and lies anterodorsad to the CO1.

According to Paxton (op. cit.), the lateral margin of the orbital portion of the third circumorbital, CO3 (jugal of some authors), in lantern fishes, is solid or split. In many forms "A keel or flag of bone projects posteriorly from the lateral margin at the level of the split. . . ." In *Dorsadena yaquinae* the lateral margin of the orbital portion of the CO3 is split. At the level of the split, the two parts contribute to the formation of a large, spine-like, posteroventrally-directed bony process (Fig. 3), also clearly visible on intact specimens. A relatively well-developed similar process is found also in *Lampa-*

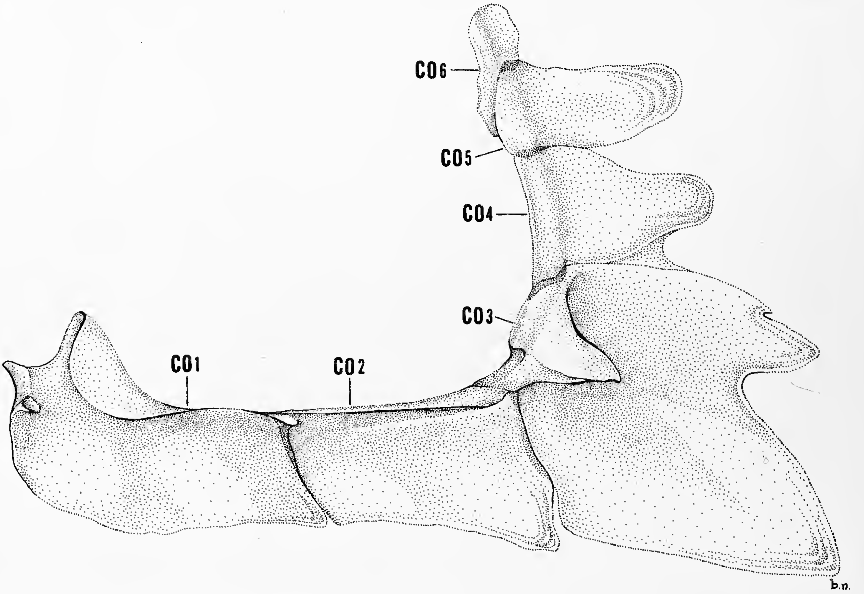


FIGURE 3. *Dorsadena yaquinae;* circumorbital bones.

dena, e.g., *L. urophaos* and *L. anomala,* and in some *Lampanyctus.*

The other circumorbital bones show no marked peculiarities.

Otoliths

Dorsadena yaquinae has a small sagitta (Fig. 4), which is almost as high as it is long–length to height ratio 1.03:1. It is not notched posterodorsally and its ventral margin is smooth. The rostrum is well developed; the antirostrum bluntly rounded but distinct. The collum divides the sulcus into two almost equal sections. The lateral face of the otolith is smooth and somewhat convex.

Nafpaktitis and Paxton (1968) have briefly discussed the trends in otolith morphology within the genus *Lampadena.* The sagittae of all the species of this genus, with the exception of *L. anomala,* are relatively large and clearly longer than they are high. Their ventral margins and, in at least two cases, dorsal margins as well, are scalloped. The rostra are little to moderately developed and the antirostra are in some cases indistinct. *L. anomala* has a relatively small otolith with a length to height ratio of 1.2:1, a smooth ventral margin and a greatly developed rostrum.

The otoliths of *L. anomala* and *D. yaquinae* are markedly similar. Figure 4 shows the otoliths of the two forms and also that of *Taaningichthys* sp., a genus closely related to *Lampadena.*

Relationships

Until thorough osteological studies are made on cleared and stained specimens of *Dorsadena,* interpretations regarding relationships of the new genus are of necessity based almost solely on external morphology.

There are several morphological similarities between *Dorsadena* and *Lampadena.* The most striking similarity is found in the structure, size and position of the supra- and infracaudal luminous glands. The body photophores in both genera are rather poorly developed and similarly arranged. With very

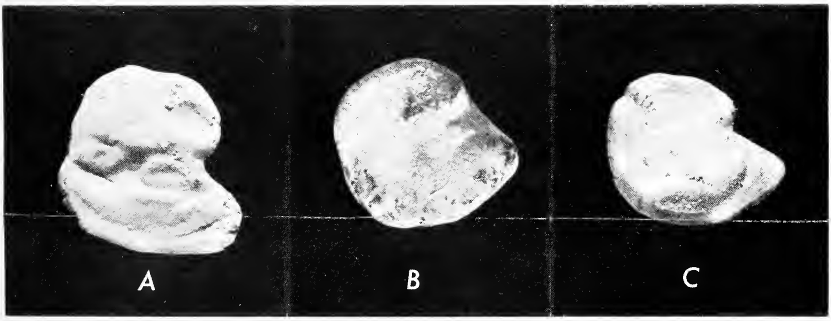


FIGURE 4. Medial views of left otoliths, anterior end to the right: (A) *Dorsadena yaquinae,* otolith 2.40 mm long, specimen 101.5 mm in SL; (B) *Taaningichthys* sp., otolith 1.90 mm long, specimen about 50 mm in SL; (C) *Lampadena anomala,* otolith 1.95 mm long, specimen about 48 mm in SL.

few exceptions, the PO and VO series are, in terms of numbers, remarkably constant within the Myctophidae. In *Dorsadena,* as in *Lampadena* and the closely related *Taaningichthys,* even the PO and VO vary in numbers. Limited osteological observations (circumorbital bones) also revealed close similarities.

Nafpaktitis and Paxton (1968) pointed out the marked differences in otolith morphology between *L. anomala* and all the rest of the species of *Lampadena.* In fact, the otolith of *L. anomala* may, in some important respects, be considered as intermediate between the long, scalloped otoliths of the rest of the species of *Lampadena* and the almost round, smooth-edged otolith of *Taaningichthys* sp. (Fig. 4). In the same manner, the otolith of *Dorsadena yaquinae* has features which may be considered intermediate between *L. anomala* and *Taaningichthys* sp., perhaps somewhat closer to the former than to the latter.

Most species of *Lampadena* appear to be among the deepest dwelling of myctophids. The very few known captures of *L. anomala* with open nets have been made below 750 meters. Shallow captures of large specimens during the night, indicative of extensive vertical migration, are known for *L. luminosa* and *L. urophaos.* Young (20-35 mm) specimens of *L. speculigera, L. dea* and *L. chavesi* have been taken during the night in the upper 200 meters.

If we assume that the body photophores of *Lampadena,* which are poorly developed (especially in *L. anomala*) and variable in numbers, reflect deep mesopelagic, or bathypelagic, existence with limited or nonexisting migratory habits, then the correlation is stronger in *Taaningichthys.* The two known species of this genus show marked degeneration of body photophores and lateral line. The photophores are small, highly superficial and their numbers as well as their arrangement vary considerably. A third species (Davy, in press) appears to have completely lost its body photophores. The lateral line components are extremely reduced. The eye, in contrast, is very large and well developed. Members of the genus *Taaningichthys* are seldom taken above 800 meters and they do not seem to undertake diel vertical migrations.

With the exception of a single specimen (MCZ 46681) taken with a 6′ Isaacs-Kidd Midwater Trawl between the surface and about 200 m, the specimens of *Dorsadena yaquinae* were captured with larger gear and at depths exceeding 2000 meters. The possibility does exist that the animals may have been caught anywhere between the surface and the maximum depth of each trawl, since the collecting gear used remained open throughout the operation. However, with the exception mentioned above, *Dorsadena* has not been taken in shallower hauls, which greatly outnumber the deep tows. In addition to capture data, several features of the body photophores suggest that *Dorsadena* occurs at depths similar to those occupied by *Lampadena* and *Taaningichthys.* If this is the case, then evolutionary convergence could account for the state of development of body photophores in the three genera. On the other hand, a detailed osteological study may support our conclusion that *Dorsadena* is closely related to *Lampadena.*

Following is a synoptic list of external characters that both relate and distinguish the three genera, *Lampadena*, *Dorsadena* and *Taaningichthys*, as they are understood at this time.

Lampadena Goode and Bean, 1896

1. Body moderately robust.
2. Ventral fins inserted under origin of dorsal fin.
3. Teeth on vomer present (absent in *L. dea*?).
4. Lateral line well developed.
5. Preadipose luminous gland absent.
6. Crescent of white tissue on dorsal half of iris present in only one species, *L. chavesi*.
7. PO 5-6; VO 3-6; SAO 3; AOa 3-8; AOp 2-5; Prc 2+1.
8. Secondary photophores absent or, if present, restricted to head.

Dorsadena, new genus

1. Body moderately robust.
2. Ventral fins inserted under origin of dorsal fin.
3. Teeth on vomer absent.
4. Lateral line well developed.
5. Preadipose luminous gland present.
6. Crescent of white tissue on iris absent.
7. PO 6-8; VO 3-5; SAO 3; AOa 5-7; AOp 3-5; Prc 2+1+1-2.
8. Secondary photophores present on head, trunk and proximal part of caudal fin.

Taaningichthys Bolin, 1959

1. Body slender.
2. Ventral fins inserted in advance of origin of dorsal fin.
3. Teeth on vomer absent.
4. Lateral line absent or very poorly developed.
5. Preadipose luminous gland absent.
6. Crescent of white tissue present on posterior half of iris.
7. PO 5-6; VO 2-10; SAO 1; AOa 1-8; AOp 1-5; Prc 2+1; or photophores absent.
8. Secondary photophores, if present, restricted to head and interradial membrane of caudal fin.

DISCUSSION

Most lanternfishes perform diel vertical migrations of several hundred meters. During their vertical migrations, these animals cross a wide range of temperature and salinity. It is therefore difficult to understand how a given set of physico-chemical factors at a particular depth could limit the horizontal distribution of these organisms. The answer, or answers, to the puzzle probably lie in the reproductive physiology on the one hand, and in the tolerance limits of the early, epipelagic stages on the other. While a large portion of the epipelagic larvae remain within the ecologically optimum area where they grow, sink and subsequently metamorphose, many may be transported by currents to waters of different physico-chemical properties. In this alien environment, some young will perish, others will survive, sink and metamorphose. However, these expatriates are usually unable to reproduce. As Bolin (1959b) points out: "While straggling adults may exist for long periods in waters far beyond the normal range of the species, permanent populations are restricted to the proximity of the areas where spawning can be successful." It is therefore necessary to exercise extreme caution in discussing ranges and distributional patterns, especially when we are dealing with oceanic, midwater organisms with epipelagic larval stages, such as myctophids, because the area in which a species can exist may be much larger than the area in which it can spawn. For instance, are the subarctic waters off Oregon within the "normal" range of *Dorsadena yaquinae*? Does this fish spawn there? The poorly developed and, in the larger specimens, regressed gonads do not seem to indicate that spawning takes place in that area. If it does, then the absence of larvae and young in the California Current System may perhaps be accounted for by the change in the physico-chemical properties of the subarctic water along the course of the California Current.

On the basis of the available data, however, it seems more likely that here we are dealing with an expatriate population originating in deep, seldom sampled waters either of the Subtropic Region or of the central and western Subarctic Region.

ACKNOWLEDGMENTS

We thank the captain, crew and scientists of the R/V YAQUINA, Oregon State University, for assisting in the work at sea. We are thankful also to William G. Pearcy of Oregon State University, Richard H. Rosenblatt and Robert L. Wisner of Scripps Institution of Oceanography for reviewing the manuscript, and to John E. Fitch and Jack W. Schott of the California Department of Fish and Game for supplying comparative otolith material and for taking the otolith photographs. Financial support by grants from AEC [AT (45-1) 1750; RLO/56] and NSF (GB-1588) is here gratefully acknowledged.

LITERATURE CITED

BOLIN, R. L. 1939. A review of the myctophid fishes of the Pacific Coast of the United States and of lower California. Stan. Ich. Bull. Vol. 1 (4): 89-156.

———. 1959a. Iniomi. Myctophidae from the "Michael Sars" North Atlantic Deep-Sea Expedition 1910. *In* Rep. Sci. Res. "Michael Sars" N. Atlantic Deep-Sea Exped. 1910, Bergen, 4, pt. 2 (7): 1-45.

———. 1959b. Differential bipolarity in the Atlantic and Pacific as expressed by the myctophid fishes. *In* International Oceanographic Congress, Reprints, 31 August-12 September 1959, Mary Sears, ed., American Association for the Advancement of Science, Washington, D.C., p. 142-143.

DAVY, B. A review of the lanternfish genus *Taaningichthys* (family Myctophidae) with the description of a new species. U.S. Dept. Com., Fish. Bull. Vol. 70 (1), (in press).

FRIZZELL, D. L., AND J. H. DANTE. 1965. Otoliths of some early Cenozoic fishes of the Gulf Coast. J. Paleontol. 39: 687-718.

GOODE, G. B., AND T. H. BEAN. 1896. Oceanic Ichthyology. U.S. Nat. Mus., Spec. Bull. 553 p.

NAFPAKTITIS, B. G. 1968. Taxonomy and distribution of the lanternfishes, genera *Lobianchia* and *Diaphus,* in the north Atlantic. Dana-Rep. 73. Copenhagen. 131 p.

NAFPAKTITIS, B. G., AND J. R. PAXTON. 1968. Review of the lanternfish genus *Lampadena* with a description of a new species. Los Angeles Co. Mus., Contrib. Sci. 138: 1-29.

PAXTON, J. R. 1972. Osteology and relationships of the lanternfishes (Family Myctophidae). Natural History Museum, Los Angeles Co., Bull. 13, (in press).

Accepted for publication Nov. 16, 1971

Printed in Los Angeles, California by Continental Grap

NUMBER 226
MARCH 21, 1972

THE *AMPHINEMURA VENUSTA* COMPLEX OF WESTERN NORTH AMERICA (PLECOPTERA: NEMOURIDAE)

By RICHARD W. BAUMANN
AND ARDEN R. GAUFIN

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1964 AIBS Style Manual for Biological Journals is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1964 AIBS Style Manual for Biological Journals in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Changes in the manuscript after galley proof will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

THE *AMPHINEMURA VENUSTA* COMPLEX OF WESTERN NORTH AMERICA (PLECOPTERA: NEMOURIDAE)

By RICHARD W. BAUMANN[1] AND ARDEN R. GAUFIN[2]

ABSTRACT: The *Amphinemura venusta* complex of Western North America contains six species where only one was previously recognized. A comparison of the *Amphinemura venusta* (Banks) holotype female with available specimens led to the re-definition of this species. The male of *A. venusta* is described and the species is recorded from Mexico, with the type locality in Southern Arizona being the northern limit of distribution. Two species, *A. mexicana* and *A. puebla* are described from near Mexico City. The material from the Rocky Mountains called *A. venusta* (Banks), as a result of the Needham and Claassen monograph (1925), is given the name *A. banksi.* Two species are named from Southwestern United States: *A. apache* and *A. mogollonica.*

The species in the complex are apparently restricted to permanently running waters. In the United States, the flight period is short, extending from July to September. The data available for Mexican species indicate that the emergence period is enlarged and may extend throughout the year.

Members of the genus *Amphinemura* occur throughout the Holarctic and Oriental regions (Illies, 1965). This study deals with a species complex found in the Western United States and Mexico. The complex is characterized by its peculiar "windowed" forewings. This type of wing, darkly infuscated with numerous clear spots in the cells (Fig. 1), is also present in some nemourids from the Himalayas. The included species represent the only North American species possessing this characteristic. Until now, these species were all included under the specific name *Amphinemura venusta* (Banks). The range of *A. venusta* was recorded by Ricker (1952) as extending from the Rocky Mountains in Wyoming to the mountains around Mexico City. This study, which was begun as part of a doctoral thesis by the senior author (1970), delineates this distributional pattern using the six species presently known in the complex.

ACKNOWLEDGMENTS

The authors are grateful to Dr. Paul H. Arnand, Jr., California Academy of Sciences (CAS); Dr. William F. Barr, University of Idaho (UI); Dr. C. J. D. Brown, Montana State University (MSU); Dr. P. J. Darlington, Jr., Museum of Comparative Zoology, Harvard University (MCZ); Dr. Oliver S. Flint, Jr., United States National Museum (USNM); Dr. W. J. Hanson and

[1] Department of Life Sciences, Southwest Missouri State College, Springfield, Missouri 65802.

[2] Department of Biology, University of Utah, Salt Lake City, Utah 84112.

Dr. George F. Knowlton, Utah State University (USU); Dr. Charles L. Hogue, Natural History Museum of Los Angeles County (LACM); Mr. Stanley G. Jewett, Jr., Portland, Oregon (SGJ); Dr. Richard W. Koss, Johns Hopkins University; Dr. Carlos Sosa Moss, Escuela Nacional de Agricultura de Mexico (ENAM); Dr. L. L. Pechuman, Cornell University (CU); Dr. William E. Ricker, Fisheries Research Board of Canada (WER); Mr. Vincent Roth, Southwest Research Station, Portal, Arizona (SWRS); Dr. Robert C. Schuster, University of California, Davis (UCD); Dr. Donald W. Webb, Illinois Natural History Survey (INHS) for making their specimens available for this study. Abbreviations for collections of the authors are: Richard W. Baumann (RWB) and University of Utah (UU).

Special thanks are given to Dr. Joachim Illies and Dr. Peter Zwick of the Max-Planck Limnology Institute, Schlitz, Germany, for their help and the use of Institute facilities for the preparation of this manuscript. The Spanish abstract was translated by Luis Benedetto. The drawing of the complete adult male was done by Michael Miner, a graduate student at the University of Utah.

This work was supported by FWPCA grant No. 1-F-2-WP-26, 393-01, NSF grant No. GB-7782 and a Sigma Xi grant-in-aid of research to the senior author.

Amphinemura apache Baumann and Gaufin, new species

Figures 2-5

Male.—Macropterous. Length of forewings 6.0-6.5 mm; length of body 4.5-5.5 mm. Body brown; legs yellowish brown, femora dark at tip, tibiae dark at base. Forewings dusky brown with 35-40 clear rounded spots in cells distributed regularly over surface; hindwings uniform dusky brown, except for 1-2 clear spots in costal space. Ninth abdominal tergite produced at posterior margin into blunt raised knob, bearing stout dark spinules. Subgenital plate rounded, broad at base, tapering gradually to narrow tip, extending to base of epiproct; lobe at base of 9th sternite four times as long as broad, lateral margins slightly sinuate, tip rounded. Paraprocts with three sclerotized processes; inner process narrow, tip blunt, lying alongside and extending slightly beyond tip of subgenital plate; middle process with large broad base, tapering abruptly to narrow tip, bearing rows of 16-18 stout spines on anterior third; outer process long and very thin, bearing 2-4 stout spines at tip (Fig. 4). Epiproct large and mostly membranous; dorsal aspect rectangular, with deep narrow sclerotized slit at bilobed tip; lateral aspect narrow at base, becoming increasingly larger, ending in large bulbous tip, lateral sclerotized band very narrow, anterior half as dark line; ventral aspect with sclerotized plate, broad at base, lateral margins sinuate, tapering to narrow tip, bearing 2-4 rows of short stout spines (Figs. 2, 3a, 3b).

Female.—Macropterous. Length of forewings 7.5 mm; length of body 6.0 mm. Body, appendages and wings similar to male. Seventh sternite very large and expanded, posterior margin extending over and completely covering middle of 8th sternite, lateral corners formed into large swollen hornlike projections (Fig. 5). Subgenital plate with median notch and lateral sinuate margins, posterior-lateral margins produced, with narrow sclerotized band.

Types.—HOLOTYPE ♂ and ALLOTYPE ♀, Rucker Creek, above Rucker Lake, Chiricahua Mountains, Cochise Co., Arizona, USA, 18-VII-1968, R. W. Baumann (LACM). PARATYPES: ARIZONA, *Cochise Co.*, same data as holotype, 6 ♂♂ (UU) (RWB); Cave Creek, Herb Martyr Campground, Chiricahua Mountains, 18-VII-1968, R. W. Baumann, 1 ♂ (dissected from mature nymph) (RWB); Upper Cave Creek, Chiricahua Mountains, 17-VIII-1970, K. Clarke and D. Sall, 1 ♂, 1 ♀ (SWRS); Upper Cave Creek, below Cave Creek Falls, 23-VIII-1970, V. Roth, 5 ♂♂, 3 ♀♀ (SWRS) (RWB).

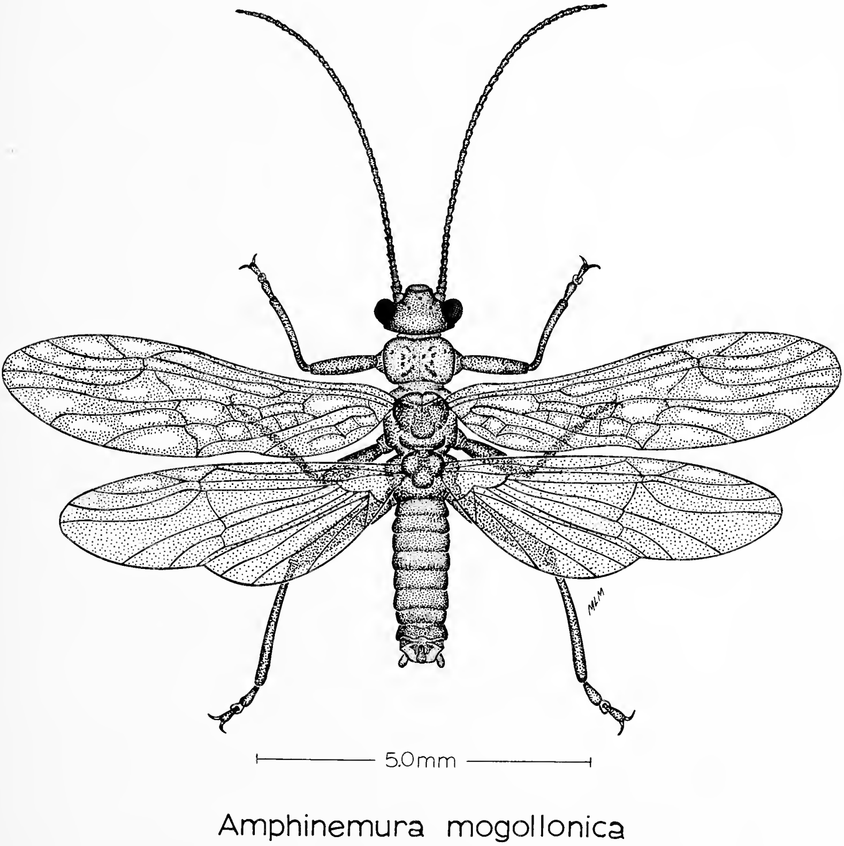
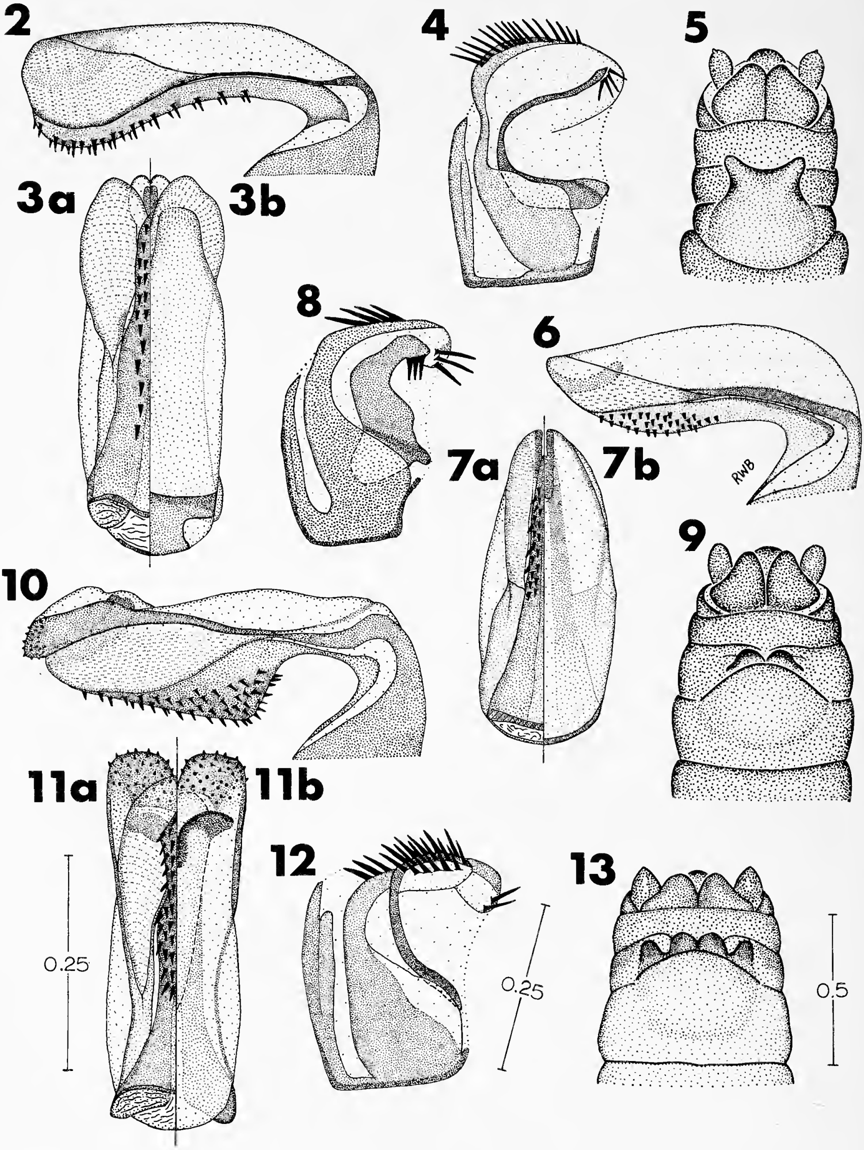


FIGURE 1. *Amphinemura mogollonica*, n. sp., adult male.



FIGURES 2-5. *Amphinemura apache,* n. sp. 2. Epiproct, lateral view. 3a. Epiproct, left half, ventral view. 3b. Epiproct, right half, dorsal view. 4. Paraproct, ventral-lateral view. 5. Female terminalia, ventral view.

FIGURES 6-9. *Amphinemura banksi,* n. sp. 6. Epiproct, lateral view. 7a. Epiproct, left half, ventral view. 7b. Epiproct, right half, dorsal view. 8. Paraproct, ventral-lateral view. 9. Female terminalia, ventral view.

FIGURES 10-13. *Amphinemura mexicana,* n. sp. 10. Epiproct, lateral view. 11a. Epiproct, left half, ventral view. 11b. Epiproct, right half, dorsal view. 12. Paraproct, ventral-lateral view. 13. Female terminalia, ventral view. (Scale in mm).

Distribution.—*Amphinemura apache* has been collected only in the Chiricahua Mountains of Southeastern Arizona. These mountains are known for their interesting endemic fauna and it is possible that this species is restricted to this area. The absence of extensive collections from the American Southwest and Mexico, however, makes such an assumption questionable.

Diagnosis.—The male of *A. apache* has an epiproct which is rectangular and narrow in dorsal view and enlarged apically in lateral view. It can be separated from the similar species. *A. mexicana* and *A. venusta,* by the broadly rounded apical portion of the epiproct as seen in lateral view. The apical portion is distinctly angular in *A. mexicana* and *A. venusta* and is produced into a downward directed process. The female can be distinguished by the greatly expanded seventh abdominal sternite which bears two hornlike processes at the posterior corners. The females of all other known species have a seventh sternite which is only slightly expanded with a broadly rounded posterior margin.

Etymology.—The specific name "apache" is a noun in apposition. It was chosen because of the importance of the Chiricahua Mountains in the history of the Apache Indians.

Amphinemura banksi Baumann and Gaufin, new species

Figures 6-9, 23

Nemoura venusta, Needham and Claassen, 1925: 209 (not holotype), 363, figs. 5-8.

Nemoura (*Amphinemura*) *venusta,* Ricker, 1952: 27 (in part).

Nemoura (*Amphinemura*) *venusta,* Gaufin, Nebeker and Sessions, 1966: 34, 35, 37 (distribution); figs. 62, 63, 72.

Amphinemura venusta, Illies, 1966: 189-190 (in part).

Additional references: *Nemoura venusta,* Dodds and Hisaw, 1925: 382; Claassen, 1931: 124 (in part); Claassen, 1940: 66 (in part); Gaufin, 1955: 117 (in part); Ricker, 1959: 949 (in part); Gaufin 1964: 222 (in part); Baumann and Gaufin, 1971: 106 (in part).

Male.—Macropterous. Length of forewings 5.0-6.0 mm; length of body 5.0-6.0 mm. Body brown; legs yellowish brown, femora dark at tip, tibiae dark at base. Forewings dusky brown with 20-25 clear rounded spots in cells beyond cord, cells between cord and base hyaline, veins brown; hindwings mostly hyaline, brown area in costal space beyond cord. Ninth abdominal tergite produced slightly at median-posterior margin, bearing fringe of small dark spinules. Subgenital plate with broad rounded base, tapering abruptly in anterior third, extending to base of epiproct, tip rounded; lobe at base of 9th sternite four times as long as broad, lateral margins parallel, tip rounded. Paraprocts with three sclerotized processes; inner process fairly broad, bluntly forked at tip, lying alongside and extending slightly beyond tip of subgenital plate; middle process with large broad base, apical portion narrow, tip located on small membranous knob bearing 3-4 stout spines, anterior sclerotized portion with row of 4-5 stout spines; outer process short, base broad, tapering slightly from angular bend to bluntly rounded tip, bearing 3-5 stout apical spines (Fig. 8). Epiproct fairly large and mostly membranous; dorsal aspect as rounded triangle, rounded tip divided by deep narrow sclerotized slit; lateral aspect quite narrow, width constant throughout, tapering to pointed tip, lateral parallel sclerotized band narrow, dorsal margin of band at base even with ventral margin of epiproct; ventral aspect with narrow sclerotized plate, broad at base, tapering gradually to pointed tip, anterior half bearing triangular patch of short stout spines (Figs. 6, 7a, 7b).

Female.—Macropterous. Length of forewings 6.5-7.5 mm; length of body 6.0-7.5 mm. Body appendages and wings similar to male. Seventh sternite large, posterior portion broadly rounded and lightly sclerotized, extending over anterior half of 8th sternite. Subgenital plate with median notch and rounded lateral sclerotized knob-like projections on posterior margin (Fig. 9). Vagina with characteristic sclerotized pattern; dorsal aspect almost square, base slightly broader, lateral-basal corners as lightly sclerotized triangles covering elongate darkly sclerotized areas, apex composed of two blunt projections which meet at junction of seminal receptacles, projections ending in blunt tips (Fig. 23).

Types.—HOLOTYPE ♂ and ALLOTYPE ♀, Hidden Valley Creek, Rocky Mountain National Park, Larimer Co., Colorado, USA, 5-VIII-1953, A. R. Gaufin (LACM). PARATYPES: ARIZONA, *Apache Co.*, Lukachukai Creek, Wagon Wheel Campground, 7-VIII-1969, R. W. Baumann, 4 ♂♂, 6 ♀♀ (RWB). COLORADO, (Rocky Mountain National Park): *Grand Co.*, Onahu Creek, Hwy. 34, 24-VIII-1967, R. W. Baumann, 1 ♂, 1 ♀ (UU). *Larimer Co.*, Cub Creek, beaver dams, 25-VII-1938, H. H. & J. A. Ross, 1 ♂ (INHS); Glacier Creek, 17-VIII-1940, T. H. Frison & T. H. Frison, Jr., 1 ♀ (INHS); same data as holotype, 10 ♂♂, 16 ♀♀ (UU) (RWB); Hidden Valley Creek, 24-VII-1960, A. R. Gaufin, 1 ♂ (UU); Fall River, Hwy. 34, 24-VII-1960, A. R. Gaufin, 1 ♀; 24-VIII-1967, R. W. Baumann, 1 ♀ (UU); creek, Hwy. 34, near Hidden Valley, 24-VIII-1967, R. W. Baumann, 4 ♂♂, 3 ♀♀ (RWB); Big Thompson River, Moraine Park, 24-VIII-1967, R. W. Baumann, 1 ♂, 2 ♀♀ (UU); Mill Creek, near Glacier Basin, 24-VIII-1967, R. W. Baumann, 2♀♀ (UU): Glacier Creek, near Bear Lake, 24-VIII-1967, R. W. Baumann, 1 ♀ (UU). UTAH, *San Juan Co.*, Pack Creek, Pack Creek Campground, 8-VIII-1969, R. W. Baumann, 4 ♂♂, 4 ♀♀ (RWB). WYOMING, *Uinta Co.*, small creek 2 miles east of Bridger, 21-VII-1967, R. W. Baumann, 60 ♂♂, 79 ♀♀ (RWB).

Additional specimens.—COLORADO, numerous specimens were examined from the following counties: *Boulder, Chaffee, El Paso, Gilpin, Grand, Jackson, Larimer, Las Animas, Mineral, Rio Blanco, Routt, Summit* and *Teller* [(MCZ) (USNM) (CU) (UU) (RWB) (INHS) (WER) (CAS).] IDAHO, *Clark Co.*, 2.5 miles northwest of Kilgore, 15-VII-1956, W. F. Barr, 6 ♂♂, 15 ♀♀ (UI). MONTANA, *Gallatin Co.*, Hyalite Creek, 9-VIII-1951, R. Hays and C. J. D. Brown, 1 ♀ (MSU); West Gallatin River, 9-VIII-1951, R. Hays and C. J. D. Brown, 1 ♀ (MSU); Beck and Border Canal, 17-VIII-1951, J. Spindler and W. D. Clothier, 8 ♂♂, 6 ♀♀ (MSU); Allison-Lewis Ditch, 12-IX-1951, J. Spindler and W. D. Clothier, 8 ♂♂, 1 ♀ (MSU). *Glacier Co.*, Kennedy Creek, 4 miles north of Babb, 13-VII-1963, A. R. Gaufin, 1 ♀ (UU). *Judith Basin Co.*, Martin Creek, 10 miles above Geyser, 7-VII-1966, J. R. Grierson, 1 ♂ (UU). SOUTH DAKOTA, *Lawrence Co.*, Roughlock Falls, near Savoy, Black Hills, 21-VIII-1954, M. W. Sanderson, 1 ♂, 3 ♀♀ (INHS). UTAH, records checked from the following counties: *Cache, Daggett, Duchesne, San Juan, Summit, Uintah, Utah* and *Wasatch* [(WER) (INHS) (UU) (RWB) (USU) (CAS).] WYOMING, numerous specimens from the following counties: *Albany, Fremont, Johnson, Lincoln, Park, Sublette, Teton* and *Uinta* [(LACM) (WER) (UU) (CAS) (USNM) (MSU) (INHS) (UCD).]

Distribution.—*Amphinemura banksi* has been recorded from Northern Montana to Northern Arizona and from Idaho to Colorado. Further collecting will probably confirm the presence of this species in Northern New Mexico. A sister species, *A. mogollonica*, is present in Arizona, New Mexico and Southwestern Utah but without an overlap in distributional area.

Diagnosis.—*Amphinemura banksi* is very similar to *A. mogollonica*. The males can be separated by the shorter and broader outer lobe of the paraprocts. The lateral projections of the female subgenital plate are simple and broadly rounded in *A. banksi* where they are bilobed and narrowly rounded in *A. mogollonica*. The female of *A. puebla* is also similar but can be distinguished by the presence of a dark triangular patch over the genital opening.

Remarks.—Needham and Claassen (1925) in their Plecoptera monograph gave descriptions and drawings of a male and female under the name *Nemoura venusta* Banks. They included collection records from Colorado, from which the descriptions and drawings were probably made. These drawings and descriptions did not agree when compared with the type female of *N. venusta* at the Harvard Museum of Comparative Zoology. This left the species figured without a name.

Etymology.—*Amphinemura banksi* was chosen in honor of the late Dr. Nathan Banks, who contributed greatly to the knowledge of the neuropteroid insects of Western North America.

Amphinemura mexicana Baumann, new species

Figures 10-13

Male.—Macropterous. Length of forewings 6.5-7.5 mm; length of body 4.5-6.0 mm. Body brown; legs yellowish brown, femora with 3 dark dorsal stripes, median stripe short, lateral stripes extending length of femur; tibiae dark at base; tarsi blackish. Forewings dark brown with 40-45 clear rounded spots in cells distributed regularly over surface; hindwings uniform dusky brown, except for 1-2 clear spots in costal space. Ninth abdominal tergite produced slightly at median-posterior margin, bearing a fringe of small dark spinules. Subgenital plate with broad oval base, tapering abruptly in anterior third, extending to base of epiproct, tip broadly rounded; lobe at base of 9th sternite four times as long as broad, lateral margins parallel, tip rounded. Paraprocts with three sclerotized processes; inner process fairly broad, forked at tip, inner prong longer than outer, lying alongside and extending beyond tip of subgenital plate; middle process with large broad base, tapering to long narrow anterior portion, tip situated on small membranous knob bearing 1-2 sharp spines, anterior sclerotized portion with 5-7 stout spines; outer process long and narrow, anterior portion located on broad membranous knob, dorsal aspect of apex bearing rows of 13-17 stout spines (Fig. 12). Epiproct large and mostly membranous; dorsal aspect rectangular, with V-shaped notch at bilobed tip, lobes covered with very small spinules, M-shaped sclerotized internal structure visible directly behind apex; lateral aspect narrow at base and greatly enlarged in anterior two-thirds; greatest width near middle, tip bluntly pointed, lateral sclerotized band narrow, widest at base and apex; ventral aspect with narrow sclerotized median portion, base broad, tapering toward apex, with enlargements near middle and slightly behind tip, bearing large patch of stout spines on anterior two-thirds (Figs. 10, 11a, 11b).

Female.—Macropterous. Length of forewings 8.0-9.0 mm; length of body 6.0-7.5 mm. Body, appendages and wings similar to male. Seventh sternite large, lightly sclerotized, posterior portion broadly rounded, extending over anterior half of eighth sternite. Subgenital plate with median notch, lateral posterior margins with two sclerotized knoblike lobes, both lobes equal in size (Fig. 13).

Types.—HOLOTYPE ♂ and ALLOTYPE ♀, La Marquesa, Las Cruces National Park, Mexico, MEXICO, 5 to 9-VII-1965, Flint and Ortiz (USNM). PARATYPES: FEDERAL DISTRICT, Desierto de los Leones National Park, 30-VII-1939, 1 ♂ (SGJ); III to V-1965, N. L. H. Krauss, 1 ♀; X-1965, 1 ♂, 1 ♀ (USNM). MEXICO, same data as holotype, 6 ♂♂, 10 ♀♀ (USNM); La Marquesa, Las Cruces National Park, 13-VII-1966, Flint and Ortiz, 5 ♂♂, 3 ♀♀ (USNM) (RWB). MORELOS, Laguanas de Zempoala National Park, 18-VIII-1939, 1 ♀ (SGJ); 10 & 11-VII-1965, Flint and Ortiz, 2 ♂♂, 2 ♀♀ (USNM).

Additional specimens.—MICHOACAN, Tuxpan, 8-VII-1965, 6 ♂♂, 4 ♀♀ (ENAM). MORELOS, Xochitepec, 14-VII-1965, 1 ♂, 1 ♀ (ENAM).

Distribution.—*Amphinemura mexicana* is known only from the mountains of Southern Mexico in the vicinity of Mexico City. The known range of this species will probably be greatly expanded with intensive collecting throughout Mexico. Based on present records, this species is the most common *Amphinemura* present in Mexico.

Diagnosis.—This species is most similar to *A. venusta*. The epiproct of the *A. mexicana* male has a large angular ventral projection. The ventral process of the epiproct is narrow and pointed in *A. venusta.* Females can be separated by the shape of the sclerotized knobs on the lateral corners of the subgenital plate. In *A. mexicana,* the knobs are equal in size and rounded, while in *A. venusta* the inner lobe is large and broadly rounded and the outer lobe is long and narrow.

Etymology.—The name is derived from Mexico where all specimens have been collected.

Amphinemura mogollonica Baumann and Gaufin, new species

Figures 1, 14-17, 24

Nemoura venusta, Ricker, 1952: 27 (in part); Ricker 1952: 949 (in part); Gaufin, 1964: 22 (in part); Gaufin, Nebeker and Sessions, 1966: 35 (in part).

Amphinemura venusta, Illies, 1966: 189-190 (in part).

Male.—Macropterous. Length of forewings 6.0-7.0 mm; length of body 5.5-6.5 mm. Body brown; legs yellowish brown, femora dark at tip, tibiae dark at base. Forewings dusky brown with 30-35 clear rounded spots in cells distributed regularly over entire surface; hindwings uniform dusky brown except for 1-2 clear spots in the costal space (Fig. 1). Ninth abdominal tergite produced slightly at median-posterior margin, bearing narrow patch of small dark spinules. Subgenital plate with broad rounded base, tapering abruptly in anterior third, extending to base of epiproct, tip rounded; lobe at base of 9th sternite four times as long as broad, lateral margins slightly sinuate, tip rounded. Paraprocts with three sclerotized processes; inner process fairly broad, bluntly forked at tip, lying alongside and extending beyond tip of subgenital plate; middle process with large base, apical portion narrow, tip located on small membranous knob bearing 2-4 sharp spines, anterior sclerotized portion with row of 4-5 stout spines; outer process long, base broad, tapering to narrow anterior portion, tip small and rounded, bearing 2-3 stout apical spines (Fig. 16). Epiproct fairly large and mostly membranous; dorsal aspect as rounded triangle, rounded tip divided by deep narrow sclerotized slit; lateral aspect quite narrow, width constant throughout, tapering to pointed tip, lateral parallel sclerotized band broad at base, dorsal margin of band at base even with dorsal margin of epiproct; ventral aspect with narrow sclerotized plate, broad at base, tapering gradually to pointed tip, anterior two-thirds bearing triangular patch of short stout spines (Figs. 14, 15a, 15b).

Female.—Macropterous. Length of forewings 7.5-8.5 mm; length of body 6.0-8.0 mm. Body, appendages and wings similar to male. Seventh sternite large, posterior portion broadly rounded and lightly sclerotized, extending over anterior half of 8th sternite. Subgenital plate with median notch and bilobed lateral sclerotized projections on posterior margin (Fig. 17). Vagina with characteristic sclerotized pattern; dorsal aspect with broad base and broadly rounded apex, lateral-basal corners as lightly sclerotized triangles partially covering elongate darkly sclerotized areas, apex with two broad projections, tips rounded above and pointed below, meeting at junction of seminal receptacles (Fig. 24).

Types.—HOLOTYPE ♂ and ALLOTYPE ♀, Christopher Creek, Hwy. 160, Christopher Creek, Gila Co., Arizona, USA, 19-VII-1968, R. W. Baumann (LACM). PARATYPES: ARIZONA, *Apache Co.,* Hall Creek, Hwy. 373, near Greer, 19-VII-1968, R. W. Baumann, 3 ♂♂ (RWB). *Cochise Co.,* stream ¼ mile below Rustler Park spring, Chiricahua Mountains, 27-VIII-1969, R. & D. Koss 1 ♂ (RWB). *Gila Co.,* same data as holotype, 27 ♂♂, 7 ♀♀ (UU) (RWB). *Graham Co.,* Wet Canyon Campground, Graham Mountains, 13-IX-1952, B. Malkin, 1 ♀ (CAS); Shannon Campground, Graham Mountains, 13-IX-1952, B. Malkin, 2 ♂♂, 1 ♀ (CAS). UTAH, *Beaver Co.,* Birch Creek, below Birch Creek Lake, Kents Lake road, 4-VIII-1969, R. W. Baumann, 1 ♂, 1 ♀ (RWB). *Emery Co.,* Joes Valley, 6-IX-1945, G. F. Knowlton, 2 ♀♀ (WER). *Sanpete Co.,* Ephraim Canyon summit, 6-IX-1945, G. F. Knowlton, 2 ♂♂, 3 ♀♀ (WER). *Sevier Co.,* Fish Lake, 2-IX-1930, 1♂ (INHS); Seven Mile Creek, above Johnson Valley Reservoir, 24-VIII-1962, R. F. Gaufin, 2 ♀♀ (UU). *Washington Co.,* North Fork Virgin River, Watchman Campground, Zion National Park, 30-VII-1967, R. W. Baumann, 1 ♀ (RWB).

Additional specimens.—ARIZONA, *Apache Co.,* 3.8 miles southeast of Nutrioso, 17-V-1964, S. G. Jewett, Jr., 1 ♂, 2 ♀♀ (dried) (SGJ); Rosey Creek, Hwy. 373, near Greer, 7-IV-1968, R. W. Baumann, 2 ♀♀ (dried) (RWB); 19-V-1970, R. W. Baumann, 1 ♂, 2 ♀♀ (dried) (RWB). NEW MEXICO, *Grant Co.,* Pinos Altos, Pinos Altos Mountains, 28-VIII-1951, E. L. Kessel, 1 ♀ (CAS).

Distribution.—*Amphinemura mogollonica* is the most common *Amphinemura* species in Arizona. It has also been recorded from the Southwestern parts of New Mexico and Utah.

Diagnosis.—This species is similar to *A. banksi* but can be distinguished by the shape of the male paraprocts and the projections on the female subgenital plate. The outer lobe of the paraproct is long and thin in *A. mogollonica*

⟶

FIGURES 14-17. *Amphinemura mogollonica,* n. sp. 14. Epiproct, lateral view. 15a. Epiproct, left half, ventral view. 15b. Epiproct, right half, dorsal view. 16. Paraproct, ventral-lateral view. 17. Female terminalia, ventral view.

FIGURES 18-21. *Amphinemura venusta* (Banks). 18. Epiproct, lateral view. 19a. Epiproct, left half, ventral view. 19b. Epiproct, right half, dorsal view. 20. Paraproct, ventral-lateral view. 21. Female terminalia, ventral view.

FIGURE 22. *Amphinemura puebla,* n. sp., Female terminalia, ventral view.

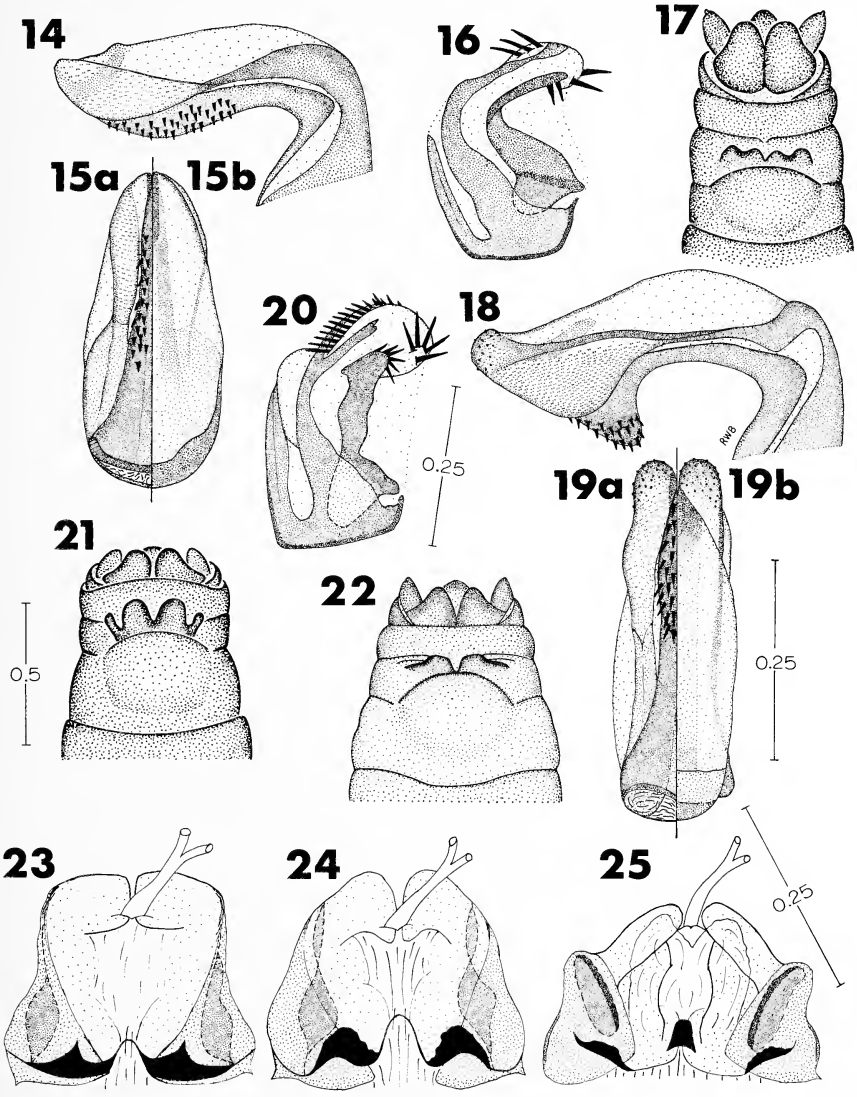
FIGURE 23. *Amphinemura banksi,* n. sp., Vagina, dorsal view.

FIGURE 24. *Amphinemura mogollonica,* n. sp., Vagina, dorsal view.

FIGURE 25. *Amphinemura puebla,* n. sp., Vagina, dorsal view. (Scale in mm).

and short and blunt in *A. banksi.* The *A. mogollonica* female has bilobed projections and the *A. banksi* female has single lobed projections. Some variation exists in the size of the outer lobe in *A. mogollonica* but usually both lobes are of similar size.

Etymology.—The name "mogollonica" is taken from the Mogollon Rim of Arizona.



Amphinemura puebla Baumann, new species

Figures 22, 25

Male.—Unknown.

Female.—Macropterous. Length of forewings 7.0-8.5 mm; length of body 6.0-6.5 mm. Body brown; legs yellowish brown, femora dark at tip, tibiae dark at base and tip, tarsi dark. Forewings dusky brown, with 25-30 clear rounded spots in cells distributed regularly over surface; hindwings uniform dusky brown. Seventh sternite large, posterior portion rounded and lightly sclerotized, extending over anterior half of 8th sternite. Subgenital plate with deep median notch and blunt lateral sclerotized projections on posterior margin (Fig. 22). Eighth sternite with elongate triangular sclerotized patch over genital opening. Vagina with characteristic sclerotized pattern; dorsal aspect short and wide, base broad, apex very broadly rounded, lateral basal corners as small sclerotized triangles covering elongate oval darkly sclerotized areas, apex with two narrow projections, tips rounded, meeting at junction of seminal receptacles (Fig. 25).

Types.—HOLOTYPE ♀, 5.2 miles west of Acultzingo (Veracruz), Puebla, MEXICO, 6-VII-1962, J. M. Campbell (INHS). PARATYPES: PUEBLA, same data as holotype, 2 ♀♀ (INHS) (RWB).

Distribution.—*Amphinemura puebla* is known only from the three type females from Puebla, Mexico.

Diagnosis.—This species is similar in the female to *A. banksi* and *A. mogollonica.* The shape of the lobes of the subgenital plate is somewhat more angular in *A. puebla* but falls within the range of variation found in the above species. The vagina is, however, quite distinctive and can be recognized by the ratio of width to length. In *A. puebla,* the width is nearly twice the length while in *A. banksi* and *A. mogollonica* the width and length are about equal. The prolonged lobes which meet at the junction of the seminal receptacles are narrow and of equal length throughout in *A. puebla* while in *A. banksi* and *A. mogollonica* they are enlarged apically.

Etymology.—The name "puebla" is taken from the Mexican state where the types were collected.

Amphinemura venusta (Banks)

Figures 18-21

Nemoura venusta Banks, 1911: 337.

Nemoura venusta, Needham and Claassen, 1925: 209 (holotype only).

Nemoura (*Amphinemura*) *venusta,* Ricker, 1952: 27 (in part).

Amphinemura venusta, Illies, 1966: 189-190 (in part).

Additional references: *Nemoura venusta*: Claassen, 1940: 66 (in part); Ricker, 1963: 949 (in part); Ricker, 1950: 205; Gaufin, 1964: 222 (in part).

Male.—Macropterous. Length of forewings 6.5-7.0 mm; length of body 5.0-5.5 mm. Body brown; legs yellowish brown, femora dark at tip, tibiae dark at base and tip, tarsi black. Forewings deep brown, with 35-40 clear rounded spots in cells distributed regularly over surface; hindwings uniform dusky brown, except for 1-2 clear areas in costal space. Ninth abdominal tergite produced slightly at median-posterior margin, bearing sparse fringe of small dark hairs, lateral-posterior margins with 2-3 long black hairs. Subgenital plate with broad oval base, tapering abruptly in anterior third, extending nearly to base of epiproct, tip broadly rounded; lobe at base of 9th sternite four times as long as broad, lateral margins parallel, tip rounded. Paraprocts with three sclerotized processes; inner process fairly broad, with slight indentation at blunt tip, lying alongside and extending beyond tip of subgenital plate; middle process broad at base, tapering abruptly to narrow median portion, tip forked and situated on large membranous bulbous lobe bearing 3-7 sharp spines, anterior sclerotized portion with row of 12-15 stout spines; outer process fairly long, broad at base, tapering slightly towards apex, with 6-9 stout spines on blunt tip (Fig. 20). Epiproct large and mostly membranous; dorsal aspect rectangular, deep sclerotized slit at bilobed tip, lobes bearing few very small dark spinules; lateral aspect narrow at base, tapering abruptly to slanted angular apex, with large median-ventral projection, lateral sclerotized band broad at base and tip, narrow medially; ventral aspect with narrow sclerotized portion, base broad, tapering towards apex, slight enlargement at anterior third, enlarged area bearing patch of short stout spines (Figs. 18, 19a, 19b).

Female.—Macropterous. Length of forewings 7.5-9.0 mm; length of body 6.0-8.0 mm. Body appendages and wings similar to male. Seventh sternite fairly large, lightly sclerotized, broadly rounded and extending over half of 8th sternite. Subgenital plate with deep median notch, two lateral knoblike projections on posterior margins, inner projections large and broadly rounded, outer projections long and very narrow (Fig. 21).

Types.—HOLOTYPE ♀, Huachuca Mountains, Cochise or Santa Cruz Co., Arizona, USA, Oslar (MCZ, #11357). ALLOTYPE ♂, La Marquesa, Las Cruces National Park, Mexico, MEXICO, 5 to 9-VII-1965, Flint and Ortiz (USNM).

Additional specimens.—FEDERAL DISTRICT, St. Rosa Nr., 24-I-1932, A. Dampf, 1 ♂ (INHS); Canada Contraras, 14-VI-1947, T. H. Hubbell, 1 ♂, 1 ♀ (WER). MEXICO, La Marquesa, Las Cruces National Park, 5 to 9-VII-1965, Flint and Ortiz, 1 ♂, 2 ♀♀ (USNM). MICHOACAN, Tuxpan, 7-VIII-1965, 2 ♀♀ (ENAM).

Distribution.—*Amphinemura venusta* is known from the United States by a single record from Southern Arizona (type). The species is recorded from three Mexican states in the vicinity of Mexico City. The distribution patterns of Trichoptera species (Flint, 1967) indicate that further collections in Northern Mexico should fill this distribution gap.

Diagnosis.—The males of this species are easily recognized by the details of the epiproct and the distinctive bulbous paraprocts. The epiproct of the most similar species, *A. mexicana*, has a wide angular ventral projection while the epiproct of *A. venusta* is narrow and pointed. *Amphinemura venusta* is the only species in this complex which has large membranous enlargements at the tip of the middle lobe of the paraprocts. The females are similar to *A. mexicana* but can be distinguished by the thin outer lobes on the median-posterior margins of the subgenital plate. These lobes are short and broad in *A. mexicana.*

Remarks.—*Amphinemura venusta* was named by Nathan Banks from a single pinned female. The apparent lack of close examination of the type by Needham and Claassen and the very general key character by Ricker (1952) led to the consideration of all specimens of *Amphinemura* from Western North America with "windowed" wings under this name.

KEY TO SPECIES

Males

(*puebla* unknown)

1. Dorsal aspect of epiproct with broad base and narrow apex; lateral aspect of epiproct of equal width throughout length; paraprocts bearing 14 or less spines. 2
   Dorsal aspect of epiproct with broad base and apex; lateral aspect of epiproct with narrow base and enlarged apex; paraprocts with 18 or more spines. 3
2. Outer sclerotized process of paraprocts short, broad and blunt at tip (Fig. 8). . . . . *banksi*
   Outer sclerotized process of paraprocts long, narrow and pointed at tip (Fig. 16). . . . . *mogollonica*
3. Lateral aspect of epiproct broadly rounded at apex, without definite ventral projection (Fig. 2). . . . . *apache*
   Lateral aspect of epiproct angular at apex, with definite ventral projection. 4
4. Ventral projection at apex of epiproct narrow and pointed; middle sclerotized process of paraprocts located on large bulbous membranous lobe, outer sclerotized process broad with large tip (Figs. 18, 20) . . . . *venusta*
   Ventral projection at apex of epiproct broad and angular; middle sclerotized process of paraprocts located on small narrow membranous lobe, outer sclerotized process narrow with small tip (Figs. 10, 12). . . . *mexicana*

Females

1. Produced portion of 7th abdominal sternite bluntly forked completely covering 8th sternite (Fig. 5). . . . . *apache*
   Produced portion of 7th abdominal sternite broadly rounded, partially covering 8th sternite. 2

2. Posterior-lateral margin of subgenital plate with one sclerotized projection on each side (bilobed in *mogollonica*). 3
   Posterior-lateral margins of subgenital plate with two sclerotized projections on each side. 5
3. Projections on subgenital plate with bilobed tip, lobes of about equal size (Fig. 17). . . . . *mogollonica*
   Projections on subgenital plate rounded or slightly angular, sometimes with small lateral extensions. 4
4. Vagina rectangular with broad base, lateral triangles small and dark, anterior projections narrow and rounded at tip; triangular sclerotized patch on 8th sternite over genital opening; projections on subgenital plate angular (Figs. 22, 25). . . . . *puebla*
   Vagina square with broad base and apex, lateral triangles large and light, anterior projections wide and blunt at tip; sclerotized patch absent from 8th sternite; projections on subgenital plate rounded (Figs. 9, 23). *banksi*
5. Outer subgenital plate projections equal in size or slightly smaller than inner projections (Fig. 13). . . . . *mexicana*
   Outer subgenital plate projections very narrow, inner projections large (Fig. 21). . . . . *venusta*

RESUMEN

El complejo *Amphinemura venusta* del oeste norteamericano muestra contener seis especies conocidas de las cuales sólo una fué previamente identificada. La comparación del holotipo hembra de *Amphinemura venusta* (Banks) con los ejemplares disponibles lleva a la rediagnosis de ésta especie en Mexico, siendo la localidad tipica en la parte sur de Arizona el limite boreal de su distribución. Se describen dos especies *A. mexicana* y *A. puebla* de las cercanias de la ciudad de Mexico. Los especimenes de las Rocalloses llamados *A. venusta* (Banks) como resultado de la monografía de Needham y Claassen (1925) son llamados *A. banksi.* Dos especies llamadas *A. apache* y *A. mogollonica* provienen del Sudoeste de los Estados Unidos.

Las especies del complejo están aparentemente restringidas a corrientes permanentes de agua. En los Estados Unidos, el período de vuelo es corto, extendiéndose desde julio a septiembre. Los datos disponibles sobre especies mexicanas indican que el período de emergencia es prolongado y puede extenderse durante todo el año.

LITERATURE CITED

BANKS, N. 1911. New species of North American Neuropteroid Insects. Trans. Amer. Entomol. Soc. 37:335-360.

BAUMANN, R. W. 1970. The Genus *Nemoura* (Plecoptera) of the Rocky Mountains. Ph. D. Thesis. Univ. Utah. 192 p. Univ. Microfilms. Ann Arbor, Mich. (Diss. Abstr. 31:3068-B).

BAUMANN, R. W., AND A. R. GAUFIN. 1971. The Stoneflies (Plecoptera) of the Wasatch Mountains, Utah. Proc. Utah Acad. Sci., Arts and Lett. 46:106-113 (1969).

CLAASSEN, P. W. 1931. Plecoptera Nymphs of America (North of Mexico). Thomas Say Found. Entomol. Soc. Amer. 3. 199 p.

————. 1940. A Catalogue of the Plecoptera of the World. Mem. Cornell Agr. Exp. Sta. 232. 235 p.

DODDS, G. S. AND F. L. HISAW. 1925. Ecological Studies on Aquatic Insects, IV. Altitudinal Range and Zonation of Mayflies, Stoneflies and Caddisflies in the Colorado Rockies. Ecology 6:380-390.

FLINT, O. S., JR. 1967. Studies of Neotropical Caddis Flies, VI: On a collection from Northwestern Mexico. Proc. Entomol. Soc. Wash. 69:162-176.

GAUFIN, A. R. 1955. The Stoneflies of Utah (Checklist). Proc. Utah Acad. Sci., Arts and Lett. 32:117-120.

————. 1964. Systemic List of Plecoptera of Intermountain Region. Proc. Utah Acad. Sci., Arts and Lett. 41:221-227.

GAUFIN, A. R., A. V. NEBEKER AND J. SESSIONS. 1966. The Stoneflies of Utah. Univ. Utah Publ. Sci. Ser. 14. 93 p.

ILLIES, J. 1965. Phylogeny and Zoogeography of the Plecoptera. Ann. Rev. Entomol. 10:117-140.

————. 1966. Katalog der rezenten Plecoptera. Das Tierreich, 82. Walter de Gruyter & Co., Berlin. 632 p.

NEEDHAM, J. G. AND P. W. CLAASSEN. 1925. A Monograph of the Plecoptera of America North of Mexico. Thomas Say Found. Entomol. Soc. Amer. 2. 397 p.

RICKER, W. E. 1950. Some Evolutionary Trends in Plecoptera. Proc. Ind. Acad. Sci. 59:197-209.

————. 1952. Systematic Studies in Plecoptera. Ind. Univ. Publ. Sci. Ser. 18. 200 p.

————. 1959. Plecoptera, p. 941-957. *In* W. T. Edmundson (ed.) Freshwater Biology. John Wiley and Sons, New York.

Accepted for publication January 14, 1972

Printed in Los Angeles, California by Continental Grap

NUMBER 227
APRIL 12, 1972

KARYOTYPIC VARIATION AND EVOLUTION OF THE LIZARDS IN THE FAMILY XANTUSIIDAE

By Robert L. Bezy

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1964 AIBS Style Manual for Biological Journals is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1964 AIBS Style Manual for Biological Journals in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Changes in the manuscript after galley proof will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

KARYOTYPIC VARIATION AND EVOLUTION OF THE LIZARDS IN THE FAMILY XANTUSIIDAE

By Robert L. Bezy[1]

Abstract: Diploid chromosome numbers of ten species of the family Xantusiidae range from 36 to 40 with 16 to 18 macrochromosomes, 18 to 22 microchromosomes, and 50 to 58 chromosome arms. Seven pericentric inversions, the loss of two pairs of microchromosomes, two centric fusions, and the formation of satellites on one pair of chromosomes explain the variation observed. Intraspecific karyotypic variation occurs in *Xantusia vigilis* and *Xantusia henshawi.* Chromosomal differences suggest that *Lepidophyma smithi* and *Lepidophyma occulor* are specifically distinct. Chromosomal similarities are consistent with the inclusion of (1) *Klauberina riversiana* in the genus *Xantusia,* and (2) *Gaigeia gaigeae* in the genus *Lepidophyma.* Of the several groups of lizards that have been considered related to xantusiids, the microteiids have the most similar karyotypes. At present, there is no evidence to indicate that hybridization preceded the evolution of unisexuality in *Lepidophyma flavimaculatum* from Panama and Costa Rica, in that (1) the karyotype is primarily diploid and homomorphic; and (2) there are no plausible parental species known to occur in the area.

INTRODUCTION

In Camp's (1923) monumental classification of lizards, the species of the family Xantusiidae bridged the morphological gap between the two divisions (Ascalabota and Autarchoglossa) of the suborder Sauria, a systematic dilemma which he resolved by arbitrarily depositing them in the Autarchoglossa. Subsequent workers have also found this morphologically ambivalent family annoying and have shifted it between these divisions. In actuality, these lizards may well be relicts of the departure point of the two major lines of saurian evolution and thus might reasonably be placed in a third division, a taxonomic honor which many systematists might be hesitant to bestow on this small family.

Not only have xantusiid lizards been troublesome to students of "higher classification," but those unforutnate taxonomists who have been lured into extensive studies of the systematics of the family have suffered greater torments. Within this handful of species there occurs nearly every conceivable degree of morphological divergence. Many problems are encountered by a systematist attempting to define subspecies, species, and genera in

---

[1] Associate Curator of Herpetology, Natural History Museum of Los Angeles County, Los Angeles, Calif. 90007.

this small family because the morphological differences between populations do not tend to fall into discrete sizes that can be easily assigned rank. In partitioning this array of only about 14 species into genera, one must steer between the Scylla of monotypic genera and the Charybdis of a monotypic family. Cope (1895) recognized five Recent genera, all of which were monotypic except *Xantusia*, and one of which (*Amoebopsis gilberti*) contained what is currently recognized as only a subspecies (*Xantusia vigilis gilberti*). Savage (1963) recognized four Recent genera of which two (*Xantusia* and *Lepidophyma*) were polytypic and two (*Cricosaura* and *Klauberina*) were monotypic. In this study, these lizards are treated as two groups: *Xantusia* (inclusive of *Klauberina*) and *Lepidophyma* (inclusive of *Gaigeia*); *Cricosaura typica* has not yet been studied karyotypically.

Xantusiids have extremely disjunct distributions, a characteristic generally attributed to primitive, receding groups. Ranges of most of the species are extremely fragmented and populations are often isolated by hundreds of miles. Particularly spectacular examples are the occurrence of *Xantusia vigilis* and *Xantusia henshawi* in Durango, Mexico, ca. 400 to 800 air-line miles southeast of the nearest known populations of these species (Webb, 1965, 1970) and the insular isolation of *Xantusia riversiana* and *Cricosaura typica.* The occurrence of the Eocene fossil, *Paleoxantusia fera* (Hecht, 1956), in Wyoming, ca. 300 miles north of the present northern limit of the family, adds a time dimension to the receding of xantusiids.

Sympatric contacts have been reported for only two pairs of currently recognized species in the family Xantusiidae: *Xantusia henshawi* and *X. vigilis* in southern California (Klauber, 1931) and Durango, Mexico (Webb, 1970) and *Lepidophyma tuxtlae* and *L. pajapanensis* in southern Veracruz (Werler, 1957). When the lack of sympatry in this family is combined with extreme variability in morphological divergence at the population level, the task of defining evolutionarily meaningful (or even morphologically consistent) species becomes difficult (Bezy, 1967b). Further, strong selective pressure for saxicolous adaptations in highly isolated populations of xantusiids has led to morphological convergence at the subspecies level (*Xantusia vigilis arizonae* and *X. v. sierrae*, Bezy, 1967a, b), at the species level (*Xantusia vigilis arizonae* and *X. henshawi*, Klauber, 1931), and at the near-generic level (*Xantusia* and *Gaigeia*, Smith, 1939).

This analysis of karyotypic variation has been undertaken in the hope of finding new data to help establish meaningful phylogenetic relationships in this small but puzzling family. Karyotypes of ten species of xantusiids are reported and discussed herein: *Xantusia henshawi* Stejneger, *X. vigilis* Baird, *X. riversiana* Cope, *Lepidophyma flavimaculatum* A. Dumeril, *L. gaigeae* Mosauer, *L. micropholis* Walker, *L. occulor* Smith, *L. pajapanensis* Werler, *L. smithi* Bocourt, and *L. tuxtlae* Werler and Shannon. The biogeographical, morphological, and karyotypic information indicates that these are all valid species as will be discussed in a separate paper on the systematics of the genus

Lepidophyma. Karyotypic data are not yet available for five rare forms of uncertain status: *Cricosaura typica* Gundlach and Peters, *Lepidophyma dontomasi* (Smith), *L. radula* (Smith), *L. sylvaticum* Taylor, and an undescribed species of *Lepidophyma* from Guatemala.

I wish to emphasize that the karyotype data can be meaningfully interpreted only by comparison with information from other sources, that is, by the process which Hennig (1966) dignified with the term "reciprocal illumination." I consider the comparison of patterns emerging from data of radically different sources to be a vital step in the establishment of meaningful phylogenetic relationships, and do not accept Sokal and Sneath's (1963) view that this is merely circular reasoning. Convergence, for example, can occur in morphology and in karyotypes, but, because of the radically different factors governing morphological and karyotypic evolution, the probability is quite low that convergence between two taxa will occur in both parameters. For these reasons data on morphological variation are discussed in this paper where the major focus is on karyotypic evolution. Moreover, the phylogenetic relationships suggested herein are based not only on an appraisal of data from both of these sources, but also on biogeographical and ecological field impressions.

MATERIALS AND METHODS

Chromosomes of cells from bone marrow, spleen, and testicular tissue were prepared in vivo by Patton's (1967) modification of the colchicine-hypotonic citrate technique of Ford and Hamerton (1956) as has been adapted for lizards by Lowe and Wright (1966) and by Lowe, Wright, and Cole (1966). The karyotype of *Lepidophyma flavimaculatum* was also determined in vitro from lung tissue culture by Dr. T. C. Hsu of the M. D. Anderson Hospital and Tumor Institute of Houston.

Good karyotype preparations were especially difficult to obtain from xantusiid lizards due, in part, to an unusually low level of mitotic activity in the bone marrow. By increasing the stressing of the peripheral circulatory system, mitotic activity was increased; unfortunately, this also increased the mortality among the lizards. The limbs of *Xantusia vigilis* and *Lepidophyma gaigeae* are quite small, and the bone marrow is consequently difficult to "flush out." Pooling of the bone marrow from several individuals was necessary to obtain the somatic karyotype of *L. gaigeae*, while the karyotype of populations of *X. vigilis* was derived primarily from study of testicular tissue.

Whenever possible, a minimum of at least ten cells was studied from each specimen "run." For each cell, the permanent slide number, the cell coordinates, the diploid chromosome number ($2n$), the number of macrochromosomes (macros) and microchromosomes (micros), the occurrence of secondary constrictions, and the numbers and relative sizes of metacentric (M), submetacentric (SM), subtelocentric (ST) and telocentric (T) macrochromosomes were recorded. The karyotype of the specimen was then determined on a modal basis.

For the family Xantusiidae the following classification of chromosomes was found to be the most useful and was employed throughout the study: metacentric S/L (= ratio of short to long arm of chromosome), 0.76-1.00; submetacentric S/L, 0.51-0.75; subtelocentric S/L, 0.01-0.50; and telocentric S/L, 0.00. Both pairing and classifying the chromosomes, however, was done "by eye" rather than by actual measurement. In counting chromosome arms (CA), metacentric to subtelocentric macrochromosomes were considered bi-armed, while telocentric macrochromosomes were considered uni-armed. Because I could not consistently distinguish their centromere positions, all microchromosomes were considered uni-armed.

KARYOTYPE DESCRIPTIONS

Xantusia vigilis. Study of 525 cells from 30 individuals (29♂, 1♀) representing eleven populations (including *X. v. arizonae*, *X. v. extorris*, *X. v. sierrae*, and *X. v. vigilis*) indicates that the 2*n* of this species is 40, with 18 macros and 22 micros (Tables 1 and 2, Fig. 1). The macro pairs were numbered from largest to smallest (Fig. 1); the micro pairs were not numbered as their small size precluded recognition of individual pairs. Pair 1 is by far

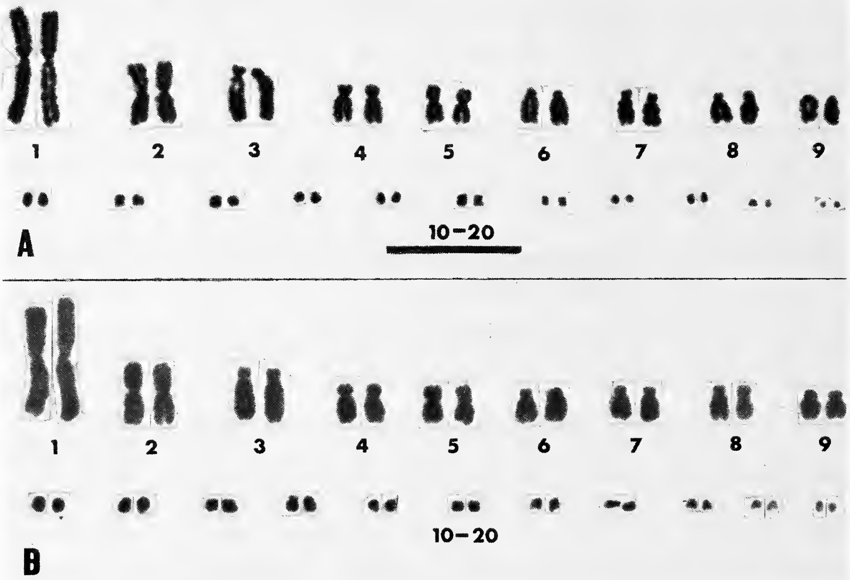


FIGURE 1. Karyotypes of *Xantusia vigilis*. A. Karyotype α; UAZ 24216, ♂, 11.3 mi (by Hwy 93) SE Burro Creek, 3200 ft, Yavapai Co., Arizona. Line represents 10 μ. B. Karyotype β; UAZ 24861, ♂, vic. Yarnell, 4750 ft, Yavapai Co., Arizona.

the largest in the complement and is metacentric to submetacentric. Pair 2 is about half the size of pair 1 and is consistently metacentric. Pair 3 is only very slightly smaller than pair 2 and is consistently subtelocentric. On the basis of size and centromere position these first three pairs are always clearly distinguishable from one another and are distinctly larger than the remaining six pairs. Pairs 4 and 5 are larger and more distinctly bi-armed than the last four pairs (6-9). Pair 4 is subtelocentric and pair 5 is submetacentric. Pairs 6, 7 and 8 are nearly identical in size and are subtelocentric; the largest (6), however, has only minute short-arms and thus occasionally appears telocentric.

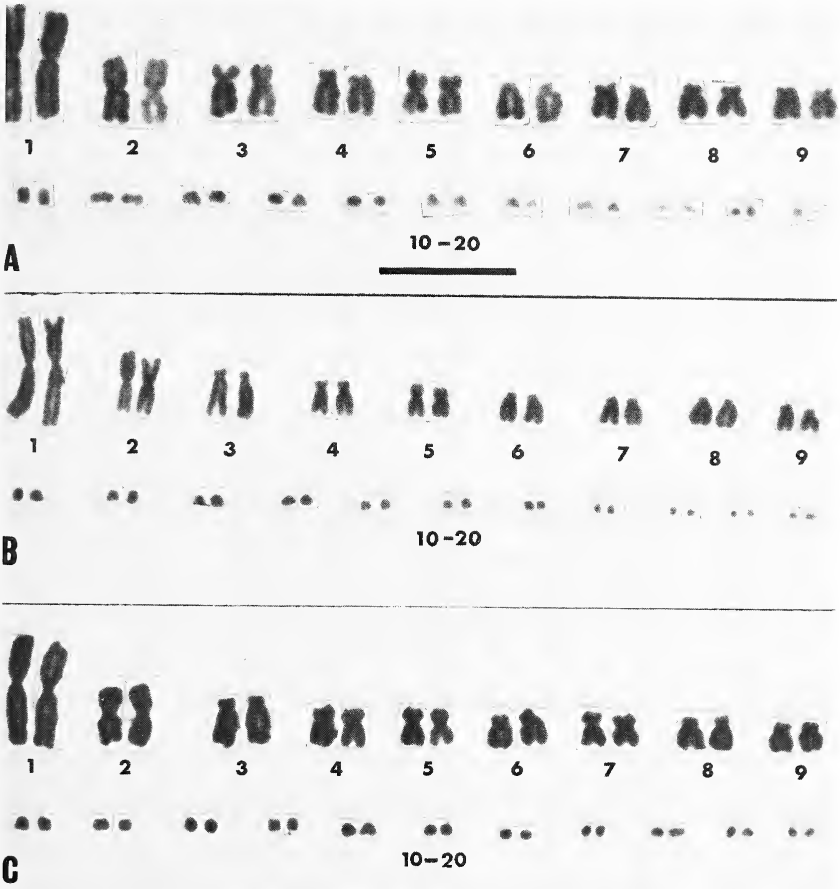


FIGURE 2. Karyotypes of two species of *Xantusia*. A. *X. riversiana*; UAZ 21688, ♀, N end of San Clemente Island, Los Angeles Co., California. Line represents 10 μ. B. *X. henshawi;* karyotype α; LACM 72325, ♀, 6.5 mi NE Pedricena, Durango, Mexico. C. *X. henshawi*; karyotype β; UAZ 21694, ♂, 2 mi (by rd to Idyllwild) S Banning, San Jacinto Mts., Riverside Co., California.

The smallest pair (9) varies among the populations of *Xantusia vigilis* studied. It appears telocentric (karyotype α, Fig. 1) in individuals from eight populations (*X. v. sierrae; X. v. vigilis* from the Mohave and Sonoran Deserts in Arizona, California, and Baja California), and subtelocentric (karyotype β) in three populations (*X. v. arizonae*; *X. v. extorris*; and *X. v. vigilis* from Desemboque, Sonora).

Xantusia henshawi. Study of 117 cells from 8 individuals (6♂, 2♀)

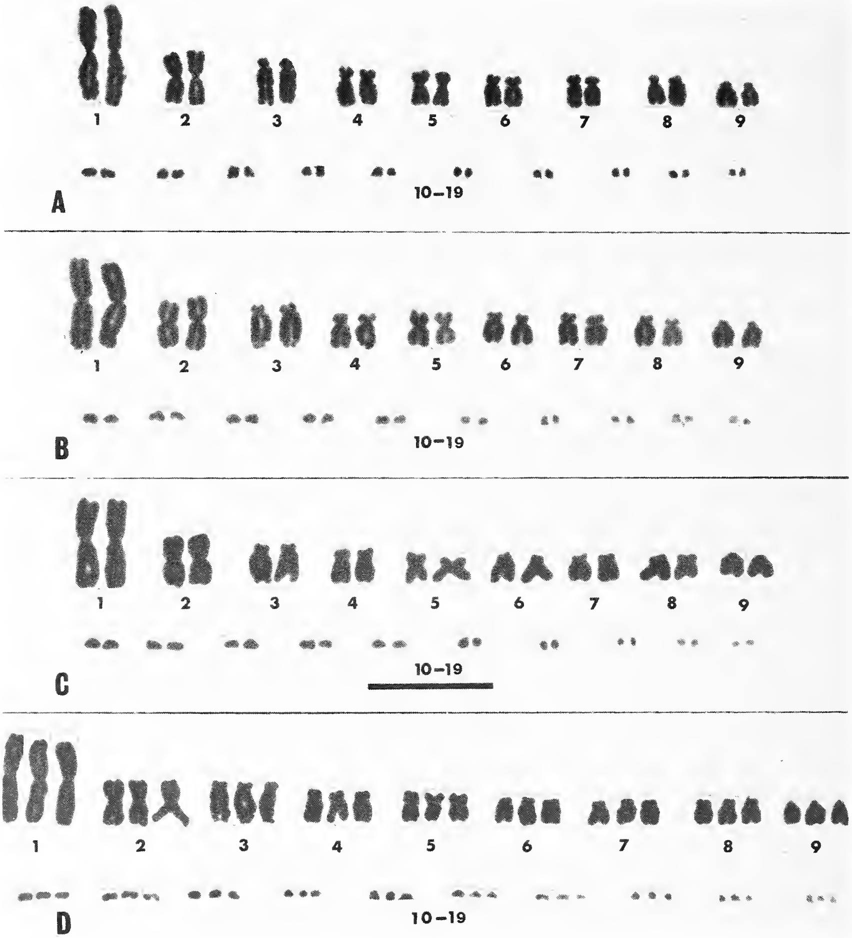


FIGURE 3. Karyotypes of *Lepidophyma flavimaculatum*. A. Bisexual population; UAZ 28805, ♀, 25 mi (by rd to Malpaso) NW Ocozocoautla, Chiapas, Mexico. B. Unisexual population; UAZ 27642, ♀, 3 mi (air line) SE Achiote, Canal Zone, Panama. C. Unisexual population. Diploid cell from UAZ 27640, ♀, same locality as UAZ 27642, above; line represents 10 μ. D. Unisexual population. Triploid cell from UAZ 27640.

from two populations (*X. h. henshawi* and *X. h. bolsonae*) indicates that the $2n$ of this species is 40, with 18 macros and 22 micros (Tables 1 and 2, Fig. 2). The karyotype of *X. h. bolsonae* ($= \alpha$) appears identical to the β karyotype of *X. vigilis*, while that of *X. h. henshawi* ($= \beta$) differs in that pair 7 has longer short-arms and is submetacentric. Matthey (1931) reported that *Xantusia henshawi* has a $2n$ of 42 with 18 macros and 24 micros. Until his count can be verified, I prefer to disregard it.

Xantusia riversiana. Study of 135 cells from 9 individuals (4♂, 5♀) of one population indicates that the $2n$ of this species is 40 with 18 macros and 22 micros (Tables 1 and 2, Fig. 2). The karyotype appears identical to the β karyotype of *X. vigilis.*

Lepidophyma flavimaculation. Study of 276 cells from 10 individuals (0♂, 10♀) representing three populations (bisexual *L. f. flavimaculatum*

FIGURE 4. Karyotypes of three species of *Lepidophyma*. A. *L. tuxtlae*. UAZ 28770, ♂, 2 mi (by rd) SE Sontecomapan, Veracruz, Mexico. B. *L. pajapanensis*. UAZ 28810, ♂, same locality as *L. tuxtlae*, above. Line represents 10 μ. C. *L. gaigeae*. UAZ 28868-73, ♀, 2 mi N Durango, Hidalgo, Mexico.

from Chiapas and unisexual *L. f. obscurum* from Panama and Costa Rica) indicates that the 2*n* of this species is 38 with 18 macros and 20 micros (rather than 22 as in *Xantusia*; Tables 1 and 2, Fig. 3). The macros in this species appear identical in morphology to those of the α karyotype of *Xantusia vigilis* except that pair 3 bears a distinct terminal satellite. The karyotypes of the unisexual populations appear to be homomorphic and identical to those of the bisexual population. However, bone marrow tissue of one individual from the all-female population in Panama appears to be composed of both diploid (2*n* = 38) and triploid (3*n* = 57) cells (Fig. 3). Eighty-two diploid and 25 triploid cells were examined from one bone marrow preparation, yielding a ratio of 3.28 diploid to 1 triploid. This condition was observed in only one of the 8 individuals studied from this all-female population. The karyotype of another individual from this same population was also determined in vitro from lung tissue culture by T. C. Hsu and found to be identical to the diploid bone marrow cells.

Lepidophyma pajapanensis. Study of 87 cells from 4 individuals (1♂, 3♀) of one population indicates that the 2*n* of this species is 38 with 18 macros and 20 micros (Tables 1 and 2, Fig. 4). The macros appear identical to those of *L. flavimaculatum.*

Lepidophyma tuxtlae. Study of 200 cells from 8 individuals (5♂, 3♀) representing two populations (Veracruz and Chiapas) indicates that the 2*n* of this species is 38 with 18 macros and 20 micros (Tables 1 and 2, Fig. 4). The karyotype of this species also appears identical to that of *L. flavimaculatum.* No differences were found between the two populations of *L. tuxtlae.*

Lepidophyma gaigeae. Study of 77 cells from 4 individuals (2♂, 2♀) of one population indicates that the 2*n* of this species is 38 with 18 macros and 20 micros (Tables 1 and 2, Fig. 4). The morphology of the macros appears identical to that in *L. flavimaculatum* except that: (1) pair 7 has longer short-arms, appearing submetacentric more often than subtelocentric; (2) pair 9 is subtelocentric rather than telocentric.

Lepidophyma micropholis. Study of 83 cells from 3 individuals (2♂, 1♀) of one population indicates that the 2*n* of this species is 36 with 16 macros and 20 micros (Tables 1 and 2, Fig. 5). The macros appear identical to those of *L. flavimaculatum*, except that: (1) pair 2A is a large metacentric that probably was formed by the fusion of pairs 6 and 8; (2) pair 3 lacks terminal satellites; (3) pair 7 is submetacentric to metacentric, thus resembling pair 7 of *L. gaigeae.*

Lepidophyma smithi. Study of 151 cells from 7 individuals (4♂, 3♀) representing two populations (*L. s. smithi* and *L. s. tehuanae*) indicates that the 2*n* of this species is 36 with 16 macros and 20 micros (Tables 1 and 2, Fig. 5). The macros appear identical to those of *L. flavimaculatum* except that pair 2A is a metacentric to submetacentric and probably was formed by centric fusion of pairs 6 and 9; thus only its long-arms are homologous with pair 2A of *L. micropholis.* That chromosome pair 2A is formed by fusion of pairs 6 and 8 in *L. micropholis* and pairs 6 and 9 in *L. smithi* is conjectured from the following: (1) pair 2A appears somewhat more submetacentric in *L. smithi* than in *L. micropholis*; (2) the smallest chromosome pair in *L. micropholis* usually appears slightly smaller than the smallest pair in *L. smithi*, and is telocentric in the former and subtelocentric in the latter. All of these differences could also be explained as resulting from inversions occurring after one centric fusion, except the difference in the size of the smallest chromosome pair. This could be made more concrete by comparing measurements from photomicrographs of the karyotypes of the two species, but the size

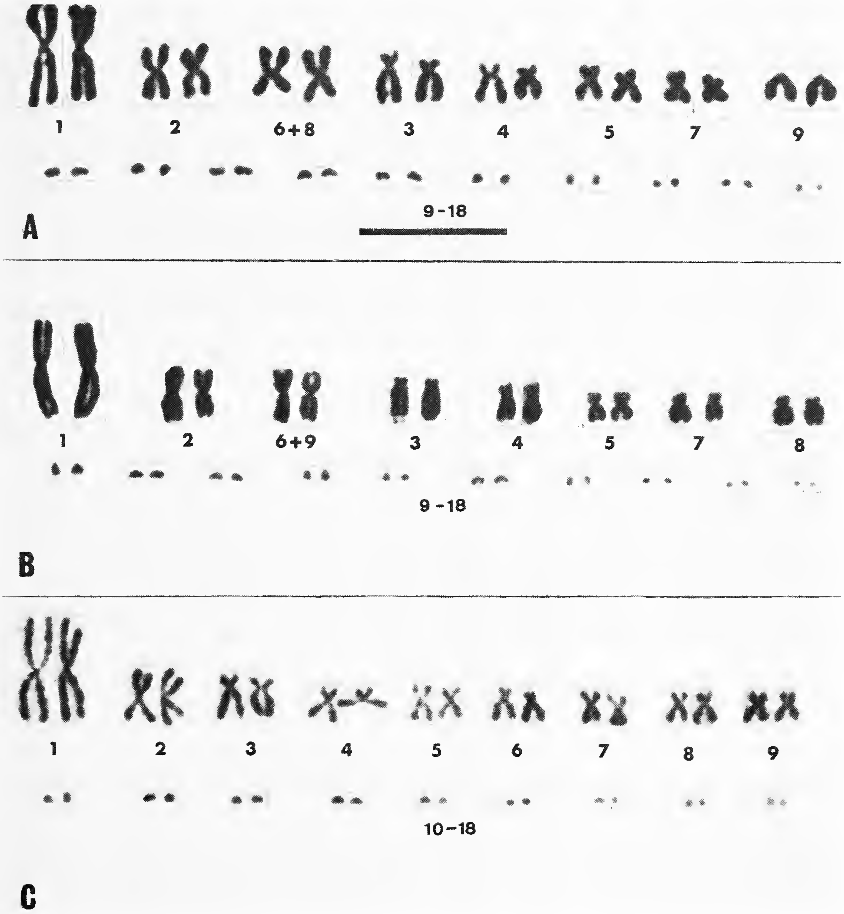


FIGURE 5. Karyotypes of three species of *Lepidophyma*. A. *L. micropholis*. UAZ 28762, ♀, cave at El Pachon, 8 km (by rd) NNE Antigua Morelos, Tamaulipas, Mexico. Line represents 10 μ. B. *L. smithi*. UAZ 28812, ♂, 4 mi NW Mapastepec, Chiapas, Mexico. C. *L. occulor*. TCWC 35605, ♂, 2.5 mi S Conca, 2000 ft, Queretaro, Mexico.

differences involved are so small that truly convincing identification of homologous chromosomes would probably require observation of synapsis in artificially produced hybrids.

Lepidophyma occulor. Study of 101 cells from one male indicates that the $2n$ of this species is 36 with 18 macros and 18 micros (Tables 1 and 2, Fig. 5). The macros are identical to those of *L. flavimaculatum*, except that (1) pair 3 lacks terminal satellites; (2) pairs 7 and 8 are submetacentric instead of subtelocentric; (3) pair 9 is submetacentric instead of telocentric.

DISCUSSION

Construction of the Karyotype Phylogeny:

The special utility of karyotype information in the study of systematics and evolution lies in three things: (1) since differences in chromosome number and form can result in decreased fertility or even sterility of hybrids, detection of karyotypic differences between two taxa increases the probability that they are not conspecific; (2) because chromosomal and morphological changes result from different evolutionary mechanisms, comparisons of the relationships indicated from karyotype analyses with those from other sources of systematic information (e.g. morphology, behavior, immunology, electrophoresis) aids in the detection of convergence; and (3) because some chromo-

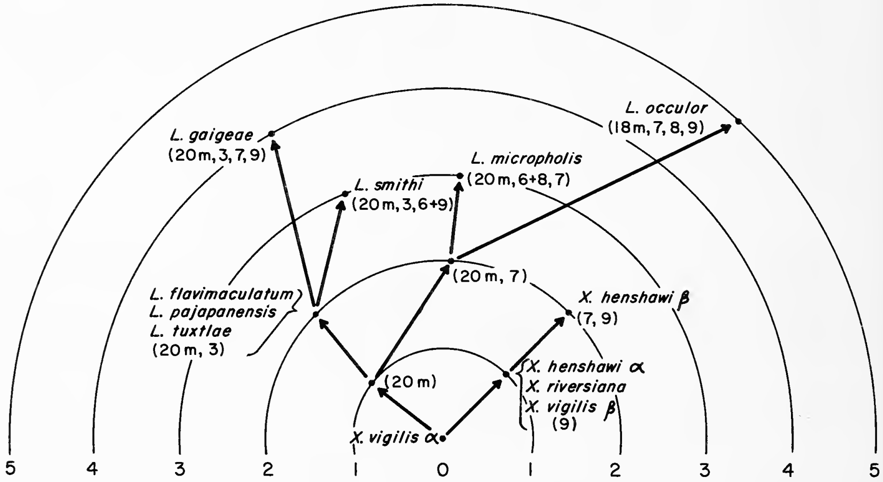


FIGURE 6. Phylogeny of the karyotypes of ten species of the family Xantusiidae. The symbols in the parentheses indicate the derived states occurring in each of the karyotypes: 18m and 20m = reductions in number of micros; 3 = formation of satellites on this pair; 6+8 and 6+9 = centric fusions of macros; 7, 8, 9 = pericentric inversions shifting the position of the centromeres on these macros. The numbers beneath the concentric half circles indicate the total number of derived states in each of the karyotypes. Data from Tables 1 and 2.

somal changes appear to be much more common than others, designation of primitive and derived character states is possible.

Although many cogent criticisms of Hennig's (1966) theory and methods have been presented (Darlington, 1970), he has, if nothing else, re-emphasized the necessity of identifying primitive (plesiomorphic) and advanced (apomorphic) character states before constructing phylogenies. In the formulation of karyotype phylogenies of lizards, two approaches have been taken to estimate the direction of evolution. One approach is to regard as primitive that karyotype which occurs most widely among the families of lizards and to derive all other karyotypes from this, using whatever cytogenetic mechanisms (centric fusion, centric fission, and inversions) are required (Gorman, Atkins, and Holzinger, 1967; Gorman, Huey, and Williams, 1969; Gorman, 1970).

The second approach to the construction of karyotype phylogenies is based on the evidence indicating that centric fusions are of much more common occurrence than fissions (Hsu and Mead, 1969). Earlier cytogenetic studies of vertebrates, especially lizards, have considered centric fusion (whole arm translocation or Robertsonian fusions; Matthey, 1951; White, 1954) to be the predominant mechanism of chromosomal rearrangement. More recently this approach has been applied to the genus *Sceloporus* (Lowe, Cole, and Patton, 1967; Cole, 1970) and *Cnemidophorus* (Lowe, Wright, Cole, and Bezy, 1970a). I have elected to utilize this approach in the present study because: (1) I feel the available evidence indicates that fissions are uncommon, and (2) the small number of taxa and karyotypes in the family Xantusiidae makes it difficult and highly arbitrary to select any one karyotype as being the most common or widespread in the family.

I thus prefer to consider karyotypes with higher diploid numbers and higher percentages of acrocentric chromosomes to be primitive, and to derive karyotypes from these by centric fusion and pericentric inversions, invoking centric fission only in those specific instances where there is compelling evidence that it has occurred (Lowe, Cole, Wright, and Bezy, 1970b).

In spite of the fact that the paracentric inversions of *Drosophila* salivary gland chromosomes form the basis for perhaps the most concrete phylogenies yet constructed, it is difficult to assign directionality to the unequal pericentric inversions that are presumed to be responsible for the shifts in centromere positions of the chromosomes in the karyotypes of xantusiids. However, as in the case of centric fusions, the general evolutionary trend in karyotypic evolution is that pericentric inversions tend to convert uni-armed chromosomes into bi-armed chromosomes, not vice versa (White, 1954:192). As with centric fusions, unequal pericentric inversions reduce the number of acrocentrics and increase the number of subtelocentric to metacentric chromosomes.

Thus, in constructing the karyotype phylogeny (Fig. 6) for each chromosome I have always considered the most nearly acrocentric condition observed

TABLE 1. Variation in the chromosomes of ten species in the family Xantusiidae. Centromere position (M = metacentric, SM = submetacentric, ST = subtelocentric, T = telocentric) and presence of satellites (*) for the macrochromosome pairs. Centromere positions in parentheses are those observed less frequently for the chromosome pair.

Chromosome Pair No.	1	2	2A	3	4	5	6	7	8	9
Xantusia										
vigilis α	M(SM)	M	—	ST	ST	SM	ST(T)	ST	ST	T(ST)
vigilis β	M(SM)	M	—	ST	ST	SM	ST(T)	ST	ST	ST
riversiana	M(SM)	M	—	ST	ST	SM	ST(T)	ST(T)	ST	ST
henshawi α	M(SM)	M	—	ST	ST	SM	ST	ST	ST	ST
henshawi β	M(SM)	M	—	ST	ST	SM	ST	SM(ST)	ST	ST
Lepidophyma										
flavimaculatum	M(SM)	M	—	ST*	ST	SM	ST	ST	ST	T
pajapanensis	M(SM)	M	—	ST*	ST	SM	ST	ST	ST	T
tuxtlae	M(SM)	M	—	ST*	ST	SM	ST	ST	ST	T
gaigeae	M(SM)	M	—	ST*	ST	SM	ST	SM(ST)	ST	ST
micropholis	M(SM)	M	M	ST	ST	SM	–	SM(M)	—	T
smithi	M(SM)	M	M(SM)	ST*	ST	SM	–	ST	ST	—
occulor	M(SM)	M	—	ST	ST	SM	ST	SM(M)	SM	SM

TABLE 2. Summary of karyotypic variation in ten species of the family Xantusiidae. Diploid chromosome number ($2n$); number of macrochromosomes (macros); number of microchromosomes (micros); number of pairs of metacentric (M), submetacentric (SM), subtelocentric (ST), and telocentric (T) macrochromosomes; presence (+) or absence (—) of satellites (Sats) on macrochromosome pair 3; number of chromosome arms (CA); and total derived states (TDS).

	$2n$	Macros	Micros	M	SM	ST	T	Sats	CA	TDS
Xantusia										
vigilis α	40	18	22	2	1	5	1	—	56	0
vigilis β	40	18	22	2	1	6	0	—	58	1
riversiana	40	18	22	2	1	6	0	—	58	1
henshawi α	40	18	22	2	1	6	0	—	58	1
henshawi β	40	18	22	2	2	5	0	—	58	2
Lepidophyma										
flavimaculatum	38	18	20	2	1	5	1	+	54	2
pajapanensis	38	18	20	2	1	5	1	+	54	2
tuxtlae	38	18	20	2	1	5	1	+	54	2
gaigeae	38	18	20	2	2	5	0	+	56	4
micropholis	36	16	20	3	2	2	1	—	50	3
smithi	36	16	20	3	1	4	0	+	52	3
occulor	36	18	18	2	4	3	0	—	54	5

among the various forms to be the primitive condition for that chromosome and have considered fused chromosomes to be a derived condition. From this line of reasoning, primitive karyotypic states in the family are: (1) a $2n$ of 40; (2) 22 micros; (3) 18 macros; (4) pairs 1 and 2, metacentric; (5) pair 5, submetacentric; (6) pairs 3, 4, 6, 7, and 8, subtelocentric; (7) pair 9, telocentric; and (8) no satellites. All of these states are present in the α karyotype of *Xantusia vigilis.*

From this primitive condition, the observed karyotypes can be derived by centric fusions and pericentric inversions using those pathways that would require the minimum number of chromosomal rearrangements and yet produce the minimum amount of karyotypic convergence (Fig. 6). A total of seven pericentric inversions, two fusions of macros, two fusions or losses of micros, and one instance of satellite formation is required to account for the chromosomal evolution observed thus far in the family Xantusiidae; a total of four instances of chromosomal convergence result (chromosomal convergence occurs when a specific derived state of a given chromosome is independently evolved in separate lineages). The phylogeny (Fig. 6) is superimposed on a scale (total derived state or TDS) that is simply the total number of character states in each karyotype that can be considered to be derived.

Species:

Although recognized species were used to some extent as guides for the sampling of populations of xantusiids for chromosomal variation, I have attempted to study as many populations as possible of each of the species.

Two karyotypes (α and β) were observed among the eleven populations of *Xantusia vigilis.* The more primitive karyotype (α) occurred in seven populations of *X. v. vigilis* from the Mohave and Sonoran Deserts of California, Arizona, and extreme northern Baja California (for localities see *Specimens Examined*) and in *X. v. sierrae* from the foothills of the Sierra Nevada in the Central Valley of California. The derived karyotype (β) was found in the three most eastern populations sampled: *X. v. vigilis* from Desemboque, Sonora, Mexico; *X. v. arizonae* from Yarnell near the southern edge of the Colorado Plateau in Arizona; and *X. v. extorris* from Durango, Mexico.

The similarity of the karyotype of *X. v. sierrae* to *X. v. vigilis* rather than to *X. v. arizonae* tends to substantiate the hypothesis (Bezy, 1967a) that the two races specialized for living under granite spalls (*arizonae* and *sierrae*) were derived independently from the widespread yucca-dwelling race (*X. v. vigilis*). The apparent lack of correspondence of chromosomal races with morphological subspecies of *X. vigilis* is interesting, and karyotypic studies of the other subspecies (*gilberti, utahensis, wigginsi*) are planned.

The two populations of *Xantusia henshawi* studied also had karyotypic differences that would appear to involve one pericentric inversion. The more primitive karyotype (α) occurs in *X. h. bolsonae* from Durango, Mexico, while the more advanced karyotype (β) occurs in the morphologically more specialized *X. h. henshawi* from southern California. Chromosomal differences of this magnitude have been found in a single population of *Sceloporus clarki* (Cole, 1970) and thus may not constitute an effective reproductive barrier.

Two forms that were considered by Walker (1955) to be subspecies of *L. flavimaculatum* have different chromosome numbers: *L. occulor* (2*n* of 36 with 18 macros and 18 micros) and *L. smithi* (2*n* of 36 with 16 macros and 20 micros). The three populations of *L. flavimaculatum* studied have a 2*n* of 38 with 18 macros and 20 micros. Such chromosomal differences rarely occur within species and may constitute genetic isolation mechanisms. Morphological and biographical data that also indicate these are distinct species will be presented in a separate paper on the systematics of the genus *Lepidophyma.*

Genera:

Mayr (1969:92-94) listed several criteria of an "ideal" genus: (1) monophyly; (2) separation from other genera by a morphological gap, the size of which is inversely proportional to the number of included species; (3) reasonable internal homogeneity; and (4) occupation of a distinctive adaptive zone. Application of these criteria to genera of xantusiids is made difficult by several factors. Convergence appears to be unusually common in the family, increasing the difficulty of accessment of monophyly. Because of the small number of xantusiid species, it is difficult to judge what size of a morphological gap should delineate a genus. Due to their secretive habits, little is known of the adaptive zones of xantusiids.

Comparisons of karyotypic phylogenies with those resulting from morphological analyses are quite useful in making decisions about monophyly and convergence, because radically different factors govern morphological and chromosomal evolution. However, for this same reason, caution must be employed in formulating generic classifications based entirely on homogeneity and gaps in chromosomal variation. For example, relying exclusively on the chromosomal data, the 10 species in this study would be partitioned into the following groupings: (1) *X. henshawi*, *X. riversiana*, *X. vigilis*; (2) *L. occulor*; (3) *L. micropholis*; (4) *L. flavimaculatum*, *L. tuxtlae*, *L. pajapanensis*, *L. smithi*; and (5) *L. gaigeae*. Although these groupings appear to be monophyletic on both karyological and morphological grounds, they do not entirely correspond to morphological clumps and gaps.

I feel that a more reasonable approach to the taxonomic interpretation of the chromosomal data is to consider the genera that have been proposed on morphological grounds as hypotheses which are, to varying degrees, testable by the chromosomal data.

During the last 50 years, a maximum of 5 Recent genera of xantusiids have been recognized (in parentheses are listed the Recent species that I consider valid): *Lepidophyma* A. Dumeril, 1851 (*flavimaculatum*, *micropholis*, *occulor*, *pajapanensis*, *smithi*, *tuxtlae*, species novum); *Xantusia* Baird, 1859 (*henshawi, vigilis*); *Cricosaura* Gundlach and Peters, 1863 (*typica*); *Gaigeia* Smith, 1939 (*dontomasi, gaigeae, radula*); and *Klauberina* Savage, 1957 (*riversiana*). In the most recent review of the genera of the family, Savage (1963) recognized 4 of these 5, placing the species formerly included in *Gaigeia* into the genus *Lepidophyma.*

No chromosomal data are yet available for *Cricosaura typica.* This is especially unfortunate because Savage (1963) considered this species to be morphologically the most distinctive in the family and placed it in a monotypic subfamily, Cricosaurinae, leaving all other species of the xantusiids in the Xantusiinae. The obtaining of chromosomal data for this species will allow further testing and comparisons of both the chromosomal and morphological phylogenetic hypotheses.

Among xantusiids the most primitive number of microchromosomes (22) is found in three of the ten species studied to date: *Xantusia henshawi, X. vigilis,* and *X. riversiana.* The similarity of the karyotypes of the three species of *Xantusia* and the consistently lower number of microchromosomes of the other 7 species xantusiids studied does not support Savage's (1957) partioning of *X. riversiana* into the monotypic genus *Klauberina.* The chromosomal evidence does not, however, unequivocably support the inclusion of *riversiana* in the genus *Xantusia* for two reasons: (1) the microchromosome number present in *X. henshawi, vigilis,* and *riversiana* is a shared *primitive* character state and this increases their phenetic similarity but does not necessarily indicate a close phylogenetic relationship; (2) as was discussed above, homogeneity and gaps in karyotypic variation do not always correspond with those of other data (morphological, ecological, behavioral, etc.). What can be said is simply that the chromosomal data lacks the pattern that Savage (1957) has reported for the morphological data, in that *X. henshawi* and *X. vigilis* do not share any chromosomal state that could be considered derived from a primitive state occurring in *X. riversiana.*

In addition to the pattern present in the chromosomal data, there are several other reasons why I prefer not to recognize the genus *Klauberina.* Genera are predictive hypotheses based on monophyly, similarities, and gaps. Monotypic genera are often the result of classifications in which there has been an overemphasis of differences. One increasingly popular solution to this problem is to use numerical techniques for quantifying species differences and then to compare these differences with standards for the minimum acceptable size of generic gaps. Short of such an analysis, I can argue against the partioning of the genus *Xantusia* only by pointing out the many similarities of the three species (*X. henshawi, riversiana,* and *vigilis*) and their differences from other xantusiids. This has already been done for the chromosomal data. The morphological evidence indicated that *Xantusia riversiana* (= *Klauberina*) is more closely related to *X. vigilis* and *X. henshawi* than any of these three species are to any of the other xantusiid (Savage, 1963). The Eocene Wyoming fossil *Paleoxantusia ferra* has been considered intermediate between *X. riversiana* (*Klauberina*) on the one hand and *X. vigilis* and *henshawi* on the other (Savage, 1963:34), suggesting that these lines diverged later than did *Lepidophyma*, *Cricosaura*, and *Xantusia*. The distributions of the species of the family suggest that each of the above three genera also occupies a somewhat consistent and distinctive adaptive zone. Species of the genus *Lepidophyma* occur primarily in wet tropical forests; *Cricosaura typica* is isolated in the Cabo Cruz area of Cuba apparently occurring under rocks and decaying leaves in forest (Barbour and Ramsden, 1919:178); while the three species of *Xantusia* have largely allopatric ranges in the arid and semiarid southwestern U.S. and northwestern Mexico. I am not trying to ignore such distinctive species ecologies as the montane limestone cap-rock habitat of *L. gaigeae* or the less restricted microhabitat enjoyed by *Xantusia riversiana* in its insular isolation, but wish simply to point out the biogeographical consistency of the three Recent genera that I feel should be recognized. Regal (1968) has recently pointed out that the pupils of some members of the genus *Lepidophyma* (perhaps exclusive of *L. gaigeae*) are round while those of other xantusiids are elliptical, an observation originally made by Cope (1900) but apparently overlooked by Savage (1963). This is a morphological observation that has broad ecological and evolutionary implications in that Regal (1968:85-86) presents the viewpoint that in xantusiids the elliptical pupil is a derived condition associated with the evolution of basking behavior. It may, then, be a derived character state shared by *Cricosaura typica*, *Xantusia henshawi*, *X. vigilis*, *X. riversiana*, and perhaps *L. gaigeae*. Further studies of pupil shape and retina structure in xantusiids are needed to determine the direction and degree of convergence in the evolution of eyes in this family.

I feel that the chromosomal, morphological, and biogeographical information summarized above indicates that the evolutionary relationships of the three species of *Xantusia* (*henshawi*, *riversiana*, and *vigilis*) are best reflected by their inclusion in one genus *Xantusia*, with two subgenera, *Xantusia* (*X. henshawi* and *X. vigilis*) and *Klauberina* (*X. riversiana*).

Smith (1939) proposed the monotypic genus *Gaigeia* in which he placed *Lepidophyma gaigeae*. He considered the genus to be intermediate between *Lepidophyma* and *Xantusia* in scale characters, having three of the distinctive character states of each of these genera, plus one unique scale character and a unique habitat. Because he felt that (1) three subsequently described species (*L. dontomasi*, *L. radula*, and *L. sylvaticum*, considered by Smith, 1942, as species of *Gaigeia*) bridged the gap in scalation between the two genera (*Lepidophyma* and *Gaigeia*) and (2) "the two supposed genera are practically identical in their skeletons," Savage (1963:33) placed all these species in *Lepidophyma*, a conclusion that was anticipated by Hecht (1956:2). Although I have karyotypic data for only one (*L. gaigeae*) of the four species that Smith (1942) considered to be in the genus *Gaigeia*, it is perhaps the most distinctive one of this group. The chromosomal information is more conclusive in this instance than it is in the case of *Xantusia riversiana*, in that *L. gaigeae* shares one definitely derived chromosomal state (loss of one pair of microchromosomes) with all other species of *Lepidophyma* studied. It also shares one character state that is probably derived (the presence of secondary constrictions on chromosome pair 3) with four other species of *Lepidophyma* (*flavimaculatum*, *pajapanensis*, *smithi*, and *tuxtlae*). The karyotype of *L. gaigeae* is one of the most highly derived in the genus *Lepidophyma* (Tables 1 and 2, Fig. 6). Interestingly enough, the karyotype of *L. gaigeae* shares two derived chromosomal states with the β karyotype of *Xantusia henshawi* in that chromosome pair 7 is submetacentric and chromosome pair 9 is subtelocentric. However, the pattern existing in the number of microchromosomes and the occurrence of secondary constrictions on the third pair of chromosomes make the conclusion inescapable that these two derived karyotypic states shared by *Xantusia h. henshawi* and *Lepidophyma gaigeae* must be the result of a certain amount of chromosomal convergence that has accompanied their morphological convergence. In this case I feel that the chromosomal data largely agree with the osteological information (Savage, 1963:33), and that *L. gaigeae* (and thus perhaps the other three species of *Gaigeia* recognized by Smith, 1942) should be included in the genus *Lepidophyma*.

Two species, *L. micropholis* and *L. occulor*, share (1) the loss of at least one pair of micros, a derived state characteristic of other species of *Lepidophyma*; (2) the absence of satellites on pair 3, a primitive state characteristic of the species of the genus *Xantusia*; and (3) submetacentric pair 7, a derived state also present in *X. henshawi* and *L. gaigeae*. Chromosomally *L. occulor* and *L. micropholis* thus appear to form a distinct species group in the genus *Lepidophyma*, a hypothesis which is to be tested by morphological data.

Inter-familial Relationships:

The evolutionary relationships of the Xantusiidae remain obscure. Cope (1900) placed the xantusiids in the suborder Leptoglossa within which he considered them to be most closely allied to the lacertids. Camp (1923) pointed out the similarities of xantusiids to both (1) the gekkonids (of the division Ascalabota) and (2) the scincids, teiids, and especially the lacertids (all of the section Scincomorpha of the division Autarchoglossa). Although the family Xantusiidae bridged the morphological gap between his two major divisions of the Sauria, Camp (1923) placed it in the Autarchoglossa, of which he considered it to be the most primitive family. McDowell and Bogert (1954) anticipated that future workers would refer the Xantusiidae to the Gekkota. Underwood (1957) placed the xantusiids in the Ascalabota; Savage (1963) referred them to the Gekkota. More recent morphological evidence has been presented which ally the family with both Gekkota (St. Girons, 1967) and Scincomorpha (Miller, 1966; Etheridge, 1967).

Available karyotype data for xantusiids, scincids, lacertids, teiids, and gekkonids are summarized in Table 3. Although there is overlap in both chromosome number and number of chromosome arms, gekkonid karyotypes differ from those of xantusiids in (1) usually being composed entirely of telocentric chromosomes; and (2) having a smooth gradation in chromosome size, thus precluding a distinction between marcros and micros. Scincid karyotypes differ in having (1) usually fewer micros, and (2) fewer chromosome arms. Those of lacertids differ in having (1) fewer micros, (2) more macros, and (3) fewer chromosome arms. Teiid karyotypes overlap those of xantusiids in all regards (numbers of chromosomes, macros, micros, and chromosome arms).

Derivation of the primitive xantusiid karyotype from known gekkonid karyotypes would require the fusion of telocentric chromosomes to form longer bi-armed macrochromosomes and the retention of the centromeres (devested of most of their euchromatin) as microchromosomes, thus increasing the number of chromosome arms while chromosome number remains approximately constant. However, because they have many primitive states, the karyotypes of gekkonids could be considered ancestral to those of most families of lizards.

Among the lizard families thought by various workers to be closely related to xantusiids, teiids appear to be karyotypically the most similar. That these two families may be closely related is suggested by: (1) the existence of macroteiids having primitive (unfused) karyotypes with numbers of chromosome arms approximating those of xantusiids; and (2) the complementary geographical distribution and the similarities in macrochromosome configuration, external morphology, and ecology of microteiids and xantusiids. I must stress that I present this simply as a phylogenetic hypothesis that should be tested by further comparisons (anatomical, karyotypic, serological, etc.) between xantusiids and other lizards, especially microteiids.

TABLE 3. Diploid chromosome number (2*n*), numbers chromosome arms (CA), macrochromosomes (Macros), and microchromosomes (Micros), and literature source (Reference) for five families of lizards.

Family	2*n*	CA	Macros	Micros	Reference
Xantusiidae	36-40	50-58	16-18	18-22	This paper
Gekkonidae	32-63	32-63	32-63		Kluge and Eckardt, 1969
Scincidae	24-32	36-46	10-32	0-18	Dutt, 1969
Lacertidae	24-38	38	24-36	0-3	Gorman, 1969
Teiidae	34-56	46-66	12-32	22-26	Gorman, 1970

Origin of Unisexuality in the Genus Lepidophyma:

Telford and Campbell (1970) reported an all-female population of *Lepidophyma flavimaculatum* in the Canal Zone (3 miles SE Achiote, Colon Province) of Panama. To help elucidate the evolutionary origin of unisexual xantusiids, I have studied karyotypes of specimens from this population and have analysed variation in sex ratio in the genus *Lepidophyma.*

As was pointed out above (see *Karyotype Descriptions*) the karyotypes of specimens from this all-female population of *L. flavimaculatum* are, with one exception, diploid and appear identical to those of individuals of this species from a bisexual population in Chiapas. This same karyotype was also found in recently obtained material from a unisexual population of *L. flavimaculatum* in southeastern Costa Rica. Thus, this case of presumed parthenogensis appears generally not to involve polyploidy. The possibility that this population is allodiploid, however, cannot be ruled out by

TABLE 4. Sample size (N), number of males (♂), number of females (♀), and percent females (% ♀) for ten species samples of *Lepidophyma* and 13 populations of *L. flavimaculatum*. Asterisk (*) indicates a sex distribution that is significantly different (.05 level) from that of *L. gaigeae* (see text).

	N	♂	♀	% ♀
dontomasi	1	0	1	100
gaigeae	260	110	150	58
micropholis	10	6	4	40
occulor	6	3	3	50
pajapanensis	13	4	9	69
radula	1	0	1	100
smithi	144	63	81	56
tuxtlae	53	24	29	55
species novum	5	1	4	80
flavimaculatum	174	29	145	83*
Tamaulipas	15	2	13	87
Queretaro	9	0	9	100*
Nuevo Leon	2	1	1	50
San Luis Potosi	1	1	0	0
Veracruz	3	0	3	100
Oaxaca	3	1	2	67
Tobasco	3	1	2	67
Chiapas	12	5	7	58
Guatemala	18	5	13	72
Honduras	17	10	7	41
Nicaragua	5	1	4	80
Costa Rica	49	2	47	96*
Panama	37	0	37	100*

the evidence at hand, since at least two other species, *L. tuxtlae* and *L. pajapanensis*, have karyotypes identical to the one under consideration. Hybridization between any of these species could result in an allodiploid in which the two separate chromosomal complements, although not distinguishable morphologically, are sufficiently different genetically to reduce the efficiency of meiosis and thereby increase the selective advantage of parthenogenetic reproduction.

Both triploid ($3n = 57$) and diploid ($2n = 38$) cells were observed in the karyotype slides from one of the eight individuals that was analysed from the Panama population (see *Karyotype Descriptions* above). It is difficult to hypothesize a reasonable mechanism for the origin of these two levels of ploidy that were observed in this one bone marrow preparation. Although the triploid and diploid cells were found in a bone marrow preparation, some type of mosaic may be involved and the two levels of ploidy may represent different types of leukocytes derived from different embryonic tissue lines. I am not aware of any really comparable phenomena among vertebrates, except perhaps the tissue mosaics involving centric fusions in *Salmo irideus*, reported by Ohno, Stenius, Fiast, and Zenges (1965) and the exparabiotic diploid-triploid leukocyte chimeraras of *Rana pipiens* reported by Volpe and Gebhardt (1966).

To survey the genus *Lepidophyma* for the occurrence of unisexuality, the sex of 666 adult specimens of the 10 recognized species was determined by examination of gonads (Table 4). Because many of the samples are small and most have greater than 50 per cent female, statistical tests were used to determine which samples have significantly different sex ratios. Choice of the appropriate test was somewhat difficult because the per cent female is greater than 50 in 9 of the 10 species. These observed deviations from the 50 per cent female (that would be theoretically expected to occur at birth in a bisexual species) may be due to: (1) chance; (2) alteration of sex ratio by a basic genetic mechanism (*e.g.* meiotic deive); (3) differences in survivorship of the sexes; or (4) differences in the "collectability" of the sexes. Since chi-square analysis ordinarily requires the use of a theoretical value, it does not aid in the task of distinguishing between (1) sex ratio deviations resulting from a basic genetic mechanism and (2) those of non-genetic origin (differential sampling and survivorship). The other available statistical test, the contingency test (Simpson, Roe, and Lewontin, 1960:186-191), requires the selection of one of the samples as a standard with which the other samples are to be compared. Although this procedure has several pitfalls of its own, it does maximize the probability of making correct distinctions between genetic and non-genetic deviations in sex ratio, if it is accepted that the samples and the standard have a similar collecting bias.

The sample of *Lepidophyma gaigeae* was chosen as the standard because it (1) is the largest available species sample; (2) was drawn from a relatively small geographic area (mountains of Queretaro and Hidalgo, Mexico); and

(3) was collected throughout the year. Using a 2x2 contingency test, with Yates' correction where applicable (see Simpson, Roe, Lewontin, 1960:186-191), the number of males and females in each species sample was tested against that of *L. gaigeae*. For only *L. flavimaculatum* was the per cent female found to be statistically different (.05 level) from that of *L. gaigeae*. As this polytypic species ranges from Tamaulipas, Mexico, to Panama, the species sample was divided into 13 geographical samples (based on the states of Mexico and the countries of Central America). When the number of males and females in each of these geographical samples was compared with that in *L. gaigeae*, only Panama (100% female), Costa Rica (96% female), and Queretaro (100% female) were found to be significantly different; Tamaulipas (87% female) almost reached the accepted level of significance (.05). The only other geographical samples large enough to allow reasonable estimates of sex ratio (Chiapas, Guatemala, and Honduras) do not differ significantly from *L. gaigeae*. Twenty of the 29 known males of *L. flavimaculatum* occur among the samples of these apparently bisexual populations. Thus *L. flavimaculatum* appears to be a polytypic species composed of (1) a central diploid bisexual population, *L. f. flavimaculatum*, in Chiapas (58% female), Guatemala (72% female), and Honduras (41% female); (2) a northern all-female or nearly all-female population (of unknown level of ploidy), *L. f. tenebrarum*, in Tamaulipas (87% female) and Queretaro (100% female); and (3) a southern all-female or nearly all-female diploid population, *L. f. obscurum*, in Costa Rica (96% female) and Panama (100% female). Samples are inadequate to determine the sex ratios of the intervening populations with any degree of accuracy.

Analysis of large samples from local populations throughout the extensive range of the polytypic *L. flavimaculatum* is required to determine whether changes in sex ratio and morphology are gradual or abrupt, and to allow an appraisal of the taxonomic status of the included forms. The two known male specimens from Costa Rica are among the northernmost available from that country, suggesting that the occurrence of males in "highly female" populations in Costa Rica might be nothing more than an artifact resulting from the accidental grouping of samples from bisexual and unisexual populations. In Tamaulipas, on the other hand, there is better evidence that males may actually occur in quite low frequency in local populations, since among the 10 adult specimens available from the Gomez Farias region, only one male was found. Comparison of sex ratios in several age classes could help to determine the relative importance of pre- and post-natal mechanisms in altering the sexual composition of the population. Before any of these questions can be addressed, adequate samples must be collected. This task is made both difficult and urgent as the devastation of the lowland tropical forests of Middle America approaches completion.

Unisexuality in the genus *Lepidophyma* appears to be similar to that of the lizards of the *saxicola* group of *Lacerta* in that (a) all forms are diploids with two identical sets of chromosomes, (b) there are forms intermediate between bisexual and unisexual; (c) the formation of small isolated populations appears to have been an important factor in the evolution of parthenogenesis (Darevsky, 1966). Known unisexual gekkos (Kluge and Eckardt, 1969) and agamids (Hall, 1970) are triploid rather than diploid. In the genus *Cnemidophorus* diploid unisexuality has been reported for *C. neomexicanus* and some *C. tesselatus,* but these, however, have been convincingly demonstrated to be allodiploids resulting from inter-specific hybridization (Lowe and Wright, 1966; Wright and Lowe, 1967), while karyotypic heteromorphism is not apparent in the unisexual *L. flavimaculatum* (Fig. 3). Vanzolini (1970) recently reported an apparently rapid shift from bisexuality to unisexuality in some Amazonian populations of *Cnemidophorus lemniscatus* and suggests that such a shift is probably not the result of inter-specific hybridization. However, Denise Peccinini (1971) reported that although these unisexual populations are diploid, they have one to three pairs of heteromorphic chromosomes and "it is possible, therefore, that the hybridization has been between subspecies of *C. lemniscatus* or even intraspecific polymorphic variants." For *Lepidophyma flavimaculatum* there is, at present, no morphological, cytogenetic, or biogeographical evidence that hybridization preceded the evolution of unisexuality. However, the paucity of the data leaves the question still open and it is certainly not unfeasible that the diploid unisexual population in Panama arose by hybridization between forms that are karyotypically similar but sufficiently different genetically to impair synapsis and thus add selective pressures for the evolution of unisexual reproduction.

During my approximately 10 years of experience with xantusiids, a number of field impressions have been formed about their ecology and probable evolutionary history. Although it is perhaps somewhat premature, I wish to here present those impressions that may help to explain the evolution of unisexuality in the family.

Xantusiids characteristically occur in localized but frequently dense populations. This distributional pattern is dictated by their narrow microenvironmental requirements. The ecological conditions to which the family is adapted were probably more widespread in the early Tertiary. This group of lizards appears to have responded to the increasingly arid continental climates of the middle and late Tertiary by becoming increasingly specialized for, and restricted to, specific limited ecological situations (e.g., under cap rocks of boulders, under bark, beneath yucca-like plants, in caves) in which their unaltered microenvironmental requirements could be met. These stresses have produced a disjunct relictual pattern of distribution. Moreover, the resulting isolated populations are frequently under tremendous pressure for colonization of new areas because of fluctuations in climate, vegetation, and habitat availability.

For example, the narrow ecological requirements of *Xantusia vigilis* result in a disjunct geographical range and in "clumped" distributions within any given area. These local "clumps" appear to occur in areas having optimal edaphic and microclimatic conditions and relatively large numbers of yuccas or other suitable plants. Because of climatic and vegetational changes, the concurrence of all these conditions is not only a rare condition, but probably also an extremely transitory one.

Field experience with *Lepidophyma flavimaculatum* leads me to believe that these generalizations are particularly valid for this species. The population located by Telford and Campbell near Achiote appears highly localized and rather dense. To date approximately 50 individuals have been collected from this population while only ca. 20 are known from the rest of Panama. My efforts to locate other individuals of this species even short distances from this population were unsuccessful (see also Telford and Campbell, 1970). Optimal conditions of forest canopy, humidity, and soil, as well as the presence of a number of extremely large logs in the proper state of decay appear to be involved; all of these factors may be related to a particular stage in the succession of this nearly mature secondary forest. Judging from the large number of *Lepidophyma* found around them, each of these logs would appear to form a "colony." As forest maturation and log decay continue, the individuals of this population are under considerable selective pressure to establish new colonies, perhaps at great distances, where the soil, humidity, forest canopy, and logs are livable.

These selective pressures would favor the evolution of unisexuality, thereby facilitating colonization by allowing each individual to reproduce in isolation and by doubling the reproductive potential. The occurrence of unisexual populations at the northern and the southern periphery of the range of *L. flavimaculatum* is thus probably indicative of a continuing contraction rather than expansion of its range. This is in marked contrast to the situation in the genus *Cnemidophorus* in which the evolution of unisexuality appears to have resulted from interspecific hybridization and expansion into new habitats (Wright and Lowe, 1968).

SPECIMENS EXAMINED

The following specimens were used in the karyotypic analysis and are deposited in the Herpetological Collection, Department of Biological Sciences, the University of Arizona (UAZ); the Natural History Museum of Los Angeles County (LACM); and the Texas Cooperative Wildlife Collection (TCWC), Texas A & M University.

Lepidophyma flavimaculatum: MEXICO: *Chiapas*: 25 mi (by rd to Malpaso) NW Ocozocoautla (UAZ 28805-06). PANAMA: *Canal Zone*: 3 mi (air line) SE Achiote (8 mi NNW Escobal) (UAZ 27637-42, 27644, 28826). COSTA RICA: *Puntarenas Prov.*: 6 km S San Vito de Java (LACM 72323).

Lepidophyma gaigeae: MEXICO: *Hidalgo*: 2 mi N Durango, 13 mi (by Hwy 85) S Jacala (UAZ 28868-72); Durango, 15 mi (by Hwy 85) S Jacala (UAZ 28880-84, 28895-905).

Lepidophyma micropholis: MEXICO: *Tamaulipas*: Cave at El Pachon, 8 km (by rd) NNE Antigua Morelos (UAZ 28762, 28767, 28769).

Lepidophyma occulor: MEXICO: *Queretaro*: 2.5 mi S Conca, 2000 ft (TCWC 35605).

Lepidophyma pajapanensis: MEXICO: *Veracruz*: Coyame, 9 mi SE Catemaco (UAZ 28804); 2 mi (by rd) SE Sontecomapan, 14 mi (by rd.) NE Catemaco (UAZ 28808-10).

Lepidophyma smithi: MEXICO: *Chiapas*: ca. ½ mi (by Hwy 200) NW Escuintla (UAZ 28788); 9 mi (by Hwy 200) NW Escuintla (UAZ 28797); 4 mi NW Mapastepec, 24 mi (by Hwy 200) NW Escuintla (UAZ 28812-15); *Oaxaca*: 1½ mi (by Hwy 190) E Tapanatepec (UAZ 28794).

Lepidophyma tuxtlae: MEXICO: *Chiapas*: 25 mi (by rd to Malpaso) NW Ocozocoautla (UAZ 28780, 28782); Veracruz: 2 mi (by rd) SE Sontecomapan, 14 mi (by rd) NE Catemaco (UAZ 28770-76).

Xantusia henshawi: MEXICO: *Durango*: 6.5 mi NE Pedricena (13.7 mi by rd SE Chocolate) (LACM 72324-25). UNITED STATES: *California*: Riverside Co.: 2 mi (by rd to Idyllwild) S Banning, San Jacinto Mts. (UAZ 21653, 21694, 21700); 3 mi (by rd to Idyllwild) S Banning, San Jacinto Mts. (UAZ 21690, 21692).

Xantusia riversiana: UNITED STATES: *California*: Los Angeles Co.: N end of San Clemente Island (UAZ 21679-81, 21683-84, 21686-89).

Xantusia vigilis: MEXICO: *Baja California del Norte*: ca. 14 mi (by rd) E La Trinidad, Valle de La Trinidad (UAZ 28961-62); *Durango*: 6.5 mi NE Pedricena (13.7 mi SW Chocolate) (LACM 72326-331); *Sonora*: 1-2 mi (by rd) S Desemboque del Rio San Ignacio (UAZ 24858, 24860, 24868, 24894). UNITED STATES: *Arizona*: Yavapai Co.: 11.3 mi (by Hwy 93) SE Burro Creek, ca. 3200 ft (UAZ 24210, 24216, 24231); vic. Yarnell, 4750 ft (UAZ 24184, 24196, 24227, 24854, 24861); Yuma Co.: E end of Palm Canyon, Kofa Mts. (UAZ 24215, 24240); *California*: Kern Co.: 0.5 mi (by rd) E Granite Station (LACM 72332-33); 0.9 mi (by Hwy 178) SE of the summit of Walker Pass (LACM 72334); 6 mi W Mojave (LACM 72335); Los Angeles Co.: 1.8 mi (by Hwy 14) N Palmdale (LACM 72336); Riverside Co.: 1 mi S, ¾ mi W Whitewater (LACM 72337-338).

ACKNOWLEDGMENTS

This paper is an expansion and revision of a part of a dissertation submitted to the University of Arizona. During my graduate work, several individuals have been exceptionally generous with their time, ideas, and constructive criticisms. I am particularly grateful to my dissertation advisor, Dr. Charles H. Lowe, for imparting an ecophysioevolutionary perspective to my interest in reptiles and amphibians; to Dr. C. Jay Cole, for his patience in helping me to find my way out of corn fields and in tutoring me in all aspects of cytotaxonomy including the art of making a pastie; to Dr. James L. Patton for discussing ideas and principles of cytogenetics; to Dr. Philip J. Regal for discussing with me his thoughts on the ecology and evolution of spectacled lizards; and to Dr. David S. Hinds for sparing me from the tragedy of the "double-nested do-loop." Dr. John Wright has helped greatly with the difficult task of revising and preparing the paper for publication, by offering encouragement, advice, and constructive criticism.

Xantusiid lizards are collected with crowbars and hard work; I am indebted to many blister-handed field friends: Kathryn Bolles, Eldon Braun, Duke Campbell, Jay Cole, Steven Goldberg, Charles Lowe, Roy McDiarmid, Philip Regal, Michael Robinson, Wade Sherbrooke, Sam Telford, David Whistler, and John, Brian, and Keith Wright. I am especially grateful to James Dixon for making available a live specimen of the rare *Lepidophyma occulor* for chromosomal analysis.

I express my thanks also to those who have read and criticized this manuscript: Drs. L. A. Carruth, L. A. Crowder, H. K. Gloyd, W. B. Heed, C. H. Lowe, J. L. Patton, F. G. Werner, and J. W. Wright. The skillful editorial efforts of Dr. Gloyd are especially appreciated.

The following persons permitted me to examine specimens under their care: Dr. James R. Dixon, Texas Cooperative Wildlife Collection, Texas A & M University; Dr. Charles L. Douglas, Texas Natural History Collection, University of Texas; Dr. William E. Duellman, University of Kansas Museum of Natural History; Dr. Donald F. Hoffmeister, University of Illinois Museum of Natural History; Dr. Charles H. Lowe, University of Arizona; Dr. James A. Peters, United States National Museum; Dr. William F. Pyburn, University of Texas, Arlington; Dr. Douglas H. Rossman, Louisana State University Museum of Zoology; Dr. Jay M. Savage, University of Southern California; Dr. Sam R. Telford, Florida State Museum; Dr. Charles F. Walker, University of Michigan Museum of Zoology; Dr. Richard G. Zweifel, American Museum of Natural History.

Dr. T. C. Hsu of the M. D. Anderson Hospital and Tumor Institute of Houston generously determined the karyotype of an individual of *Lepidophyma flavimaculatum* by lung tissue culture.

The Computer Center of the University of Arizona facilitated the data reduction.

This study was partially supported by a NASA traineeship at the University of Arizona.

LITERATURE CITED

BARBOUR, T., AND C. T. RAMSDEN. 1919. The herpetology of Cuba. Mem. Mus. Comp. Zool. 47(2): 77-166.

BEZY, R. L. 1967a. A new night lizard *(Xantusia vigilis sierrae)* from the southern Sierra Nevada in California. J. Ariz. Acad. Sci. 4:163-167.

———. 1967b. Variation, distribution, and taxonomic status of the Arizona night lizard *(Xantusia arizonae)*. Copeia 1967:653-661.

CAMP, C. L. 1923. Classification of the lizards. Bull. Amer. Mus. Nat. Hist. 48: 289-481.

COLE, C. J. 1970. Karyotypes and evolution of the *spinosus* group of lizards in the genus *Sceloporus*. Amer. Mus. Nov. 2431:1-47.

COPE, 1895. The genera of Xantusiidae. Amer. Nat. 29:757-758.

COPE, E. D. 1900. The crocodilians, lizards, and snakes of North America. Ann. Rep. U. S. Nat. Mus. for 1898, part II:151-1294.

DAREVSKY, I. S. 1966. Natural parthenogenesis in a polymorphic group of Caucasian rock lizards related to *Lacerta saxicola* Eversmann. J. Ohio Herp. Soc. 5:115-152.

DARLINGTON, P. S. 1970. A practical criticism of Hennig-Brundin "Phylogenetic Systematics" and Antarctic biogeography. Syst. Zool. 19:1-18.

DUTT, K. 1969. Study of chromosomes in two species of Indian lizards. Microscope 17:213-218.

ETHERIDGE, R. 1967. Lizard caudal vertebrae. Copeia 1967:699-721.

FORD, C. E., AND J. L. HAMERTON. 1956. A colchicine, hypotonic citrate, squash sequence for mammalian chromosomes. Stain Tech. 31:247-254.

GORMAN, G. C. 1969. New chromosome data for 12 species of lacertid lizards. J. Herpetol. 3:49-54.

———. 1970. Chromosomes and the systematics of the family Teiidae (Sauria, Reptilia). Copeia 1970:230-245.

GORMAN, G. C., L. ATKINS, AND T. HOLZINGER. 1967. New karyotypic data on 15 genera of lizards in the family Iguanidae, with a discussion of taxonomic and cytological implications. Cytogenetics 6:286-299.

GORMAN, G. C., R. B. HUEY, AND E. E. WILLIAMS. 1969. Cytotaxonomic studies on some unusual iguanid lizards assigned to the gerera *Chamaeleolis, Polychrus,* and *Phenacosaurus,* with behavioral notes. Breviora 316:1-17.

HALL, W. P. III. 1970. Three probable cases of parthenogenesis in lizards (Agamidae, Chamaeleontidae, Gekkonidae). Experientia 26:1271-73.

HECHT, M. K. 1956. A new xantusiid lizard from the Eocene of Wyoming. Amer. Mus. Nov. 1774:1-8.

HENNIG, W. 1966 Phylogenetic systematics. Univ. Ill. Press, Urbana.

HSU, T. C., AND R. A. MEAD. 1969. Mechanisms of chromosomal changes in mammalian speciation, p. 8-17. *In* Comparative Mammalian Cytogenetics (Kurt Benirschke, ed.). Springer-Verlag, N. Y.

KLAUBER, L. M. 1931. A new species of *Xantusia* from Arizona, with a synopsis of the genus. Trans. San Diego Soc. Nat. Hist. 7:1-16.

KLUGE, A. G., AND M. J. ECKARDT. 1969. *Hemidactylus garnoti* Dumeril and Bibron, a triploid all-female species of gekkonid lizard. Copeia 1969:651-664.

LOWE, C. H., AND J. W. WRIGHT. 1966. Evolution of parthenogenetic species of *Cnemidophorus* (whiptail lizards) in western North America. J. Ariz. Acad. Sci. 4:81-87.

LOWE, C. H., C. J. COLE, AND J. L. PATTON. 1967. Karyotype evolution and speciation in lizards (genus *Sceloporus*) during evolution of the North American Desert. Syst. Zool. 16:296-300.

LOWE, C. H., J. W. WRIGHT, AND C. J. COLE. 1966. Chromosomes and karyotypes of sceloporine iguanid lizards in the North American Southwest. Mamm. Chrom. Newsletter 22:201-203.

LOWE, C. H., J. W. WRIGHT, C. J. COLE, AND R. L. BEZY. 1970a. Chromosomes and evolution of the species groups of *Cnemidophorus* (Reptilia: Teiidae). Syst. Zool. 19:128-141.

________. 1970b. Natural hybridization between the teiid lizards *Cnemidophorus sonorae* (parthenogenetic) and *Cnemidophorus tigris* (bisexual). Syst. Zool. 19:114-127.

MATTHEY, R. 1931. Chromosomes de Reptiles Sauriens, Ophidiens et Cheloniens. L'evolution de la formule chromosomiale chez les Sauriens. Revue Suisse de Zoologie 38:117-184.

MATTHEY, R. 1951. The chromosomes of the vertebrates. Adv. Genet. 4:159-180.

MAYR, E. 1969. Principles of systematic zoology. McGraw-Hill, New York.

MCDOWELL, S. M., AND C. M. BOGERT. 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bull. Amer. Mus. Nat. Hist. 105:1-142.

MILLER, M. R. 1966. The cochlear duct of lizards. Proc. Calif. Acad. Sci. 23: 255-359.

OHNO, S., C. STENIUS, E. FAISST, AND M. T. ZENZES. 1965. Post-zygotic chromosomal rearrangements in rainbow trout (*Salmo irideus* Gibbons). Cytogenetics 4:117-129.

PATTON, J. L. 1967. Chromosome studies of certain pocket mice, genus *Perognathus* (Rodentia: Heteromyidae). J. Mamm. 48:27-37.

PECCININI, D. 1971. Chromosome variation in populations of *Cnemidophorus lemniscatus* in the Amazon valley. Ciencia e Cultura 23(2):133-136.

REGAL, P. J. 1968. An analysis of heat-seeking in a lizard. Ph.D. dissertation, UCLA.

ST. GIRONS, H. 1967. Morphologie comparee de l'hypophyse chez les Squamata: Donnees complementaires et apport a la phylogenie des reptiles. Ann. des Sci. Nat. Zool. (Paris) 12:229-308.

SAVAGE, J. M. 1957. Studies on the lizard family Xantusiidae. III. A new genus for *Xantusia riversiana* Cope, 1883. Zoologica 42:83-86.

________. 1963. Studies of the lizard family Xantusiidae IV. The genera. Los Angeles Co. Mus., Contrib. Sci. 71:1-38.

SIMPSON, G. G., A. ROE, AND R. C. LEWONTIN. 1960. Quantitative Zoology. Harcourt, Brace, New York.

SMITH, H. M. 1939. Notes on Mexican reptiles and amphibians. Zool. Ser., Field Mus. Nat. Hist. 24:15-35.

SMITH, H. M. 1942. Mexican herpetological misellany. Proc. U. S. Nat. Mus. 92: 349-395.

SOKAL, R. R., AND P. H. A. SNEATH. 1963. Principles of numerical taxonomy. W. H. Freeman, San Francisco.

TELFORD, S. R., AND H. W. CAMPBELL. 1970. Ecological observations on an all-female population of the lizard *Lepidophyma flavimaculatum* (Xantusiidae) in Panama. Copeia 1970:379-381.

UNDERWOOD, G. 1957. On the lizards of the family Pygopodidae. A contribution to the morphology and phylogeny of the Squamata. J. Morphol. 100(2): 207-268.

VANZOLINI, P. E. 1970. Unisexual *Cnemidophorus lemniscatus* in the Amazonas Valley: a preliminary note (Sauria, Teiidae). Papeis avulsos de Zoologia, S. Paulo, 23(7):63-68.

VOLPE, E. P., AND B. M. GEBHARDT. 1966. Evidence from cultured leucocytes of blood cells chimerism in ex-parabiotic frogs. Science 154:1197-1199.

WALKER, C. F. 1955. Two new lizards of the genus *Lepidophyma* from Tamaulipas. Occ. Pap. Mus. Zool., Univ. Mich. 564:1-10.

WEBB, R. G. 1965. A new night lizard (genus *Xantusia*) from Durango, Mexico. Amer. Mus. Nov. 2231:1-16.

———. 1970. Another new night lizard (*Xantusia*) from Durango, Mexico. Los Angeles Co. Mus., Contrib. Sci. 194:1-10.

WERLER, J. E. 1957. A new lizard of the genus *Lepidophyma* from Volcan San Martin Pajapan. Herpetologica 13:223-226.

WHITE, M. J. D. 1954. Animal cytology and evolution. 2nd ed., Cambridge Univ. Press, Cambridge.

WRIGHT, J. W., AND C. H. LOWE. 1967. Evolution of the allodiploid parthenospecies *Cnemidophorus tesselatus* (Say). Mamm. Chrom. Newsletter 8:95-96.

———. 1960. Weeds, polyploids, parthenogenesis, and the geographical and ecological distribution of all-female species of *Cnemidophorus*. Copeia 1968(1): 128-138.

Accepted for publication July 12, 1971

NUMBER 228
JUNE 7, 1972

TYPE SPECIMENS OF AVIAN FOSSILS IN THE COLLECTIONS OF THE NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

By HILDEGARDE HOWARD

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1964 AIBS Style Manual for Biological Journals is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1964 AIBS Style Manual for Biological Journals in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Changes in the manuscript after galley proof will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

TYPE SPECIMENS OF AVIAN FOSSILS IN THE COLLECTIONS OF THE NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

By Hildegarde Howard[1]

Abstract: Fossil bird types in the collections of the Natural History Museum of Los Angeles County are listed with their catalog numbers under the original published names. Included, in addition to the type series, are subsequently described or figured specimens that provide information concerning skeletal elements not included in the original description. Bibliographic references and locality data are provided throughout.

The International Code of Zoological Nomenclature (1964, Art. 72D) recommends not only that each institution mark and carefully preserve all type specimens deposited therein, but that it publish a list of all such material in its possession. Accordingly, the following catalog of avian fossil types in the collections of the Natural History Museum of Los Angeles County (LACM) is presented. The help of Pierce Brodkorb in reviewing the completed manuscript is gratefully acknowledged.

Included are *holotypes, syntypes, paratypes,* and *lectotypes* as defined by the International Code (op. cit., Arts. 73 and 74) as well as casts of specimens in these categories designated with the prefix *plasto.*

In Avian Paleontology, specimens remaining after designating the holotype are usually listed as "referred." The term paratype (or in older publications, cotype) is reserved for outstanding specimens in the type series. However, in strict adherence to recommendation 73D of the International Code, all specimens (other than the holotype) listed in the original description of a species should be known as paratypes. This catalog follows the Code recommendation, but the term will appear in quotes ("paratype") unless it is also used by the original describer.

Also included are described or figured specimens, recorded subsequent to the original type description, that provide additional information regarding the species. This material falls within the definition of the *hypotype* (Zullo and Hertlein, 1970:3) and is listed under this term. As complete fossil skeletons are rarely found, paratypes and hypotypes, which often represent different skeletal elements than the holotype, are of particular importance in Avian Paleontology. Tentatively identified paratypes and hypotypes are included if figured.

Species are grouped according to Order and Family and arranged alphabetically by genus as first described. The following information is included for each entry: author, bibliographic reference, type category, skeletal element (and portion thereof if incomplete), geologic age, Formation (if known) and

---

[1] Research Associate in Palaeornithology, Natural History Museum of Los Angeles County, Los Angeles, Calif. 90007.

locality. Specimen numbers refer to the latest LACM Vertebrate Paleontology catalog. Specimens described from the former California Institute of Technology collection (now incorporated with the LACM collections) are prefixed (CIT). Each holotype bears an individual catalog number; a few "paratypes" or hypotypes have been grouped under one number. Wherever possible, elements described without designation of catalog numbers have been traced and their numbers included here. However, hypotypes in this category are omitted unless figured. For plastotypes, the catalog number of the original institution is provided as well as the LACM cast number, and all data included in the entry refer to the specimen from which the cast was made. In a few instances, the specimens for which we have plastotypes were not illustrated in the original description; reference to a review by a later author is, therefore, included.

The catalog includes 53 holotypes, 3 syntypes, 525 paratypes, 214 hypotypes (168 figured) and 46 plastotypes of 112 species and two subspecies. In a few instances a specimen is listed with more than one species, owing to reidentification. Parenthetical reference to the most recent assignment is given under the earliest listing. In the alphabetical species index at the end of the catalog, the latest taxonomic designations are given in brackets.

Holotypes, syntypes and plastotypes are housed in a separate case in the Department of Vertebrate Paleontology apart from the general collections. Paratypes and hypotypes are filed by locality within the Vertebrate Paleontology collections, except that some Rancho La Brea hypotypes have been used in the composite mounts of the several species from that locality, and "paratypes" and hypotypes of *Mancalla* from the San Diego Formation are included in the composite mount of that flightless bird. See Howard (1962, figs. 8, 10-21) for illustrations of the mounted specimens.

Avian fossils have been recorded from 50 LACM collecting areas, 33 of which contain the material listed herein. Broken down into separate localities, the number is considerably greater, as for example, the various pits at Rancho La Brea and the separate street roadcuts in San Diego where the San Diego Formation was accessible. Another 20 or more LACM collecting sites contain unrecorded avian fossils.

List of Abbreviations

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences, Philadelphia
BM	British Museum
CAS	California Academy of Sciences
CIT	California Institute of Technology
CM	Canterbury Museum, Christchurch, New Zealand
FGS	Florida Geological Survey
LACM	Natural History Museum of Los Angeles County (formerly Los Angeles County Museum)

MCZ	Museum of Comparative Zoology, Harvard
SBMNH	Santa Barbara Museum of Natural History
SDSM	South Dakota School of Mines
SU	Stanford University
UCLA/VP	University of California, Los Angeles, Vertebrate Paleontology Department
UCMP	University of California Museum of Paleontology (Berkeley)
UF	University of Florida
USNM	United States National Museum
YPM	Yale Peabody Museum
(dist.)	distal end preserved
(prox.)	proximal end preserved
(frag.)	fragmentary specimen
(tent.)	tentative identification

GAVIIFORMES: GAVIIDAE

Gavia concinna Wetmore

WETMORE, 1940: 25, figs. 1-4.

Plastoholotype ulna (prox.) USNM 16160; cast C681 Early Pliocene, Etchegoin Formation, Sweetwater Canyon near King City, Monterey County, California.

HOWARD, 1949b: 185-187, pl. 3, figs. 5, 6, 6a.

Hypotypes (tent.) upper mandible 2110 (figs. 6, 6a), and humerus 2133 (fig. 5) (see G. *howardae* Brodkorb); Pliocene, San Diego Formation, San Diego, California.

BRODKORB, 1953: 211.

Hypotypes: cranium, rostrum and mandible 2109, rostrum 2110 (figured tentatively, Howard 1949b, pl. 3, figs. 6, 6a), humerus (prox.) 2444; Pliocene, San Diego Formation, San Diego, California.

Gavia howardae Brodkorb

BRODKORB, 1953: 212-213, fig. 1B.

Holotype humerus (dist.) 2111 (fig. 1B); "paratypes" humeri (dist.) 2133, 2175; Pliocene, San Diego Formation, San Diego, California.

MILLER and BOWMAN, 1958: 4, fig. 1 (p. 11).

Hypotype tibiotarsus (dist.) 2314; Pliocene, San Diego Formation, San Diego, California.

PODICIPEDIFORMES: PODICIPEDIDAE

Colymbus subparvus Miller and Bowman

MILLER and BOWMAN, 1958: 6, figs. 5a, 5b (p. 11).

Holotype femur (dist.) 2568 (figs. 5a, 5b); paratype femur (dist.) 2118; "paratypes" tibiotarsus (prox.) 2129, coracoid 2354; Pliocene, San Diego Formation, San Diego, California.

PROCELLARIIFORMES: DIOMEDEIDAE

Diomedea californica Miller

HOWARD, 1966d: 2, fig. 1-I.

Hypotype humerus (dist.) 16468; Middle Miocene, Temblor Formation, Sharktooth Hill, Kern County, California; Loc. 1625.

Diomedea milleri Howard

HOWARD, 1966d: 2-4, fig. 1C.

Holotype ulna (prox.) 7319 (fig. 1C); "paratype" tarsometatarsus (prox.) 16474; Middle Miocene, Temblor Formation, Sharktooth Hill, Kern County, California; Locs. 1655 and 1625.

PROCELLARIIFORMES: PROCELLARIIDAE

Fulmarus hammeri Howard

HOWARD, 1968b: 9, figs. 2F, 2K (p. 4).

Holotype carpometacarpus (prox.) 18262 (figs. 2F, 2K); "paratype" humerus (dist.) 18263; Late Miocene, Leisure World, Laguna Hills, Orange County, California; Loc. 1945.

Puffinus calhouni Howard

HOWARD, 1968b: 6, figs. 2A-2E (p. 4).

Holotype humerus (dist.) 17508 (figs. 2A, 2E); "paratypes" tarsometatarsus (prox.) 17582 (figs. 2B, 2C, 2D), humerus (dist.) 17539, ulna (prox.) 17530; Late Miocene, Leisure World, Laguna Hills, Orange County, California; Loc. 1945.

Puffinus conradi Marsh

MARSH, 1870: 212 (figured SHUFELDT, 1915, pl. 8, figs. 63-64).

Plastoholotype humerus (dist.); plasto "paratype" ulna (dist.), both ANSP 13360; cast C688; Middle Miocene, Calvert Formation, Calvert County, Maryland.

Puffinus diatomicus Miller

MILLER, 1925b: 111, pls. 1-2.

Plastoholotype complete skeletal impression UCMP 26541 (pl. 1), 2 casts (one in relief, one impressed) C692; plastoparatype impression left wing bones SU 1 (pl. 2), cast (in relief) C693; Miocene, diatomaceous shales, Lompoc, Santa Barbara County, California.

Puffinus felthami Howard

HOWARD, 1949b: 194, pl. 2, figs. 4, 6.

Holotype humerus (dist.) 2037 (fig. 6); paratype tarsometatarsus (prox.) 2038 (fig. 4); Early Pliocene, Repetto Formation, 3 miles north of Corona del Mar, Orange County, California; Loc. 1067.

Puffinus inceptor Wetmore

WETMORE, 1930: 86, figs. 1-3.

Plastoholotype humerus (dist.) CAS 5223; cast C678; Middle Miocene, Temblor Formation, Sharktooth Hill, Kern County, California.

Puffinus kanakoffi Howard

HOWARD, 1949b: 187, pl. 2, figs. 3, 5.

Holotype tarsometatarsus 2122 (fig. 3); paratypes, humerus (dist.) 2120 (fig. 5), femur 2124; "paratypes" tarsometatarsus 2126, tibiotarsus (prox.) 2123, 4 humeri 2114, 2116, 2146, 2160; Pliocene, San Diego Formation, San Diego, California.

Puffinus mitchelli Miller

MILLER, 1961: 400, fig. 1.

Plastoholotype humerus (dist.) UCMP 58184; cast C684; Middle Miocene, Temblor Formation, Sharktooth Hill, Kern County, California.

Puffinus priscus Miller

MILLER, 1961: 399, fig. 1.

Plastoholotype humerus (dist.) UCMP 58185; cast C683; Middle Miocene, Temblor Formation, Sharktooth Hill, Kern County, California.

Puffinus tedfordi Howard

HOWARD, 1971: 2, figs. 1A, 1B, 1E, 1F.

Holotype tarsometatarsus (prox.) 15386 (figs. 1B, 1E); paratype tarsometatarsus 15387 (figs. 1A, 1F); Early Pliocene, Almejas Formation, SE corner Cedros Island, Baja California, Mexico; Loc. 65151.

PELECANIFORMES: ELOPTERYGIDAE

Elopteryx nopcsai Andrews

ANDREWS, 1913: 195, figs. 1-2.

Plastoholotype femur (prox.) BM A1234 (fig. 1); cast C699; plastoparatype tibiotarsus (dist.) BM A1234 (fig. 2); cast C700; Late Cretaceous (Maestrichtian) Szentpeterfalva near Hatszeg, Transylvania, Rumania.

LAMBRECHT, 1929: 1266, figs. 2-10 (p. 1263).

Plastohypotypes 2 tibiotarsi (dist.) BM A1588 (figs. 2, 6, 9, 10); cast C702; BM A1528 (figs. 3, 5, 7, 8); cast C701; Late Cretaceous (Maestrichtian) Szentpeterfalva near Hatszeg, Transylvania, Rumania.

PELECANIFORMES: CYPHORNITHIDAE

Palaeochenoides mioceanus Shufeldt

SHUFELDT, 1916: 347, pl. 15.

Plastoholotype femur (dist.) YPM 2176; cast C742; Early Miocene, Hawthorne Formation, Stono River, Charleston County, South Carolina.

HOPSON, 1964: 8, fig. 2.

Plastohypotype (tent.) tarsometatarsus (dist.) MCZ 2514; cast C741; Early Miocene, Hawthorne Formation, Ashley River, Charleston County, South Carolina.

PELECANIFORMES: PSEUDODONTORNITHIDAE

Osteodontornis orri Howard

HOWARD, 1957a: 3, figs. 2-8.

Plastoholotype nearly complete skeleton in shale SBMNH 309 (skull, figs. 4, 6; foot bones, figs. 7, 8; complete skeleton, figs. 2, 3); casts (sections from skeleton) C703-C714; Miocene, flagstone quarry, west side Tepusquet Creek, Santa Barbara County, California.

HOWARD and WHITE, 1962: 4-11, figs. 2, 3, 5.

Hypotypes upper and lower jaw fragments 2707B and 2707A (figs. 2, 3), atlas vertebra 2707D (fig. 5); Miocene diatomaceous shales, Del Gado Drive near Sepulveda and Ventura Blvds., Sherman Oaks, Los Angeles County, California; Loc. 1267.

Pseudodontornis stirtoni Howard and Warter

HOWARD and WARTER, 1969: 348, pls. 1-3.

Plastoholotype incomplete skull and jaws CM AV20569; cast C690; ?Pliocene Greta Siltstone, Waitotaran Stage; concretion found on Motunau Beach, 36 miles north of Christchurch, New Zealand.

PELECANIFORMES: SULIDAE

Miosula media Miller

MILLER, 1925b: 114, pl. 5.

Plastoholotype impression of incomplete skeleton UCMP 26543; cast (in relief) C696; Miocene diatomaceous shales, Lompoc, Santa Barbara County, California.

Miosula recentior Howard

HOWARD, 1949b: 190, pl. 2, figs. 1, 2.

Holotype tibiotarsus 2117 (pl. 2, figs. 2, 2a) partype ulna (prox.) 2112 (pl. 2, fig. 1) (see *Sula humeralis*); Pliocene, San Diego Formation, San Diego, California; Loc. 1071.

Moris reyana Howard

HOWARD, 1936: 213, figs. 37a-b.

Holotype coracoid 991 (figs. 37a-b); “paratype” pedal phalanx 996; Late Pleistocene, Lincoln Blvd., Del Rey Hills, northeast of Playa del Rey, Los Angeles County, California; Loc. 1024.

HOWARD, 1949a: 21, 24.

Hypotypes tarsometatarsus (prox.) 2052, radius 2043; Late Pleistocene, Newport Bay Mesa, Orange County, California; Loc. 1066.

Moris vagabundus Wetmore

HOWARD, 1966d: 5, figs. 1A, 1B, 1J.

Hypotypes humerus 7432 (figs. 1A, 1J), ulna (prox.) 16473 (fig. 1B), 3 humeri (incomplete) 16467, 13980, 16471, 2 ulnae (prox.) 16472, 16470; Middle Miocene, Temblor Formation, Sharktooth Hill, Kern County, California.

Sula humeralis Miller and Bowman

MILLER and BOWMAN, 1958: 9.

“Paratypes” femur 2522, ulna (prox.) 2112; Pliocene, San Diego Formation, San Diego, California.

Sula lompocana Miller

MILLER 1925b: 114, pl. 4.

Plastoholotype impression of incomplete skeleton UCMP 26544; cast (in relief) C697; Miocene, diatomaceous shales, Lompoc, Santa Barbara County, California.

Sula pohli Howard

HOWARD, 1958: 4, fig. 1.

Holotype wing bones on slab 2674 (fig. 1); "paratype" humerus 2532; Middle Miocene, Ventura Blvd. between Whitsett and Coldwater Canyon Road, Studio City, Los Angeles County, California; Loc. 1229.

Sula stocktoni Miller

MILLER, 1935: 75, fig. 2.

Plastoholotype part skeleton in shale UCMP 32105; cast C743; Miocene, Lomita diatomite, Los Angeles County, California.

HOWARD, 1958: 12, fig. 3.

Hypotype humerus 2533; Miocene, Round Drive near Chester St., El Sereno, Los Angeles County, California; Loc. 6455.

Sula willetti Miller

MILLER, 1925b: 112, pl. 3.

Plastoholotype impression of nearly complete skeleton UCMP 26542; cast (in relief) C698; Miocene, diatomaceous shales, Lompoc, Santa Barbara County, California.

PELECANIFORMES: PLOTOPTERIDAE

Plotopterum joaquinensis Howard

HOWARD, 1969a: 68, fig. 1.

Holotype coracoid (dist.) 8927; Early Miocene, Vaqueros Formation, Pyramid Hill, Kern County, California; Loc. 1626.

PELECANIFORMES: PHALACROCORACIDAE

Graculus macropus Cope

COPE, 1878: 386 (figured, SHUFELDT, 1892, pl. 15, figs. 7, 8; lectotype selected, HOWARD, 1946: 153).

Plastolectotype tarsometatarsus AMNH 3555; cast C665; Late Pleistocene, Fossil Lake, Oregon.

Phalacrocorax femoralis Miller

MILLER, 1929: 167, fig. 58.

Plastoholotype posterior skeletal impression UCLA/VP 2754; cast C736; Late Miocene, Modelo Formation, Poyer quarry, near Calabasas, Los Angeles County, California.

Phalacrocorax goletensis Howard

HOWARD, 1965a: 51, figs. 1A-1D.

Holotype coracoid 4632 (figs. 1A-1D); "paratype" humerus (dist.)

3166; Pliocene, Goleta Formation, Morelia lacustrine basin near La Goleta, Morelia, Michoacan, Mexico; Loc. 1136.

Phalacrocorax kennelli Howard

HOWARD, 1949b: 188, pl. 3, figs. 7-8.

Holotype coracoid (dist.) 2127 (pl. 3, figs. 7, 7a); "paratype" humerus (prox.) 2121 (pl. 3, figs. 8, 8a); Pliocene, San Diego Formation, San Diego, California; Loc. 1080.

MILLER and BOWMAN, 1958: 12, fig. 3.

Hypotypes tibiotarsus 2566 (prox.) (fig. 3), femur 2528, ulna 2529; Pliocene, San Diego Formation, San Diego, California.

Ardea paloccidentalis Shufeldt

SHUFELDT, 1892: 411, pl. 17, fig. 31.

Plastoholotype tarsometatarsus (dist.) AMNH 3484; cast C670; Late Pleistocene, Fossil Lake, Oregon.

ARDEIFORMES: CICONIIDAE

Ciconia maltha Miller

MILLER, 1932: 215, fig. 23C.

Hypotype lower mandible (CIT)293; Late Pleistocene, McKittrick asphalt deposits, Kern County, California; Loc. (CIT) 138.

MILLER, 1938: 458, pl. 37B.

Hypotype cranium (CIT) 1894; Late Pleistocene, McKittrick asphalt deposits, Kern County, California; Loc. (CIT) 138.

HOWARD, 1942: 193-195, figs. 1, 1a.

Hypotype rostrum (CIT) 1894; Late Pleistocene McKittrick asphalt deposits, Kern County, California; Loc. (CIT) 138.

Jabiru? weillsi Sellards

SELLARDS, 1916: 146, pl. 26, fig. 1.

Plastoholotype humerus USNM (FGS) 5961; cast C682; Late Pleistocene, stratum 2, canal bank, Vero, Florida.

Mycteria wetmorei Howard

HOWARD, 1935b: 253, fig. 47.

Holotype lower mandible (frag.) K3527 (fig. 47, 1 and 2); "paratype" tarsometatarsus (prox.) K3528 (fig. 47, 3 and 4); Late Pleistocene, Rancho La Brea, Los Angeles, California.

PHOENICOPTERIFORMES: PALAELODIDAE

Megapaloelodus connectens A. Miller

A. MILLER, 1944: 86, figs. 1-2.

Plastoholotype tarsometatarsus (dist.) UCMP 37367; cast C689; Early Miocene, Upper Rosebud Formation, Flint Hill, Bennett County, South Dakota; UCMP Loc. V3417.

Megapaloelodus opsigonus Brodkorb

HOWARD, 1971: 6, figs. 1K, 1M, 1N.

Hypotype (tent.) tarsometatarsus (dist.) 15423; Early Pliocene, Almejas Formation, SE corner Cedros Island, Baja California, Mexico; Loc. 65148.

PHOENICOPTERIFORMES: PHOENICOPTERIDAE

Phoenicopterus minutus Howard

HOWARD, 1955b: 202, pl. 50, figs. 1-7.

Holotype tibiotarsus (fig. 3-7) and associated (prox.) tarsometatarsus (figs. 1, 2) 2445; "paratype" tarsometatarsus (prox.) 2473; Pleistocene, Manix Lake, Mohave Desert, California; Loc. 1093.

Phoenicopterus stocki Miller

MILLER, 1944b: 77, figs. 1-2.

Holotype tibiotarsus (dist.) (CIT)3245 (fig. 1); "paratypes" (catalogued subsequent to publication) tibiotarsi (prox.) 4623 (fig. 2), (dist.) 4624, 4626, humeri (dist.) 4629, 4630, ulna (prox.) 4627, carpometacarpus 4628, tarsometatarsus (dist.) 4625; Middle Pliocene, Rincon-Yepomera area, Chihuahua, Mexico; Loc. (CIT)289.

HOWARD, 1966a: 3.

Hypotypes scapula (frag.) 9731, radii (prox.) 9732, (dist.) 9733; Middle Pliocene, Rincon-Yepomera area, Chihuahua, Mexico; Locs. (CIT)289 and 276.

ANSERIFORMES: ANATIDAE: CYGNINAE

Cygnus paloregonus Cope

HOWARD, 1946: 162, 164.

Plastohypotypes furcula AMNH 3536, carpometacarpus AMNH 3554; casts C666 and C664; Late Pleistocene, Fossil Lake, Oregon.

Olor matthewi Shufeldt

SHUFELDT, 1913: 151, pl. 35, fig. 422.

Plastosyntype, carpometacarpus AMNH 3554 (see *Cygnus paloregonus*); cast C664; Late Pleistocene, Fossil Lake, Oregon.

ANSERIFORMES: ANATIDAE: ANSERINAE

Anser condoni Shufeldt

SHUFELDT, 1892: 406, pl. 16, fig. 19.

Plastoholotype furcula AMNH 3536 (see *Cygnus paloregonus* Cope); cast C666; Late Pleistocene, Fossil Lake, Oregon.

Branta dickeyi Miller

MILLER, 1944a: 27, fig. 6.

Hypotype coracoid (CIT)3236; Pliocene, Owyhee, east side Dry Creek, Malheur County, Oregon; Loc. (CIT)62.

Branta minuscula Wetmore

WETMORE, 1924: 6, figs. 3-4.

Plastoholotype humerus (prox.) USNM 10548; cast C679; Early Pleistocene (late Pliocene?) 2 miles south of Benson, Arizona.

Branta propinqua Shufeldt

SHUFELDT, 1892: 407, pl. 15, fig. 17.

Plastoholotype humerus AMNH 3547; cast C667; Late Pleistocene, Fossil Lake, Oregon.

Eremochen russelli Brodkorb

HOWARD, 1966a: 4, fig. 1J.

Hypotype (tent.) scapula 9734; Middle Pliocene, Rincon-Yepomera area, Chihuahua, Mexico; Loc. (CIT)289.

Presbychen abavus Wetmore

HOWARD, 1966d: 8, figs. 1D-1F (p.3).

Hypotype tarsometatarsus (prox.) 16466; Middle Miocene, Temblor Formation, Sharktooth Hill, Kern County, California; Loc. 1625.

ANSERIFORMES: ANATIDAE: TADORNINAE

Anabernicula gracilenta Ross

ROSS, 1935: 107, fig. 6.

Holotype tarsometatarsus (CIT)1169 (fig. 6); paratypes two tarsometatarsi (CIT)1168, (CIT)1170; "paratypes" tarsometatarsi (CIT)1171-1175; Late Pleistocene, McKittrick asphalt deposits, Kern County, California; Loc. (CIT)138.

HOWARD, 1964b: 286, pl. 7A-H.

Hypotype humerus 27349 (pl. 7A, 7B); Late Pleistocene, McKittrick asphalt deposits, Kern County, California; Loc. (CIT)138. Hypotypes carpometacarpus K4744 (pl. 7C, 7D), femur K4789 (pl. 7E, 7F), tarsometatarsus K4797 (pl. 7G, 7H); Late Pleistocene, Rancho La Brea, Los Angeles, California.

Anabernicula oregonensis Howard

HOWARD, 1964d: 5, figs. 1A, 1B.

Plastoholotype humerus AMNH 3548; cast C676 (figs. 1A, 1B), "paratype" coracoid (CIT)3279; Late Pleistocene, Fossil Lake, Oregon.

Brantadorna downsi Howard

HOWARD, 1963: 8, pl. 1, figs. G, H, I.

Holotype humerus (prox.) 3911 (fig. G); paratype coracoid (dist.) 3910 (figs. H, I); "paratype" humerus (dist.) 3911; Middle Pleistocene, Upper Palm Spring Formation, Mesquite Oasis, Vallecito Creek, Anza-Borrego Desert, San Diego County, California; Loc. 1323.

ANSERIFORMES: ANATIDAE: ANATINAE

Nettion bunkeri Wetmore

HOWARD, 1966a: 7, figs. 1F, 1G.

Hypotype coracoid 4621; Middle Pliocene, Rincon-Yepomera area, Chihuahua, Mexico; Loc. (CIT)289.

Wasonaka yepomerae Howard

HOWARD, 1966a: 5, figs. 1A-1E, 1H, 1-I.

Holotype humerus 4620 (figs. 1A, 1B); paratypes furcula 4618 (figs. 1H, 1-I), ulna 4619 (figs. 1C, 1D, 1E); Middle Pliocene, Arroyo de las Barrancas Blancas, ¼ mile east of Yepomera, Chihuahua, Mexico; Loc. (CIT)286.

ANSERIFORMES: ANATIDAE: MERGINAE

Bucephala fossilis Howard

HOWARD, 1963: 11, pl. 1, figs. A-C.

Holotype carpometacarpus (prox.) 2787 (figs. A, B); paratype humerus (prox.) 2885 (fig. C); "paratypes" two carpometacarpi (prox. 2886, 2887); Middle Pleistocene, Upper Palm Spring Formation, Arroyo Tapiado, Vallecito Creek, Anza-Borrego Desert, San Diego County, California; Loc. 1430.

Chendytes lawi Miller

HOWARD, 1947: 76, fig. 15.

Hypotypes coracoid (dist.) 2042 (fig. 15), humerus 2030; Late Pleistocene, Newport Bay Mesa, Orange County, California; Loc. 1066.

HOWARD, 1949a: 21 and 25.

Hypotypes pelvis and synsacrum (frag.) 2055, 3 pedal phalanges 2025; Late Pleistocene, Newport Bay Mesa, Orange County, California; Loc. 1066.

HOWARD, 1955a: 136, figs. 1b, 1c, 1h, 2a, 2d.

Hypotypes humerus 2455 (figs. 1b, 1c), premaxilla 2059, femur 2015 (figs. 2a, 2d); Late Pleistocene Newport Bay Mesa, Orange County, California; Loc. 1066. Hypotype scapula 2006 (fig. 1h); Late Pleistocene, Lincoln Blvd., Del Rey Hills, northeast of Playa del Rey, Los Angeles County, California; Loc. 1024.

MILLER, MITCHELL and LIPPS, 1961: 4-10, pls. 1-2.

Hypotypes coracoid 2697 (pl. 1, fig. b), humerus 2698 (pl. 1, fig. c), cranium and part lower jaw (missing) (pl. 1, figs. a, d) and associated atlas, axis and cervical vertebra 2699, pelvis 2696 (pl. 2, figs. a, b), eight associated vertebrae 2702; Late Pleistocene, north shore of east end of West Anacapa Island, California.

HOWARD, 1964c: 372-376, fig 1.

Hypotypes sternum 2725 (figs. 1a, 1h), humerus 4868 (figs. 1b, 1c), ulnae 2736 (fig. 1d), 2764, carpometacarpus 5536 (figs. 1e, 1f, 1g), scapulae 2713, 2733, 2733a, 5538, coracoid 2730; Late Pleistocene, north shore of east end of West Anacapa Island, California.

Chendytes milleri Howard

HOWARD, 1955a: 137, figs. 1-3.

Holotype humerus 2364 (figs. 1a, 1d); paratypes femur 2378 (figs. 2b, 2c), ulna 2387 (figs. 1f, 1g), scapula 2386 (figs. 1e, 1i); "paratypes" incomplete coracoids, scapulae, humeri, ulnae, pelvis, femora, tibiotarsi, fibula, tarsometatarsi, phalanges and vertebrae 2379-2385, 2388-2390, 2392-2415 (including illustrated pelvis 2395, figs. 3a, 3b); Early? Pleistocene, north side San Nicolas Island, California; Loc. 1085.

ANSERIFORMES: ANATINAE: OXYURINAE

Oxyura bessomi Howard

HOWARD, 1963: 13, pl. 1, figs. D, E.

Holotype carpometacarpus 2785 (figs. D, E); "paratypes" ulna (dist.) 2784, coracoids 2535 and 4966, carpometacarpus (prox.) 2888; Middle Pleistocene, Upper Palm Spring Formation, Vallecito Creek, Anza-Borrego Desert, San Diego County, California.

FALCONIFORMES: TERATORNITHIDAE

Cathartornis gracilis Miller

MILLER, 1910: 14, figs. 4a, 4b (p. 9).

Plastoholotype tarsometatarsus UCMP 12598 (figs. 4a, 4b); cast C686; plastocotype tarsometatarsus UCMP 12600; cast C687; Late Pleistocene, Rancho La Brea, California.

Teratornis incredibilis Howard

HOWARD, 1952: 51, pl. 10.

Holotype cuneiform (CIT)5067; Late Pleistocene, Smith Creek Cave, White Pine County, Nevada; Loc. (CIT)251.

HOWARD, 1963: 16, pl. 2A, 2C.

Hypotype radius (dist.) 3803; Middle Pleistocene, Upper Palm Spring Formation, Vallecito Creek, Anza-Borrego Desert, San Diego County, California; Loc. 1318.

HOWARD, 1972: (in press).

Hypotype (tent.) incomplete rostrum 26697; Late Pliocene (Blancan), Fish Creek, Anza-Borrego Desert, San Diego County, California; Loc. 6747.

Teratornis merriami Miller

MILLER, 1925a: 87, pls. 1-4.

Hypotypes skull B1380 (pl. 1), furcula B1366 (pl. 2A-B), coracoid B1369 (pl. 2C), sternum B1365 (pl. 2D-E, and pl. 3A), partial pelvis B1368 (pl. 3B); humerus B1370 (pl. 3C-F), carpometacarpus B1373 (pl. 4A), femur B1374 (pl. 4C-D), tarsometatarsus D542 (pl. 4G-H), wing phalanx B1376 (pl. 4B), tibiotarsus B1372 (pl. 4E-F); Late Pleistocene, Rancho La Brea, Los Angeles, California.

FALCONIFORMES: VULTURIDAE

Coragyps occidentalis mexicanus Howard

HOWARD, 1968a: 124.

Holotype tarsometatarsus 20455; paratypes 21 tarsometatarsi 3358 and 20307-20326, 38 coracoids 3354 and 20327-20363, 15 humeri 3352 and 20364-20377, 20 ulnae 3356 and 20378-20396, 21 carpometacarpi 3355 and 20397-20416, 23 femora 3353 and 20417-20438, 17 tibiotarsi 3357 and 20439-20454; Late Pleistocene, San Josecito Cave, Nuevo Leon, Mexico; Loc. (CIT)192.

Gymnogyps amplus Miller

FISHER, 1944: 290, figs. 43, 45, 46.

Hypotypes cranium B5415 (figs. 43, 45, 46), rostrum B6513, mandible B7591; Late Pleistocene, Rancho La Brea, Los Angeles, California.

Sarcorhamphus clarki Miller

MILLER and HOWARD, 1938: 171, pl. 2a-c.

Hypotypes cranium and rostrum K3158 (pl. 2a), cranium B2148 (pl. 2b, 2c); Late Pleistocene, Rancho La Brea, Los Angeles, California.

HOWARD, 1969b: 5.

Hypotype axis vertebra 4638; Late Pleistocene, Tequixquiac, Mexico; Loc. (CIT)310.

Vultur kernensis Miller

MILLER, 1931: 70, fig. 16.

Holotype humerus (dist.) (CIT)454; Pliocene, Pozo Creek, Kern River Divide, Kern County, California; Loc. (CIT)49.

FALCONIFORMES: ACCIPITRIDAE: BUTEONINAE

Aquila pliogryps Shufeldt

SHUFELDT, 1892: 416, p. 17, fig. 33.

Plastoholotype pedal phalanx 1, digit 1 AMNH 3471; cast C668; Late Pleistocene, Fossil Lake, Oregon.

Aquila sodalis Shufeldt

SHUFELDT, 1892: 417, pl. 15, fig 5.

Plastoholotype tarsometatarsus (prox.) AMNH 3470; cast C663; Late Pleistocene, Fossil Lake, Oregon.

Buteo typhoius Wetmore

WETMORE, 1923: 489, figs. 3, 4.

Plastoholotype tarsometatarsus (dist.) AMNH 1754; cast C680; Late Miocene, Snake Creek beds, Sioux County, Nebraska.

Geranoaetus fragilis Miller

HOWARD, 1932: 16-25, pls. 1-6.

Hypotypes cranium D1184 (pl. 1, figs. 1, 1a), rostrum D1142 (pl. 1, figs. 2, 2a), mandible D2029 (pl. 1, fig. 3), furcula C8184 (pl. 1, figs. 4, 4a), scapula C5485 (pl. 1, figs. 5, 5a, 5b), sternum C7929 (pl. 2, figs. 1, 1a), coracoid E4079 (pl. 2, figs. 2, 2a, 2b), humerus C8735 (pl. 3, figs. 1, 1a), carpometacarpus E1091 (pl. 3, fig. 3), ulna C5261 (pl. 4, figs. 1, 1a, 1b), radius D8354 (pl. 4, figs. 2, 2a), pelvis C6481 (pl. 5, figs. 1, 1a, 1b), femur C684 (pl. 5, figs. 2, 2a, 2b), tibiotarsus C7332 (pl. 6, figs. 2, 2a, 2b, 2c), tarsometatarsus E893 (pl. 6, figs. 1, 1a, 1b); Late Pleistocene, Rancho La Brea, Los Angeles, California.

Geranoaetus grinnelli Miller

HOWARD, 1932: 33-43, pls. 14-19.

Hypotypes crania E3600 (pl. 14, fig. 1) and D4284 (pl. 14, figs. 1a, 1b), rostrum F3071 (pl. 14, figs. 2, 2a), mandible C5852 (pl. 14, fig. 3), furcula C2508 (pl. 14, figs. 4, 4a), sternum D5981 (pl. 15, figs. 1, 1a), coracoid C5842 (pl. 15, figs. 2, 2a, 2b, 2c), scapula C4450 (pl. 15, figs. 3, 3a, 3b), humerus D2365 (pl. 16, figs. 1, 1a), carpometacarpus C1587 (pl. 16, figs. 2, 2a), ulna C1937 (pl. 17, figs. 1, 1a, 1b), radius D9637 (pl. 17, figs. 2, 2a), pelvis C1036 (pl. 18, figs. 2, 2a, 2b), femur C1028 (pl. 18, figs. 1, 1a), tibiotarsus C3103 (pl. 19, figs. 1, 1a, 1b), tarsometatarsus C6804 (pl. 19, figs. 2, 2a, 2b); Late Pleistocene, Rancho La Brea, Los Angeles, California.

Miohierax stocki Howard

HOWARD, 1944: 236, fig. 40.

Holotype tarsometatarsus (dist.) metatarsal 1 and 9 phalanges (CIT) 1396; Miocene, Tick Canyon Formation, Vasquez Canyon, Los Angeles County, California; Loc. (CIT)201.

Morphnus daggetti Miller

MILLER, 1915: 179, fig. 63.

Holotype tarsometatarsus K3114 (old no. A380); Late Pleistocene, Rancho La Brea, Los Angeles, California.

MILLER, 1925a: 97, pl. 5, fig. F.

Hypotype tibiotarsus J9744; Late Pleistocene, Rancho La Brea, Los Angeles, California.

HOWARD, 1932: 16 (footnote), text figs. 1A, 1B.

Hypotype coracoid D1217; Late Pleistocene, Rancho La Brea, Los Angeles, California.

Morphnus woodwardi Miller

HOWARD, 1932: 25-30, pls. 7-12.

Hypotypes cranium F3172 (pl. 7, figs. 1, 1a), rostrum C6846 (pl. 7, figs. 2, 2a), mandibular symphysis D1019 (pl. 7, fig. 3), furcula D3056 (pl. 7, figs. 4, 4a), coracoid D4676 (pl. 7, figs. 5, 5a, 5b), sternum D2398 (pl. 8, figs. 1, 1a), scapula D4816 (pl. 8, figs. 2, 2a, 2b), humerus D6743 (pl. 9, figs. 1, 1a), radius (prox.) C4224 (pl. 9, fig. 2), carpometacarpus D1702 (pl. 9, fig. 3), ulnae (prox.) C9264 (pl. 10, figs. 1, 1a, 1b), and G7554 (pl. 10, fig. 2), (dist.) D5177 (pl. 10, figs. 3, 3a, 3b), pelvis C8858 (pl. 11, figs. 1, 1a), tibiotarsus D1974 (pl. 11, figs. 2, 2a, 2b), femur C1111 (pl. 12, figs. 1, 1a, 1b), tarsometatarsus C6644 (pl. 12, figs. 2, 2a, 2b); Late Pleistocene, Rancho La Brea, Los Angeles, California.

Spizaetus willetti Howard

HOWARD, 1935a: 207, fig. 40.

Holotype tarsometatarsus (dist.) (CIT)1791; Late Pleistocene, Smith Creek Cave, White Pine County, Nevada; Loc. (CIT)251.

FALCONIFORMES: ACCIPITRIDAE: PALAEOPLANCINAE

Palaeoplancus sternbergi Wetmore

WETMORE, 1933: 7, figs. 15-16.

Plastoholotype (part) tarsometatarsus (dist.) from skeleton USNM 12479; cast C677; Middle Oligocene, Brule Formation, Plum Creek, Niobrara County, Wyoming.

FALCONIFORMES: ACCIPITRIDAE: GYPAETINAE

Arikarornis macdonaldi Howard

HOWARD, 1966c: 2, figs. 1A-1D.

Holotype tarsometatarsus (dist.) 9357; Early Miocene, Middle Sharp's Formation, Sharp's Cut-off Road, Shannon County, South Dakota; Loc. 1821.

Neogyps errans Miller

HOWARD, 1932: 45-62, pls. 20-25.

Hypotypes cranium C2053 (pl. 20, figs. 1, 1a), rostrum D4615 (pl. 20, figs. 2, 2a), mandible C694 (pl. 20, fig. 4), furculae D6522 (pl. 20, fig. 3), B8633 (pl. 20, fig. 3a), sternum C1118 (pl. 21, figs. 1, 1a), coracoid C5467 (pl. 21, figs. 2, 2a), scapula C7922 (pl. 21, figs. 3, 3a), humerus C2946 (pl. 22, figs. 1, 1a), ulna C4049 (pl. 23, figs. 1, 1a, 1b), radii (prox.) C3849 (pl. 23, figs. 2, 2a), (dist.) C1528 (pl. 23, fig. 3), carpometacarpus D3374 (pl. 22, fig. 2), pelvis C1314 (pl. 24, figs. 1, 1a, 1b), femur J7555 (pl. 25, figs. 2, 2a, 2b), tibiotarsus C4982 (pl. 25, figs. 1, 1a, 1b), tarsometatarsus F2017 (pl. 24, figs. 2, 2a); Late Pleistocene, Rancho La Brea, Los Angeles, California.

Neophrontops americanus Miller

HOWARD, 1932: 62-70, pls. 26-29.

Hypotypes cranium D7752 (pl. 26, figs. 1, 1a), rostrum J9068 (pl. 26, figs. 2, 2a), mandible C7398 (pl. 26, fig. 3), sternum E2033 (pl. 26, figs. 4, 4a), furcula E3859 (pl. 26, figs. 5, 5a), coracoid E2661 (pl. 27, fig. 1), scapula E3453 (pl. 27, figs. 2, 2a), humerus G1987 (pl. 27, figs. 3, 3a), ulna D8188 (pl. 28, figs. 1, 1a, 1b), radius D7841 (pl. 28, figs. 2, 2a), carpometacarpus H2477 (pl. 27, fig. 4), pelvis E2051 (pl. 29, figs. 1, 1a), femur D9765 (pl. 29, figs. 2, 2a, 2b), tibiotarsus F1958 (pl. 29, figs. 3, 3a, 3b), tarsometatarsus E2159 (pl. 29, figs. 4, 4a); Late Pleistocene, Rancho La Brea, Los Angeles, California.

Neophrontops vallecitoensis Howard

HOWARD, 1963: 17, pl. 3, fig. B.

Holotype tarsometatarsus (dist.) (pl. 3B) with associated metatarsal 1 and 8 phalanges 2866; paratype tarsometatarsus (dist.) 3769; Middle Pleistocene (Irvingtonian), Upper Palm Spring Formation; Vallecito Creek, Anza-Borrego Desert, San Diego County, California; Locs. 1299 and 1356.

FALCONIFORMES: FALCONIDAE

Polyborus prelutosus Howard

HOWARD, 1938: 226, pls. 1-3.

Holotype humerus E4398 (pl. 1, fig. 1, pl. 2, fig. 3); "paratypes" humeri E3927 (pl. 1, fig. 3, pl. 2, fig. 1), E4356 (pl. 1, fig. 2, pl. 2, fig. 4), E9852 (pl. 1, fig. 4), E3255 (pl. 1, fig. 5), E1318 (pl. 2, fig. 2), E1804 (pl. 2, fig. 5), rostrum E4485 (pl. 3, fig. 2), carpometacarpus E3556 (pl. 3, figs. 4, 4a), femora E1210 (pl. 3, fig. 6), E4012 (pl. 3, fig. 7), E651 (pl. 3, fig. 8), tarsometatarsi E681 (pl. 3, fig. 10), E3446 (pl. 3, fig. 11), and 747 specimens not listed by catalog numbers. It is impossible to trace all of these specimens. However, the following, derived from the author's notes, are representative of the unillustrated elements described: coracoids E3080, E9884, H4545, H4606, ulnae E905, E1339, E1583, E3367, pelves D9083, D9619, E4678, E9617, tibiotarsi E3954, E4267, E4327, E4493; Late Pleistocene, Rancho La Brea, Los Angeles, California.

Polyborus prelutosus grinnelli Howard

HOWARD, 1940: 41.

Holotype tarsometatarsus (CIT)2709; "paratypes" 10 tarsometatarsi (CIT)2710-2719, 3 humeri (CIT)2720-2722, 3 ulnae (CIT)2723-2725, 5 carpometacarpi (CIT)2726-2730, 4 femora (CIT)2731-2734, 2 tibiotarsi (CIT)2735-2736, coracoid (CIT)2737; Late Pleistocene, San Josecito Cave, Nuevo Leon, Mexico; Loc. (CIT)192.

GALLIFORMES: CRACIDAE

Procrax brevipes Tordoff and Macdonald

TORDOFF and MACDONALD, 1957: 179, pl. 10, fig. 1.

Plastoholotype incomplete skeleton in matrix SDSM 511; cast C538; Early Oligocene, top of Chadron Formation, Pennington County, South Dakota.

GALLIFORMES: TETRAONIDAE

Palaeotetrix gilli Shufeldt

SHUFELDT, 1892: 415, pl. 17, fig. 34.

Plastoholotype carpometacarpus AMNH 3474; cast C672; Late Pleistocene, Fossil Lake, Oregon.

Pediocaetes lucasi Shufeldt

SHUFELDT, 1892: 414, pl. 17, fig. 30.

Plastoholotype ulna AMNH 3476; cast C675; Late Pleistocene, Fossil Lake, Oregon.

GALLIFORMES: PHASIANIDAE

Miortyx aldeni Howard

HOWARD, 1966c: 5, fig. 1E.

Holotype humerus (prox.) 9388; Early Miocene, Middle Sharp's Formation, gully beside Sharp's Cut-off Road, Shannon County, South Dakota; Loc. 1982.

GALLIFORMES: MELEAGRIDIDAE

Agriocharis anza Howard

HOWARD, 1963: 19, pl. 3, fig. A.

Holotype humerus 3753 (pl. 3, fig. A); paratypes humerus (prox.), sternum (frag.), sacrum and ulna collected with type 3753; Middle Pleistocene, Upper Palm Spring Formation, Vallecito Creek, Anza-Borrego Desert, San Diego County, California; Loc. 1358.

Meleagris crassipes Miller

MILLER, 1940: 154, fig. 45A.

Holotype tarsometatarsus (CIT)2708; Late Pleistocene, San Josecito Cave, Nuevo Leon, Mexico; Loc. (CIT)192.

Pavo californicus Miller

HOWARD, 1927: 3-27, pls. 1-13.

Hypotypes cranium E5226 (pl. 1, fig. 3, and pl. 2, fig. 1), two sterna E5173 (pl. 3, fig. 1), E5691 (pl. 4, fig. 1), furcula J6535 (pl. 5, figs. 4 and 7), scapula E5445 (pl. 7, fig. 5, and pl. 8, fig. 1), coracoid E7239 (pl. 6, figs. 1, 5, and pl. 7, fig. 3), humerus E7108 (pl. 2, fig. 5), ulna E6192 (pl. 8, fig. 5), radius D9790 (pl. 7, figs. 9, 13), carpometacarpus E6666 (pl. 9, fig. 1), femur old no. 3 + 4 (pl. 9, fig. 5), tibiotarsus F6993 (pl. 10, fig. 1, pl. 11, fig. 1), tarsometatarsus E6839 (pl. 12, fig. 1, pl. 13, fig. 1); Late Pleistocene, Rancho La Brea, Los Angeles, California.

HOWARD, 1928: 90.

Hypotypes five beaks K2474-2478; Late Pleistocene, Rancho La Brea, Los Angeles, California.

HOWARD, 1945: 597, pl. 25.

Hypotypes tarsometatarsi (age stages) K1681 (upper fig. a), K8364 (upper fig. b), G6282 (upper fig. c), E7224 (upper fig. d), E8569 (upper fig. e), E6732 (upper fig. f), E6697 (upper fig. g), E7737 (upper fig. h), E6793 (lower fig. a), E5075 (lower fig. b), E6801 (lower fig. c), E6173 (lower fig. d), E5333 (lower fig. 3); Late Pleistocene, Rancho La Brea, Los Angeles, California.

GRUIFORMES: PHORUSRHACIDAE

Titanis walleri Brodkorb

BRODKORB, 1963: 113, fig. 2.

Plasto"paratype" pedal phalanx 1, digit 3 UF 4109; cast C427; Late Pleistocene, Santa Fe River, Gilchrist/Columbia County line, Florida.

GRUIFORMES: RALLIDAE

Epirallus natator Miller

MILLER, 1942: 43, fig. 1a.

Holotype tarsometatarsus (CIT)2943; Late Pleistocene, San Josecito Cave, Nuevo Leon, Mexico; Loc. (CIT)192.

Fulica hesterna Howard

HOWARD, 1963: 22, pl. 1, fig. F (p. 10).

Holotype tibiotarsus (dist.) 2873 (pl. 1, fig. F); paratype tarsometatarsus and 5 pedal phalanges 2873; "paratype" tibiotarsus (dist.) 2875; Middle Pleistocene, Upper Palm Spring Formation, Vallecito Creek, Anza-Borrego Desert, San Diego County, California; Locs. 1433 and 1299.

Fulica minor Shufeldt

SHUFELDT, 1892: 412, pl. 17, fig. 32.

Plastoholotype humerus AMNH 3480 (name preoccupied; see *Fulica shufeldti* Brodkorb); cast C673; Late Pleistocene, Fossil Lake, Oregon.

Fulica shufeldti Brodkorb

BRODKORB, 1964b: 186.

Plastoholotype humerus AMNH 3480; cast C673; Late Pleistocene, Fossil Lake, Oregon.

CHARADRIIFORMES: SCOLOPACIDAE

Palnumenius victima Miller

MILLER, 1942: 45, fig. 1b.

Holotype tarsometatarsus (CIT)2944; Late Pleistocene, San Josecito Cave, Nuevo Leon, Mexico; Loc. (CIT)192.

CHARADRIIFORMES: LARIDAE

Larus oregonus Shufeldt

SHUFELDT, 1892: 398, pl. 15, fig. 3.

Plastoholotype humerus (prox.) AMNH 3494; cast C662; Late Pleistocene, Fossil Lake, Oregon.

Larus robustus Shufeldt

SHUFELDT, 1892: 398, pl. 15, figs. 1-2.

Plastoholotype coracoid AMNH 3497; cast C674; Late Pleistocene, Fossil Lake, Oregon.

CHARADRIIFORMES: STERCORARIIDAE

Stercorarius shufeldti Howard

HOWARD, 1946: 184, pl. 2, figs. 1, 2.

Plastoholotype humerus AMNH 3491; cast of proximal end only C671; Late Pleistocene, Fossil Lake, Oregon.

CHARADRIIFORMES: ALCIDAE: ALCINAE

Aethia rossmoori Howard

HOWARD, 1968b: 16, figs. 2-I, 2-J (p. 4).

Holotype ulna 18948 (fig. 2-J); "paratype" humerus (dist.) 18949 (fig. 2-I); Late Miocene, Leisure World, Laguna Hills, Orange County, California; Loc. 1945.

Brachyramphus pliocenus Howard

HOWARD, 1949b: 191, pl. 3, figs. 1, 2.

Holotype humerus 2119 (pl. 3, fig. 2); "paratypes" cranium 2166 (pl. 3, fig. 1), humerus (dist.) 2152, articular end mandible 2172; Pliocene, San Diego Formation, San Diego, California.

Cerorhinca dubia Miller

MILLER, 1925b: 115, pl. 2.

Plastoholotype impression of leg bones in shale UCMP 26546; cast (in relief) C695; Late Miocene, diatomaceous shales, Lompoc, Santa Barbara County, California.

Cerorhinca minor Howard

HOWARD, 1971: 9, figs. 1D, 1G, 1H, 1J.

Holotype humerus (prox.) 15408 (fig. 1J); "paratypes" ulna (prox.) 15406 (fig. 1G), tarsometatarsus 15407 (fig. 1D), humerus (prox.) 15420, coracoid (dist.) 15421 (fig. 1H); Early Pliocene, Almejas Formation, SE corner Cedros Island, Baja California, Mexico; Locs. 65153 and 65148.

CHARADRIIFORMES: ALCIDAE: MANCALLINAE

Alcodes ulnulus Howard

HOWARD, 1968b: 18, figs. 2G, 2H, 2L (p. 4).

Holotype ulna 18277 (fig. 2H); "paratypes" ulna (dist.) 18279, carpometacarpus (prox.) 18278 (figs. 2G, 2L); Late Miocene, Leisure World, Laguna Hills, Orange County, California; Loc. 1945.

Mancalla californiensis Lucas

LUCAS, 1901: 133, figs. 1, 2.

Plastoholotype humerus (prox.) USNM 4976; cast C685; Early Pliocene, Repetto Formation, Third Street Tunnel, Los Angeles, California.

HOWARD, 1949b: 196, pl. 3, figs. 3, 3a, 4, 4a.

Hypotypes carpometacarpus (prox.) 2033 (figs. 3, 3a), tarsometatarsus (shaft) 2034 (figs. 4, 4a), vertebra 2035; Early Pliocene, Repetto Formation, 3 miles north of Corona del Mar, Orange County, California; Loc. 1067.

HOWARD, 1970: 2.

Hypotypes humeri (prox.) 2576, (dist.) 2577, coracoid 2581, ulna 2580, radius 2579, carpometacarpus 2578, tibiotarsus 2424, tarsometatarsus 2250; Early Pliocene, Repetto Formation, 3 miles north of Corona del Mar, Orange County, California; Loc. 1067.

Mancalla cedrosensis Howard

HOWARD, 1971: 11, figs. 1L and 2A-K.

Holotype incomplete skeleton 15373 including essentially complete right scapula (fig. 2H), coracoid (figs. 2C, 2G, 2J), humerus (fig. 2B), ulna, femur (fig. 2K), and tibiotarsus (figs. 2A and 2D), left ulna (fig. 2E), radius (fig. 2F), carpometacarpus (fig. 2I), distal end right radius, carpometacarpus and left tibiotarsus, proximal end right tarsometatarsus and left femur, and fragmentary vertebrae; "paratypes" complete right tarsometatarsus (fig. 1L) and associated fragmentary pelvis, femur, tibiotarsi and vertebrae 15425; associated leg bones 23739; associated furcula, sternum, scapulae, coracoids, carpometacarpus 15410; and 50 separate elements nos. 15364-15372, 15374-15385, 15388-15402, 15408-15409, 15411-15412, 15415-15419, 15424, 15427; Early Pliocene, Almejas Formation, Cedros Island, Baja California, Mexico.

Mancalla milleri Howard

HOWARD, 1970: 7, figs. 1A-1C.

Holotype femur 2185 (figs. 1A, 1B; figured Miller and Howard, 1949, pl. 5, fig. 3 as *Mancalla diegense*); paratype humerus 2813 (fig. 1C); "paratypes" (Miller and Howard, 1949, pls. 1-6, figured as *M. diegense*; see *Pliolunda diegense*) scapula 2070 (pl. 4, fig. 4), humeri 2066, 2096 (pl. 2, figs. 2, 3), ulnae 2069 (pl. 1, fig. 1) 2082 (pl. 1, fig. 2, pl. 3, fig. 8), 2079 and 2101 (pl. 3, figs. 9-10), 2179 (pl. 5, fig. 2), carpometacarpus 2068 (pl. 4, fig. 15), femur 2097 (pl. 4, fig. 1), tibiotarsi 2083, 2100, 2108, 2134 (pl. 4, figs. 8, 10, 13, 14), sterna 2063 (pl. 2, fig. 7), 2180 (pl. 6, fig. 1), pelvis 2182 (pl. 6, fig. 2); "paratypes" cranium 2204, sterna 2325, 2661, scapulae 2167, 2252, 2257, 2278, 2297, 2506, 2536, coracoids 2208, 2229, 2243, 2276, 2338, 2498a, 2555, 2559, 2627, humeri 2096a and b, 2206, 2219, 2292, 2303, 2326, 2427, 2442, 2480a, b, and c, 2504, 2553, 2679, 2850, ulnae 2342, 2439, 2484, 2497a and b, 2552, 2558, 6426, radii 2335, 2632, carpometacarpus 2825, femora 2508, 2848, tibiotarsi 2088, 2209, 2286, 2478, 2549, 2628, tarsometatarsi 2327, 2488, 2548, 2682, 6454; Pliocene, San Diego Formation, San Diego, California.

Pliolunda diegense Miller

MILLER and HOWARD, 1949: 201-228, pl. 1-6.

Hypotypes scapulae 2176, 2049 (pl. 4, figs. 5, 7), coracoids 2087, 2067 (pl. 3, figs. 2, 3), ulna 2064 (pl. 3, fig. 7), carpometacarpus (prox.) 2068 (pl. 4, fig. 16), tibiotarsi 2125 (pl. 4, fig. 9), 2177 (pl. 5, fig. 1), tarsometatarsi 2178, 2177 (pl. 5, figs. 4-5); (see *Mancalla milleri* for reassignment of other figured specimens); Pliocene, San Diego Formation, San Diego, California.

HOWARD, 1970: 7, fig. 1D.

Hypotype humerus 2670; Pliocene, San Diego Formation, San Diego, California.

Praemancalla lagunensis Howard

HOWARD, 1966b: 4, figs. 1A, C, D, E, G.

Holotype humerus (dist.) 15288 (fig. 1E, 1G); paratype carpometacarpus (prox.) 15287 (fig. 1A); "paratypes" carpometacarpus (prox.) 15290, coracoid (dist.) 15289 (figs. 1C, 1D), scapula 15294, lower mandible (articular end) 15428; Late Miocene, Leisure World, Laguna Hills, Orange County, California; Loc. 1945.

CUCULIFORMES: CUCULIDAE

Geococcyx conklingi Howard

HOWARD, 1931: 208, fig. 50.

Syntypes humerus (dist.) 118 (figs. 50c, 50c′), ulna 119 (fig. 50b), femur 113 (figs. 50a, 50a′); "paratypes" femora (shafts) 114, 115, humerus (shaft) 117, tibiotarsus (dist.) 116; Late Pleistocene, Conkling Cavern, Doña Ana County, New Mexico; Loc. 1009.

STRIGIFORMES: PROTOSTRIGIDAE

Protostrix californiensis Howard

HOWARD, 1965b: 350, pl. 49, figs. 1, 3.

Holotype humerus 6171; Eocene, Poway Formation, 300 yards north of intersection of Lake Shore and Jackson drives, San Diego, California; Loc. 1723.

STRIGIFORMES: STRIGIDAE

Asio priscus Howard

HOWARD, 1964a: 28, fig. 1.

Holotype tibiotarsus 4712; Late Pleistocene, Arlington Canyon, Santa Rosa Island, California; Loc. (CIT) 106.

Strix brea Howard

HOWARD, 1933: 66, fig. 15.

Holotype tarsometatarsus E9379 (fig. 15); "paratypes" rostra C7125, K2713, sterna E2477, D9615, coracoids E9273, E9687, H4850, H4872, H4881, H4889, H4904, H4911, H4923, scapulae E2720, H6610, H6613, H6629, H6636, H6656, H6659, H6673, humeri E8911, E9051, E9425, E9804, F9305, G1229, carpometacarpi H3096-H3098, H3107, H3126. femora E9439, E9647, E9909, F4884, tibiotarsi E1139, E9267, E9414, E9545, E9606, E9758, E9888, E9919, E9932, E9942, F7456, tarsometatarsi E9416, E9417, E9575, E9892, E9911, G3933, G3957, G3958; Late Pleistocene, Rancho La Brea, Los Angeles, California.

PASSERIFORMES: PALAEOSCINIDAE

Palaeoscinis turdirostris Howard

HOWARD, 1957b: 6, figs. 1-2.

Holotype complete skeleton on two slabs of matrix 2604; Miocene, Tepusquet Creek, Santa Barbara County, California; Loc. 1127.

PASSERIFORMES: ICTERIDAE

Pandanaris convexa A. Miller

A. MILLER, 1947: 22, fig. 4a-d.

Holotype upper mandible K7278 (figs. 4a, 4b, 4c); "paratype" lower mandible K7279 (figs. 4b, 4d); Late Pleistocene, Rancho La Brea, Los Angeles, California.

Pyelorhamphus molothroides A. Miller

A. MILLER, 1932: 39, pl. 4, figs. 1-5.

Holotype lower mandible 320 (pl. 4, figs. 1, 2, 3); "paratype" upper mandible 338 (pl. 4, figs. 2, 4, 5); Quaternary (?Late Pleistocene), Shelter Cave, Doña Ana County, New Mexico; Loc. 1010.

PASSERIFORMES: FRINGILLIDAE

Pipilo angelensis Dawson

DAWSON, 1948: 59, fig. 16.

Holotype upper mandible K7291 (fig. 16); paratype upper mandible K7292; "paratypes" six upper mandibles, all K7293; Late Pleistocene, Rancho La Brea, Los Angeles, California.

LITERATURE CITED

ANDREWS, C. W. 1913. On some bird remains from the Upper Cretaceous of Transylvania. Geol. Mag. decade 5, 10 (5): 193-196, figs. 1-2.

BRODKORB, P. 1953. A review of the Pliocene loons. Condor 55:211-214, fig. 1.

———. 1963a. Catalogue of Fossil Birds, Part 1. Bull. Fla. St. Mus., Biol. Sci. 7 (4):179-293.

———. 1963b. A giant flightless bird from the Pleistocene of Florida. Auk 80:111-115, figs. 1-2.

———. 1964a. Catalogue of Fossil Birds, Part 2. Bull. Fla. St. Mus., Biol. Sci. 8 (3):195-335.

———. 1964b. A new name for *Fulica minor* Shufeldt. Quart. J. Fla. Acad. Sci., 27 (3):186.

———. 1967. Catalogue of Fossil Birds, Part 3. Bull. Fla. St. Mus., Biol. Sci. 11 (3):99-220.

———. 1971. Catalogue of Fossil Birds, Part 4. Bull. Fla. St. Mus., Biol. Sci. 15 (4):163-266.

COPE, E. D. 1878. Descriptions of new extinct vertebrata from the Upper Tertiary and Dakota formations. Bull. U.S. Geol. and Geog. Surv. Terr. 4 (2):379-396.

DAWSON, W. R. 1948. Records of fringillids from the Pleistocene of Rancho La Brea. Condor 50:57-63, fig. 16.

FISHER, H. I. 1944. The skulls of the cathartid vultures. Condor 46:272-296, figs. 42-47.

HOPSON, J. A. 1964. *Pseudodontornis* and other large marine birds from the Miocene of South Carolina. Postilla, Peabody Mus. Nat. Hist., Yale Univ. No. 83, 19 p., figs. 1-3.

HOWARD, H. 1927. A review of the fossil bird, Parapavo californicus (Miller) from the Pleistocene asphalt beds of Rancho La Brea. Univ. Calif. Publ. Bull. Dept. Geol. Sci. 17:1-56, pls. 1-13.

———. 1928. The beak of Parapavo californicus (Miller). Bull. So. Calif. Acad. Sci. 27:90-91.

________. 1931. A new species of road-runner from Quaternary cave deposits in New Mexico. Condor 33:206-209, figs. 48-50.

________. 1932. Eagles and eagle-like vultures of the Pleistocene of Rancho La Brea. Carnegie Inst. Wash., Publ. 429, 82 p., 3 figs. in text, 29 pls.

________. 1933. A new species of owl from the Pleistocene of Rancho La Brea, California. Condor 35:66-69, fig. 15.

________. 1935a. A new species of eagle from a Quaternary cave deposit in eastern Nevada. Condor 37:206-209, fig. 40.

________. 1935b. The Rancho La Brea Wood Ibis. Condor 37:251-253, fig. 47.

________. 1936. A new fossil bird locality near Playa del Rey, California, with description of a new species of sulid. Condor 38:211-214, fig. 37.

________. 1938. The Rancho La Brea Caracara, a new species. Carnegie Inst. Wash., Publ. 487:217-240, 3 pls.

________. 1940. A new race of Caracara from the Pleistocene of Mexico. Condor 42:41-44.

________. 1942. A review of the American fossil storks. Carnegie Inst. Wash., Publ. 530:187-203, 2 text figs., 1 pl.

________. 1944. A Miocene hawk from California. Condor 46:236-237, fig. 40.

________. 1945. Observations on young tarsometatarsi of the fossil turkey, *Parapavo californicus* (Miller). Auk 62:596-603, 1 text fig., pl. 25.

________. 1946. A review of the Pleistocene birds of Fossil Lake, Oregon. Carnegie Inst. Wash., Publ. 551:141-195, 2 pls.

________. 1947. Wing elements assigned to Chendytes. Condor 49:76-77, fig. 15.

________. 1949a. Avian fossils from the marine Pleistocene of southern California. Condor 51:20-28.

________. 1949b. New avian records for the Pliocene of California. Carnegie Inst. Wash., Publ. 584:177-199, 3 pls.

________. 1952. The prehistoric avifauna of Smith Creek Cave, Nevada, with a description of a new gigantic raptor. Bull. So. Calif. Acad. Sci. 51 (2):50-54, pl. 10.

________. 1955a. New records and a new species of Chendytes, an extinct genus of diving geese. Condor 57:135-143, figs. 1-3.

________. 1955b. Fossil birds from Manix Lake, California. U.S. Geol. Surv. Prof. Paper No. 264-J:199-205, pl. 50, and text fig. 42.

________. 1957a. A gigantic "toothed" marine bird from the Miocene of California. Santa Barbara Mus. Nat. Hist., Bull. Dept. Geol. 1:1-23, figs. 1-8.

________. 1957b. A new species of passerine bird from the Miocene of California. Los Angeles Co. Mus., Contrib. Sci. 9:1-16, figs. 1-2.

________. 1958. Miocene sulids of southern California. Los Angeles Co. Mus., Contrib. Sci. 25:1-15, figs. 1-3.

________. 1962. Fossil Birds. Los Angeles Co. Mus., Sci. Ser. 17, Paleontol. 10, 44 p., 22 figs.

________. 1963. Fossil birds from the Anza-Borrego Desert. Los Angeles Co. Mus., Contrib. Sci. 73:1-33, 1 fig., 3 pls.

________. 1964a. A fossil owl from Santa Rosa Island, California, with comments on the eared owls of Rancho La Brea. Bull. So. Calif. Acad. Sci. 63(1):27-31, 1 fig.

________. 1964b. Fossil Anseriformes. *In* "Waterfowl of the World," by Jean Delacour, vol. 4, p. 233-326, 5 text figs., 10 pls. Country Life Ltd., London.

________. 1964c. Further discoveries concerning the flightless "diving geese" of the genus Chendytes. Condor 66:372-376, 1 fig.

________. 1964d. A new species of the "Pigmy Goose," *Anabernicula,* from the Oregon Pleistocene, with a discussion of the genus. Amer. Mus. Novitates 2200:1-14, 2 figs.

———. 1965a. A new species of cormorant from the Pliocene of Mexico. Bull. So. Calif. Acad. Sci. 64 (1):50-55, 1 fig.

———. 1965b. First record of avian fossils from the Eocene of California. J. Paleontol. 39(3):350-354, pl. 49.

———. 1966a. Pliocene birds from Chihuahua, Mexico. Los Angeles Co. Mus., Contrib. Sci. 94:1-12, 1 fig.

———. 1966b. A possible ancestor of the Lucas Auk (Family Mancallidae) from the Tertiary of Orange County, California. Los Angeles Co. Mus., Contrib. Sci. 101:1-8, 1 fig.

———. 1966c. Two fossil birds from the Lower Miocene of South Dakota. Los Angeles Co. Mus., Contrib. Sci. 107:1-8, 1 fig.

———. 1966d. Additional avian records from the Miocene of Sharktooth Hill, California. Los Angeles Co. Mus., Contrib. Sci. 114:1-11, 1 fig.

———. 1968a. Limb measurements of the extinct vulture, Coragyps occidentalis, with a description of a new subspecies. Papers Archaeol. Soc. New Mex. 1:115-128.

———. 1968b. Tertiary birds from Laguna Hills, Orange County, California. Los Angeles Co. Mus., Contrib. Sci. 142:1-21, 2 figs.

———. 1969a. A new avian fossil from Kern County, California. Condor 71:68-69, 1 fig.

———. 1969b. Avian fossils from three Pleistocene sites in central Mexico. Los Angeles Co. Mus., Contrib. Sci. 172:1-11, 1 fig.

———. 1970. A review of the extinct avian genus, *Mancalla.* Los Angeles Co. Mus., Contrib. Sci. 203:1-12, 1 fig.

———. 1971. Pliocene avian remains from Baja California. Los Angeles Co. Mus., Contrib. Sci. 217:1-17, 2 figs.

———. 1972. The Incredible Teratorn again. Condor 74:(in press).

HOWARD, H., AND S. L. WARTER. 1969. A new species of bony-toothed bird (*Family Pseudodontornithidae*) from the Tertiary of New Zealand. Rec. Canterbury Mus. 8(4):345-357, 4 pls.

HOWARD, H., AND J. A. WHITE. 1962. A second record of *Osteodontornis,* Miocene "toothed" bird. Los Angeles Co. Mus., Contrib. Sci. 52:1-12, 5 figs.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1964. International code of zoological nomenclature, adopted by the XV International Congress of Zoology. Int. Trust Zool. Nomenclature, London. 176 p.

LAMBRECHT, K. 1928. Mesozoische und tertiäre Vogelreste aus Siebenburgen. Proc. X International Congr. Zool., Budapest, 1927, Sect. VIII, Paleozoologie et Zoogeographie, p. 1262-1275, figs. 1-16.

LUCAS, F. A. 1901. A flightless auk, Mancalla californiensis, from the Miocene of California. Proc. U.S. Nat. Mus. 24(1245):133-134, figs. 1-2.

MARSH, O. C. 1870. Notice of some fossil birds from the Cretaceous and Tertiary formations of the United States. Amer. J. Sci. ser. 2, 49(46):205-217.

MILLER, A. H. 1932. An extinct icterid from Shelter Cave, New Mexico. Auk 49:38-41, pl. 4.

———. 1947. A new genus of icterid from Rancho La Brea. Condor 49:22-24, fig. 4.

MILLER, L. H. 1910. The condor-like vultures of Rancho La Brea. Univ. Calif. Publ. Bull. Dept. Geol. 6:1-19, figs. 1-5.

———. 1915. A walking eagle from Rancho La Brea. Condor 17:179-181, fig. 63.

———. 1925a. The birds of Rancho La Brea. Carnegie Inst. Wash., Publ. 349: 63-106, pls. 1-6, 20 text figs.

———. 1925b. Avian remains from the Miocene of Lompoc. Carnegie Inst. Wash., Publ. 349:107-117, pls. 1-9, 1 text fig.

———. 1929. A new cormorant from the Miocene of California. Condor 31: 167-172, figs. 58-59.

———. 1931. Bird remains from the Kern River Pliocene of California. Condor 33:70-72, fig. 16.

———. 1932. The Pleistocene storks of California. Condor 34:212-216, fig. 23.

———. 1935. New bird horizons in California. Publ. Univ. Calif. Los Angeles, Biol. Sci. 1(5):73-80, 2 figs.

———. 1938. A study of the skull of the Pleistocene stork, Ciconia maltha Miller. Trans. San Diego Soc. Nat. Hist. 8:455-462, pl. 37.

———. 1940. A new Pleistocene turkey from Mexico. Condor 42:154-156, fig. 45.

———. 1942. Two new bird genera from the Pleistocene of Mexico. Univ. Calif. Publ. Zool. 47:43-46, fig. 1.

———. 1944a. Some Pliocene birds from Oregon and Idaho. Condor 46:25-32, fig. 6.

———. 1944b. A Pliocene flamingo from Mexico. Wilson Bull. 56:77-82, figs. 1-2.

———. 1961. Birds from the Miocene of Sharktooth Hill, California. Condor 63:399-402, fig. 1.

MILLER, L., AND R. I. BOWMAN. 1958. Further bird remains from the San Diego Pliocene. Los Angeles Co. Mus., Contrib. Sci. 20:1-15, figs. 1-5.

MILLER, L., AND H. HOWARD. 1938. The status of the extinct condorlike birds of the Rancho La Brea Pleistocene. Publ. Univ. Calif. Los Angeles, Biol. Sci. 1: 169-176, pl. 2, 2 text figs.

———. 1949. The flightless Pliocene bird Mancalla. Carnegie Inst. Wash. Publ. 584(7):201-228, pls. 1-6.

MILLER, L., E. D. MITCHELL, AND J. H. LIPPS. 1961. New light on the flightless goose, *Chendytes lawi.* Los Angeles Co. Mus., Contrib. Sci. 43:1-11, pls. 1-2.

ROSS, R. 1935. A new genus and species of pigmy goose from the McKittrick Pleistocene. Trans. San Diego Soc. Nat. Hist. 8(15):107-114, figs. 1-6.

SELLARDS, E. H. 1916. Human remains and associated fossils from the Pleistocene of Florida. 8th Ann. Rept. Fla. Geol. Surv., p. 121-160, pls. 15-31, text figs. 1-15.

SHUFELDT, R.W. 1892. A study of the fossil avifauna of the Equus beds of the Oregon desert. J. Acad. Nat. Sci. Phila. 9(3):389-425, pl. 15-17.

———. 1913. Review of the fossil fauna of the desert region of Oregon, with a description of additional material collected there. Bull. Amer. Mus. Nat. Hist. 32(6):123-178, pls. 9-43.

———. 1915. Fossil birds in the Marsh collection of Yale University. Trans. Connecticut Acad. Arts and Sci. 19:1-110, 15 pls.

———. 1916. New extinct bird from South Carolina. Geol. Mag. n.s. 3(8):343-347, pl. 15.

TORDOFF, H. B., AND J. R. MACDONALD. 1957. A new bird (family Cracidae) from the early Oligocene of South Dakota. Auk 74:174-184, pl. 10, and text fig. 1.

WETMORE, A. 1923. Avian fossils from the Miocene and Pliocene of Nebraska. Bull. Amer. Mus. Nat. Hist. 48(12):483-507, figs. 1-20.

———. 1924. Fossil birds from southeastern Arizona. Proc. U.S. Nat. Mus. 64(5):1-18, figs. 1-9.

———. 1930. Fossil bird remains from the Temblor Formation near Bakersfield, California. Proc. Calif. Acad. Sci. 19(8):85-93, 7 text figs.

———. 1933. An Oligocene eagle from Wyoming. Smithsonian Misc. Coll. 87(19): 1-9, figs. 1-19.

———. 1940. Fossil bird remains from Tertiary deposits in the United States. J. Morphol. 66:25-37, figs. 1-14.

ZULLO, V. A., AND L. G. HERTLEIN. 1970. Catalog of specimens in the type collection of the Department of Geology, California Academy of Sciences. Cephalopoda. Occas. Papers Calif. Acad. Sci. 82:1-130.

SPECIES INDEX

Names in brackets indicate latest taxonomic assignments (see Brodkorb, 1963a, 1964a, 1967, 1971).

Accepted for publication March 24, 1972

Printed in Los Angeles, California by Continental Graph

NUMBER 229
JUNE 12, 1972

A NEW SPECIES OF SWIFT OF THE GENUS *CYPSELOIDES* FROM NORTHEASTERN SOUTH AMERICA (AVES: APODIDAE)

By Charles T. Collins

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1964 AIBS Style Manual for Biological Journals is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1964 AIBS Style Manual for Biological Journals in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Changes in the manuscript after galley proof will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

A NEW SPECIES OF SWIFT OF THE GENUS *CYPSELOIDES* FROM NORTHEASTERN SOUTH AMERICA (AVES: APODIDAE)[1]

By CHARLES T. COLLINS[2]

ABSTRACT: A review of the Chestnut-collared Swift, *Cypseloides rutilus,* indicates that the labelled type specimen of *Hirundo rutila* Vieillot, 1817 is from Trinidad, that Vieillot's original description agrees with the type, and that the distinctive population from the Pantepui area of southern Venezuela and neighboring Guyana and Brazil, long believed to the the same as the Trinidad population and also called by that name by recent authors, is deserving of separate species status. Although characterized nearly 100 years ago, this species lacks a valid name, and *Cypseloides phelpsi,* the Tepui Swift, is here proposed.

In the course of field studies of the Chestnut-collared Swift (*Cypseloides rutilus*) in Trinidad (Collins, 1968) I became increasingly aware that the plumages of some individuals, particularly those of females and juveniles, were sharply at odds with some published accounts. A subsequent review of the molts and plumages of this species throughout its range (Collins, in preparation) has also pointed out a particularly distinct population which, although accurately characterized nearly 100 years ago, lacks a valid scientific name. Correcting this situation entails first a review of the taxonomic history of *C. rutilus* and this distinctive population.

The Chestnut-collared Swift (*Cypseloides rutilus*) was first described by Vieillot (1817) under the name of *Hirunda rutila.* The type specimen, stated by Vieillot to be in the collections of the Muséum National d'Histoire Naturelle, (Paris), is extant in the collections of that museum, mounted on a small stand as was then the custom. No locality for the type was given by Vieillot although "La Trinité" (i.e., Trinidad) is written on the underside of the base of the stand. This omission is not surprising as it is well known that Vieillot often described new species from mounted specimens he did not handle but only observed in locked exhibit cases in the Paris museum. In any event Vieillot's description agrees with the specimen. Also appearing on the underside of the stand are the determinations *"Chaetura rutila* Vieillot" and *"Hirundo robini* Lesson," the latter being a long accepted junior synonym published in 1831 with type locality given as "l'île de la Trinité." Later authors

---

[1] EDITORIAL COMMITTEE FOR THIS CONTRIBUTION
Eugene Eisenmann
Herbert Friedmann
Kenneth E. Stager

[2] Research Associate in Ornithology, Natural History Museum of Los Angeles County; and Department of Biology, California State College, Long Beach, California 90801.

(Sclater, 1855; Salvin and Sclater, 1860; Orton, 1871) state that this species was collected by M. Robin in Trinidad and that his *specimens* form the *types* of Vieillot's and Lesson's descriptions. I have been able to find only the single specimen. There is no evidence that there were ever more and I suggest that both descriptions were based on the same specimen, as indicated by the labels on the stand. As indicated below there is no reason to doubt that the specimen described by Vieillot is that marked as type in the Paris museum and labeled as being from Trinidad, and this should be designated as the type locality for *Hirundo rutila* Vieillot and *H. robini* Lesson in future studies.

In the next 100 years Chestnut-collared Swifts were collected in most parts of their present known range: in mountainous country from Mexico to Bolivia. Additional taxa were described from Colombia (*Chaetura brunnitorques* Lafresnaye, 1844 = *Cypseloides rutilus brunnitorques*); and from Mexico (*Cypselus brunneitorques* (sic) *griseifrons* Nelson, 1900 = *Cypseloides rutilus griseifrons*; *Chaetura nubicola* Brodkorb, 1938 = *Cypseloides rutilus nubicola*). A full review of these taxa and a yet to be described subspecies from South America will be presented later (Collins, in preparation).

During this period authors have not been in full agreement as to whether *brunnitorques* and *rutilus* were races of a single species, *C. rutilus,* or alternatively, separate species, with *griseifrons* and *nubicola* being races of *C. brunnitorques.* Species limits will be discussed in detail below. Although several fairly recent authors, mostly following Peters (1940), have included these birds in the genus *Chaetura,* as was also done by some very early workers, the current consensus favors inclusion in *Cypseloides.* This is based both on various aspects of the reproductive biology (Lack, 1956; Snow, 1962; Collins, 1968) but also on more traditional morphological characters (Zimmer, 1953; Eisenmann and Lehmann, 1962).

In the last century two specimens of an allied but strikingly different swift, one of which is presently located in the collections of the British Museum, were collected by H. Whitely in the Merumé Mountains of British Guiana (Guyana). As described by Salvin and Godman (1882:82), these specimens differed from those of other areas in having a "brighter" chestnut collar and a tail "much longer and distinctly forked." Also, the chestnut of the collar included the chin, an area normally brown in specimens from all other populations. These are in fact some of the salient characteristics of this population. However, the following statement made by Salvin and Godman with regard to the correct name applicable to these specimens was evidently made without examining Vieillot's type and in disregard of a salient aspect of his description: "There can be little doubt that the species described as *Hirundo rutila* by Vieillot was the Guiana bird, though the origin of the specimens was unknown."

This view is contradicted by Vieillot's original description of *Hirundo rutila* in which, among other things, the tail is stated to be square (not forked), and the chin is not chestnut colored. Salvin and Godman further suggested that the name *Hirundo robini* be applied to these Guianan birds as well and that the island of Trinidad be included in the range. The erroneous assumption was made that the two populations were the same. The designation of "Guiana" as the type locality for *H. rutila* by Peters (1940) ,following Salvin and Godman, is not supportable on the basis of the known facts. Peters did correctly include Trinidad in the range of this form, not realizing that two very different forms were included under one designation.

I have examined most of the available specimens of the Chestnut-collared Swifts from all portions of their range and they are in agreement with Vieillot's original description of *H. rutila* and the type specimen, which I have also examined. It is important to note that in all populations the tail is relatively short, essentially square and unforked. In worn plumages the rectrices may become abraded thus exposing the terminal portion of the shafts of some feathers. This gives them the superficial appearance of having the bare terminal "spines" typical of species of *Chaetura.* The specimen described by Vieillot had these characteristics, for he stated "la queue carrée; les deux pennes intermediares terminees en pointe; les autres arrondies a leur extremite," which I translate as "the tail square; the two middle feathers ending in a point; the others rounded at their ends." Personal observations made on numerous living birds netted in the field confirm that these characteristics are also true of the Chestnut-collared Swifts presently breeding on the island of Trinidad. Surprisingly there are but two museum specimens of these swifts from Trinidad, and only one is of an adult. I have examined both and they are of the form described by Vieillot.

The correct view that *Cypseloides rutilus* (Vieillot) is applicable to the birds inhabiting the island of Trinidad has been uniformly accepted by all authors considering the avifauna of this island from Léotaud (1866) to the present day. However, the erroneous conclusion of Salvin and Godman (1882) that Guianan birds were the same was repeated by Salvin (1885), and unfortunately was uncritically followed by Peters and nearly all later authors. This gave rise to the view that the name *Cypseloides rutilus* was applicable not only to the Trinidad form (which is square-tailed), but to the distinctive, fork-tailed birds now known from many specimens from the tabletop mountains (tepuis) south of the Orinoco River in Venezuela and the immediate adjacent parts of Guyana and Brazil ("Pantepui Area" of Mayr and Phelps, 1967). This situation was abetted by a near absence of specimens of these swifts from the mountains of northern Venezuela, thus giving the impression that there existed a large discontinuity in the range of these swifts and that the nearest continental population to Trinidad was in fact that inhabiting Pantepui. With the collection of specimens of *C. rutilus* from various localities in northern Venezuela (Phelps and Phelps, 1958), and the filling of this seeming discontinuity in their range, it is now obvious that the zoogeographical affinities of the population in Trinidad (*Cypseloides rutilus sensu stricto*) are with northern Venezuela and Colombia (so-called *brunnitorques*). There is much less morphological resemblance and less close relationship with the distinctive population inhabiting Pantepui. In fact, *rutilus* and *brunnitorques* are so similar as to be doubtfully distinct even as subspecies, and after further study the latter may prove to be synonymous with *rutilus* which has priority. The Pantepui swifts, characterized by Salvin and Godman (1882) form a distinctive allopatric population for which I now propose the name:

Cypseloides phelpsi, new species

TYPE: Adult male, AMNH 324213, original expedition number 1594; collected 14 February 1938, on Cerro Auyan-tepui, Bolivar, Venezuela at an elevation of 1100 meters by the Phelps Venezuela Expedition.

DIAGNOSIS: Adults of *C. phelpsi* are readily separable from those of all populations of *C. rutilus* (whatever the subspecies) in having a longer "softer" (less stiffened) and deeply forked tail lacking the stiffened, and sometimes bare-tipped shafts and square tail of *C. rutilus* and in longer wings. Moreover, in color they also differ from all populations of *C. rutilus* in 1) having the plumage more nearly black rather than a blackish brown, 2) the collar a more orange-chestnut tone rather than a deep red-brown or chestnut-brown, and 3) in having the coloration of the collar extend upward over all of the chin or interramal area. The extent of this coloration is the same in both sexes although the breast is a bit paler and mixed with brown in some females. The white supraocular streak is present in nearly all individuals. In *C. rutilus* only exceptional females have the full male coloration; most females have no chestnut collar, or only a partial one confined to the nape and part of the sides of the neck. In both *C. phelpsi* and *C. rutilus* there is a tendency for males to be larger than females in most linear measurements, although even the smallest females of *C. phelpsi* are generally larger than the largest males of *C. rutilus.* Table 1 presents measurements of the available specimens of *C. phelpsi* (both from Venezuela and Guyana) and, for comparison, a series of *C. rutilus* from the mountainous areas of northern Venezuela in the states of Táchira, Mérida, Barinas, Yaracuy, Carabobo, Aragua, Distrito Federal, Miranda and Sucre.

As mentioned earlier, specimens from all parts of the range of *C. rutilus* have been examined in this study, although only measurements from this one nearby part of the range are presented here. The darkness of the body and flight feathers, the more orange color and extent of the collar, the length of wing and tail, and depth of forking of the tail, individually as well as collectively, serve to separate *C. phelpsi* from this or any other population of *C. rutilus* throughout its range. The degree of whiteness of the supraocular stripe in *C. phelpsi* is approached in one population of *C. rutilus* in Middle America (*nubicola*). As also usually (but not invariably) true in *C. rutilus,* the outermost (tenth) primary of *C. phelpsi* is shorter than the ninth (see tip measurement, Table 1).

TABLE 1

Measurements[a] of *Cypseloides phelpsi* and *Cypseloides rutilus* from Venezuela

	phelpsi Males (N = 12)[c]	*phelpsi* Females (N = 18)	*rutilus* Males (N = 22)	*rutilus* Females (N = 20)
Wing (Flattened)	136.92 ±0.61 (133–140.5)	133.92 ±0.64 (129.5–138)	122.50 ±0.89 (116–130.5)	119.15 ±0.71 (112–124.5)
Wing Tip[b]	5.15 ±0.42 (3.0–7.5)	4.86 ±0.28 (2.5–7.5)	4.98 ±0.53 (2.5–10.0)	4.31 ±0.18 (2.5–5.5)
Tail	61.31 ±0.81 (56.5–66)	58.87 ±0.36 (56.5–61.5)	44.84 ±0.58 (39.5–48.5)	42.68 ±0.49 (37.5–47.0)
Depth of Tail Fork	9.61 ±0.45 (7.0–11.5)	9.71 ±0.48 (5.5–13.0)	2.79 ±0.62 (1.0–3.0)	1.36 ±0.29 (0.0–4.5)
Culmen (from nostril)	4.18 ±0.06 (4.0–4.5)	4.21 ±0.06 (3.7–4.5)	4.17 ±0.09 (3.7–4.5)	4.16 ±0.05 (3.7–4.5)
Tarsus	13.76 ±0.13 (12.7–14.5)	13.60 ±0.11 (12.7–14.3)	12.33 ±0.11 (11.5–13.0)	12.03 ±0.11 (11.3–13.0)

a. All measurements in millimeters; presented are: Mean ± standard error and (range).

b. Difference in length of ninth and tenth primaries (ninth longest).

c. Does not include extralimital specimen from Aragua: wing, 139; wing tip, ? (primary 10 not full length); tail, 59.2; depth of fork, 9.8; culmen, 4.0; tarsus, 14.0.

DESCRIPTION OF TYPE: Dark sooty black all over except for pronounced orange-chestnut collar including nape, upper breast, throat, chin and sides of head up to level of eyes; light white streak above eyes on edge of dark crown. Tail deeply forked; shafts of rectrices not markedly stiffened nor projecting beyond vane. Soft parts (on label): iris brown, bill black, feet purplish gray. Wing (flattened) 136 mm, tail 61.5 mm; culmen (from nostril) 4 mm; tarsus 14.5 mm; depth of tail fork 8.5 mm; gonads not fully enlarged; no appreciable molt but not in fresh plumage.

RANGE: Pantepui area of southeastern Venezuela, northwestern Guyana, and probably (no specimen) extreme northeastern portion of Territorio Federal de Roraima, Brazil. A single extralimital specimen has been taken at Rancho Grande, Aragua, in northern Venezuela.

SPECIFIC STATUS: *C. phelpsi* is unquestionably a distinctive population, but, it may be argued, no more so than numerous insular or otherwise isolated populations of other birds entitled to only subspecific rank. It should be remembered, however, that swifts are exceedingly mobile animals and that the geographic distances which restrict gene flow between populations of many bird species may be encompassed by the daily foraging flights of swifts. Thus it is unlikely that in itself the distance between Pantepui and the nearest breeding populations of *C. rutilus* in northern Venezuela (900 ± kms) is enough of a barrier to gene flow to justify considering the striking differences of *C. phelpsi* as simply those of a geographically isolated but potentially interbreeding population. The Mexican and Bolivian populations of *C. rutilus* are more like those of Trinidad and northern Venezuela than is the comparatively nearby Pantepui population of *C. phelpsi.* As has also been pointed out by Orr (1963) and Brooke (1971), good species of swifts frequently show little divergence in appearance so that seemingly minor morphological difference may be of greater importance in delimiting species than in other avian taxa. Thus the striking difference in wing and tail length, degree of forking of the tail, and decreased sexual dimorphism in plumage of *C. phelpsi* seem especially significant in appraising specific limits in this case. Two further bits of evidence are available. Firstly, if the Pantepui area is as isolated for swifts as it is for the other less mobile species, we should expect to find similar degrees of difference in other swift species living there. Such is not the case! *Aëronautes montivagus* and *Chaetura chapmani* show little or no geographic variation over this part of their ranges. A second bit of evidence that *C. phelpsi* is not sedentary is the existence of a single specimen collected at the Rancho Grande Biological Station in Aragua on 16 February 1960. This specimen, now housed in the collection at that station, is typical in every way of the Pantepui specimens of *C. phelpsi.* Rancho Grande is well within the breeding range of *C. rutilus,* which has also been collected there (Beebe, 1949; Collins, in preparation). This indicates that at least an occasional individual of *C. phelpsi* may occur in the range of *C. rutilus* and that the appreciable morphological differences between these birds are maintained despite this possible sympatry and potential for genetic interchange. For these reasons I feel that tentatively full specific status is warranted for *Cypseloides phelpsi.* This is essentially a reversion, although with new nomenclature, to the treatment prevailing before Peters (1940).

REMARKS: There is no information available on the ecology, feeding habits, or body weight of *C. phelpsi.* It was observed flying in large flocks around Cerro Auyan-tepui in the non-breeding season by Gilliard (1941). Although Mayr and Phelps (1967:297) include the Tepui Swift in a list of "cliff dwellers," this, although probably true, is still a supposition, for its nesting and roosting habits are presently unreported. In all likelihood, it will show the same affinities for nest and roosting sites in damp, dark areas with high relief, near or behind waterfalls, exhibited by other *Cypseloides* swifts including *C. rutilus* (Snow, 1962; Collins, 1968). Nest sites of *C. phelpsi* should be looked for in the vicinity of the numerous waterfalls coming off the tepuis.

Two specimens showing early stages of molt of the wing feathers, typical of the end of the breeding season, were taken on 26 July. This probably indicates a late "spring"- early "summer" breeding season (in the northern hemisphere sense) closely tied to the onset of the rainy season in this area. Only one of a large series collected in February showed even slightly enlarged gonads (Gilliard, 1941). Two specimens show from three to six white feathers in the central breast region at the lower border of the collar. These specimens, both of female (AMNH 323327 and 324266), were collected on Cerro Auyan-tepui on 14 February and 13 March 1938. Such cases of partial albinism have been recorded for several other neotropical swifts including *C. rutilus* (Eisenmann and Lehmann, 1962; Collins, 1967).

The name *Cypseloides phelpsi,* based on information provided by me, has appeared as a *nomen nudum* in two recent faunal lists but without any diagnosis or description (Brooke, 1970a, 1970b).

Since most of the possible vernacular names incorporating the color of the collar have been used in reference to *C. rutilus,* Tepui Swift would seem the most appropriate English name for *Cypseloides phelpsi* in recognition of its range in Pantepui.

ETYMOLOGY: It is my pleasure to name this swift after William H. Phelps, Jr., who, by so ably continuing the efforts devoted by his father, the late William H. Phelps, to the study and preservation of the avifauna of Venezuela and the Pantepui area in particular, has contributed so much to our ornithological knowledge of these areas.

SPECIMENS EXAMINED

Cypseloides phelpsi

Venezuela, Bolivar, Mt. Auyan-tepue: 9 males, 14 females (AMNH, R.G.)
  Cerro Duida: 1 female (AMNH)
  Gran Sabana: 1 male, 1 female (P.)
  Cerro Serrania: 1 male, 1 female (P.)
Territory Amazonas, Cerro Yapacana: 1 female (R.G.)
  Aragua, Rancho Grande: 1 male (R.G.)
British Guiana (Guyana): Merumé Mountains: 1 male (B.M.)

Cypseloides rutilus

Over 250 specimens from all parts of the range of this species have been examined in this study including a sample of 44 from northern Venezuela (localities listed in text). A complete analysis of this species will be presented later (Collins, in preparation).

(AMNH = American Museum of Natural History, New York; P. = Phelps Ornithological Collection, Caracas; R.G. = Estacion Biologica de Rancho Grande, Aragua; B.M. = British Museum, Tring.)

ACKNOWLEDGMENTS

This study of *Cypseloides rutilus* and *C. phelpsi,* part of a wider study of the biology of Neotropical swifts, has been generously supported by research awards for field studies in Trinidad and Venezuela and a post-doctoral fellowship from the Frank M. Chapman Memorial Fund of the American Museum of Natural History. Without this support this work would not have been possible. I am grateful to the curators of the many museum collections from which I borrowed specimens for this study, and patricularly the authorities of the Muséum National d'Histoire Naturelle for allowing me to examine Vieillot's type of *Hirundo rutila.* I am also most grateful to E. Eisenmann and R. K. Brooke for their most helpful comments which improved an earlier draft of this paper.

RESUMEN

Una revisión del vencejo de collar castaño, *Cypseloides rutilus,* ha indicado que el espécimen tipo (*Hirundo rutila* Vieillot, 1817) es de Trinidad, y que la población distintiva del área de Pantepui del sur de Venezuela, la vecina Guayana y Brasil, desde hace mucho asociada con este nombre, merece ser separada en categoría de especie. Aunque caracterizada hace cerca de 100 años, esta especie carece de nombre válido y *Cypseloides phelpsi* es propuesto aquí para el vencejo tepuiano.

LITERATURE CITED

BEEBE, W. 1949. The swifts of Rancho Grande, North-Central Venezuela, with special reference to migration. Zoologica 34: 53–62.

BRODKORB, P. 1938. New birds from the district of Soconusco, Chiapas. Oc. Papers. Mus. Zool., Univ. Mich. 369: 1–7.

BROOKE, R. K. 1970a. Zoogeography of Swifts. Ostrich, Supplement 8: 47–54.

————. 1970b. Taxonomic and evolutionary notes on the subfamilies, tribes, genera and subgenera of the swifts. Durban Mus. Novitates 9: 13–24.

————. 1971. Geographical variation in the Little Swift *Apus affinis* (Aves: Apodidae). Durban Mus. Novitates 9: 93–103.

COLLINS, C. T. 1967. Partial albinism in the Chestnut-collared Swift in Trinidad. Bull. Brit. Orn. Club 87: 122–123.

————. 1968. The comparative biology of two species of swifts in Trinidad, West Indies. Bull. Fla. St. Mus. 11: 257–320.

EISENMANN, E., AND F. C. LEHMANN V. 1962. A new species of swift of the genus *Cypseloides* from Colombia. Amer. Mus. Novitates 2117: 1–16.

GILLIARD, E. T. 1941. The birds of Mt. Auyan-tepui, Venezuela. Bull. Amer. Mus. Nat. Hist. 77: 439–508.

LACK, D. 1956. A review of the genera and nesting habits of swifts. Auk 73: 1–32.

LAFRESNAYE, M. DE 1844. Nouvelles especes d'oiseaux de Colombie. Revue Zoologique 1844: 80–??

LEOTAUD, A. 1866. Oiseaux de L'Île de la Trinidad. Chronicle Publishing Office, Port of Spain. 560 p.

LESSON, R. P. 1831. (type description of *Hirundo robini*) *Traité d'Ornithologie,* Paris.

MAYR, E., AND W. H. PHELPS, JR. 1967. The origin of the bird fauna of the south Venezuelan highlands. Bull. Am. Mus. Nat. Hist. 136: 269–328.

NELSON, E. W. 1900. Descriptions of thirty new North American birds in the Biological Survey collection. Auk 17: 253–270.

ORR, R. T. 1963. Comments on the classification of swifts of the subfamily Chaeturinae. Proc. XIII Internat. Ornith. Cong. 1: 126–134.

ORTON, J. 1871. Notes on some birds in the Museum of Vassar College. Amer. Nat. 4: 711–717.

PETERS, J. L. 1940. Check-list of Birds of the World. Vol. 4. Harvard Univ. Press, Cambridge.

PHELPS, W. H., AND W. H. PHELPS, JR. 1958. Lista de las aves de Venezuela con su distribucion. Tomo 2, Parte 1, No Passeriformes.

SALVIN, O. 1885. A list of the birds obtained by Mr. Henry Whitely in British Guiana. Ibis 3 (5th Ser.): 418–439.

SALVIN, O., AND F. D. GODMAN. 1882. Notes on birds from British Guiana. Ibis 6 (4th Ser.): 76–84.

SALVIN, O., AND P. L. SCLATER. 1860. Contributions to the ornithology of Guatemala. Ibis 2: 28–45.

SCLATER, P. L. 1855. On the birds received in collections from Santa Fe de Bogota. Proc. Zool. Soc. Lond. 1855: 131–166.

SNOW, D. W. 1962. Notes on the biology of some Trinidad swifts. Zoologica 47: 129–139.

VIEILLOT, L. J. P. 1817. Nouveau Dictionnaire D'Historie Naturelle, Vol. 14.

ZIMMER, J. T. 1953. Studies of Peruvian birds. No. 64. The Swifts: Family Apodidae. Am. Mus. Novitates 1609: 1–20.

Accepted for publication April 17, 1972

NUMBER 230
JUNE 23, 1972

HYPSOCEPHALUS ATLANTICUS, A NEW GENUS AND SPECIES OF LUTJANID FISH FROM MARINE EOCENE LIMESTONES OF NORTHERN FLORIDA

By CAMM SWIFT AND BROOKS ELLWOOD

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1964 AIBS Style Manual for Biological Journals is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1964 AIBS Style Manual for Biological Journals in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Changes in the manuscript after galley proof will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

HYPSOCEPHALUS ATLANTICUS, A NEW GENUS AND SPECIES OF LUTJANID FISH FROM MARINE EOCENE LIMESTONES OF NORTHERN FLORIDA[1]

By CAMM SWIFT[2] AND BROOKS ELLWOOD[3]

ABSTRACT: A single neurocranium (and a few other bone fragments) representing an undescribed genus and species of hoplopagrine lutjanid was discovered in solution caverns in Eocene limestones in Jackson County, Florida. It is quite distinct from the only living member of this subfamily, *Hoplopagrus guntheri*, known from southern Baja California to Panama in the eastern Pacific Ocean. The Hoplopagrinae are distinct from other lutjanids in possessing: 1) strong, blunt, conical teeth on the premaxillary, dentary, vomer and palatine; 2) a largely vertical posterior face on the basioccipital; 3) exoccipital condylar surfaces which fail to meet in the midline; 4) relatively small otic capsules; and 5) a strong, globular, ventral swelling near the posterior end of the parasphenoid, apparently serving as a brace for the upper pharyngeals.

In Eocene times when the sea was deeper and warmer, the hoplopagrine lutjanids were present near the northern Gulf of Mexico of today. For some reason the group disappeared on the Atlantic side but persisted in the eastern Pacific Ocean. This subfamily is not known outside the New World.

The snappers, family Lutjanidae, are common, worldwide fishes in tropical and subtropical marine shore waters. A few species enter estuaries, and several others are little known species occurring about hard substrate in deep water. Despite this recent abundance, snappers are scarce in the fossil record, and only two records could be found for fossil snappers in North America (Gregory, 1930; Jordan and Gilbert, 1919). Elsewhere in the world three genera (*Caesio, Lednevia, Lutjanus*) have been recorded from Eocene and Miocene deposits of Europe, and *Lutjanus* has been noted from the Miocene of Australia (Romer, 1966). Summary works on fossil fishes by Smith-Woodward (1901), Casier (1966), Danil'chenko (1967), and Lehman (1966) mention no lutjanid genera. Six other doubtful fossil records for the family are based on otoliths (Weiler, 1968), five from the London Clay and one of *Lutjanus* from Borneo.

[1] EDITORIAL COMMITTEE FOR THIS CONTRIBUTION
William A. Gosline
Robert J. Lavenberg
Stanley H. Weitzman

[2] Associate Curator of Fishes, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

[3] Graduate School of Oceanography, University of Rhode Island, Kingston, Rhode Island 02881.

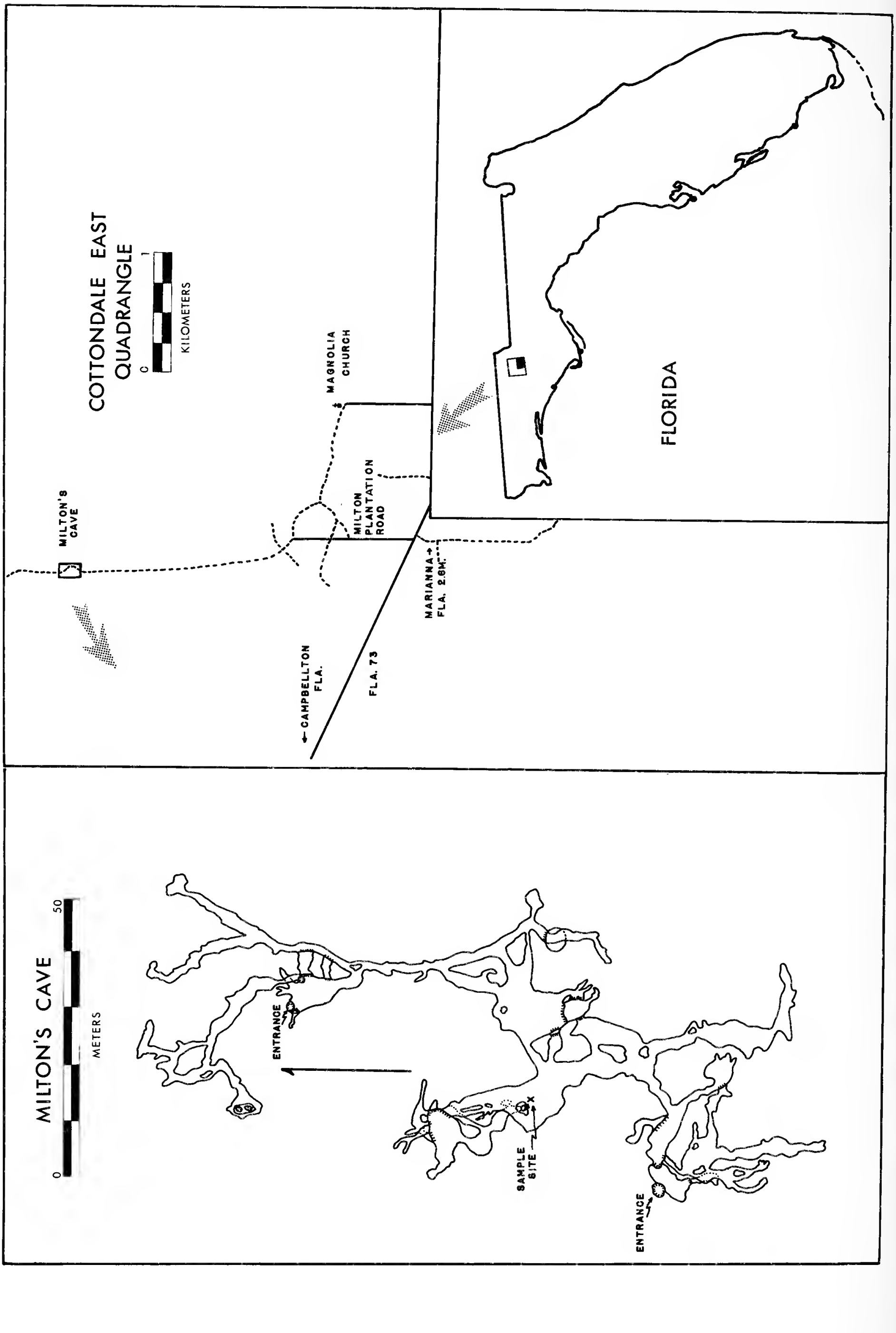


FIGURE 1. Map showing the type locality of *Hyssocephalus atlanticus*

The lutjanid fossils known from North America come from the Miocene of California, *Lutianus hagari* Jordan and Gilbert, 1919, and the Oligocene of Florida, *Lutjanus avus* Gregory, 1930. The first known fossil of a hoplopagrine snapper (described below) comes from within a few miles of the site of collection of *Lutjanus avus* in northwest Florida (Figure 1). The Hoplopagrinae are otherwise known only by the sole living species, *Hoplopagrus guntheri Gill* (1862a) which ranges from Abreojos (UCLA S-392) and Magdelena (LACM 32086-3) Bays on the west coast of Baja California and Guaymas (CAS IU 7749) in the Gulf of California south to Panama (Walford, 1937). It occurs about reefs from shore to "deep, cold water near the Pearl Islands" (Walford, 1937) in the Gulf of Panama.

Previous authors have compared the hoplopagrines with other lutjanids and with the sparids when searching for the affinities of the subfamily (Gill, 1862a, 1862b; Jordan and Evermann, 1898; Regan, 1913). All agree that the hoplopagrines resemble lutjanids more than sparids, and this seems to be true based on our comparison of the skeletons of most of the North American genera of both families. The new fossil has been compared primarily with North American lutjanids, but osteological resemblances to sparids and pomadasyids have been recorded. References to characters of those families are based on examination of materials listed below. Several old world genera of both families have not been examined, and this should be considered in assessing the comparisons.

MATERIALS AND METHODS

The comparison below of the fossil with recent species of lutjanids, pomadasyids and sparids are based on the following specimens. Neurocranium length was measured from the anterior end of the vomer to the posterior end of the basioccipital. Abbreviations are: California Academy of Sciences (CAS), University of California at Los Angeles (UCLA), and Natural History Museum of Los Angeles County (LACM).

Lutjanidae

Hoplopagrus guntheri Gill: CAS 14158, 460 mm SL, Mexico, Cerralvo Is., 4 March 1945; LACM-VP-F422, Mexico, Gulf of California, Cabo Lobos, 14 Feb. 1970, S. P. Applegate; UCLA S-392, about 410 mm SL, Mexico, Baja California, Abreojos Bay, May, 1954; LACM 31774-1, 208 mm SL, Mexico, Gulf of California, Baja California, just S Pta. Arena, R/V Searcher Sta. 44, 2 Feb. 1971.

Lutjanus apodus (Walbaum): LACM 31732-1, SL unknown (neurocranium 48.9 mm long), Bahamas, San Salvador Island, Graham Harbor, 10 June 1966, E. S. Wing.

Lutjanus campechanus (Poey): LACM 31737-1, 523 mm SL, Florida, Gulf of Mexico, Middle Grounds, Sept. 1969, P. McCaffrey.

Lutjanus griseus (Linnaeus): LACM 31735-1, 393 mm SL, Florida, Monroe Co., Tortugas, 17 or 18 Dec. 1968, C. Combs, H. Austin, H. Mattraw;

LACM 31852-1, 460 mm SL, Broward Co., off Hollywood Beach, 18 March 1969, H. Yaffa; LACM 31736-1, 215 mm SL, Florida, Okaloosa Co., mouth Choctawhatchee Bay, 12 Oct. 1968, R. Hastings.

Lutjanus synagris (Linnaeus): LACM 31731-1, ca. 335 mm SL, Florida, Volusia Co., vic. Daytona Beach, summer 1966, M. Gomon.

Ocyurus chrysurus (Bloch): LACM 31853-1, 461 mm SL, Florida, Gulf of Mexico, Middle Grounds. 28° 25′ N, 84° 18′ W, 10 Nov. 1969, J. Bishop, H. Austin; LACM 31734-1, 245 mm SL, Panama, Atlantic Ocean, San Blas, Holandes Cay, 27 Sept. 1970, J. E. McCosker.

Pristipomoides aquilonaris (Goode and Bean): LACM 31730-1, ca. 110 mm SL, Oregon Station 10892, Gulf of Mexico.

Rhomboplites aurorubens (Cuvier): LACM 31738-1, 190 mm SL, Florida, Okaloosa Co., vic. Destin, 2 April 1966, C. Swift; LACM 31733-2, 219 mm SL, and LACM 31733-1, 165 mm SL, Gulf of Mexico, 23 mi SSE of Pensacola, 29 June 1969, S. Bortone.

Pomadasyidae

Anisotremus davidsoni (Steindachner): LACM 32587-1, 319 mm SL, California, Orange Co., Huntington Beach, 8 Aug. 1970, C. Swift, et al.; LACM 32588-1, 298 mm SL, California, Orange Co., Huntington Beach, 5 July 1970, J. Fitch.

Brachydeutereus corvinaeformis Steidachner: LACM 32585-1, neurocranium 38 mm long, Panama, Atlantic, Bahia Limon, 1970, J. E. McCosker.

Haemulon aurolineatum Cuvier: LACM 32584-2, 129 mm SL, Florida, Franklin Co., 15 mi S Alligator Harbor, 10 May 1969, S. Bortone; LACM 31849-6, 151 mm SL, Florida, Gulf of Mexico, Middle Grounds, 12, 13 June 1969, C. Swift and party.

Haemulon plumieri (Lacepede): LACM 32584-1, neurocranium 72 mm long, Florida, Franklin Co., ca. 15 mi S Alligator Harbor, 10 May 1969, S. Bortone; LACM 31849-5, 383 mm SL, Florida, Gulf of Mexico, Middle Grounds, 12, 13 June 1969, C. Swift and party.

Haemulon sciurus (Shaw): LACM 32586-1, neurocranium 52 mm long, Florida, Monroe Co., Vaca Key, June, 1964, K. Ainslie and party.

Orthopristis chrysoptera (Linnaeus): LACM 31848-3, 177 mm SL, LACM 31848-4, 170 mm SL, Florida, Franklin Co., mouth Alligator Harbor, 4 July 1968, C. Swift and party; LACM 32583-1, 188 mm SL, LACM 32583-2, 179 mm SL, Florida, Franklin Co., St. George Island, 11 June 1968, F. W. Vockell.

Sparidae (all from Florida)

Archosargus probatocephalus (Walbaum): LACM 31591-3, 270 mm SL, Okaloosa Co., mouth Choctawhatchee Bay, 11 Sept. 1969, C. Swift and party; LACM 31850-1, SL unknown (neurocranium 32.9 mm long), Santa Rosa Co., Santa Rosa Sound at Gulf Breeze, 15 July 1966, R. W. Hastings.

Calamus nodosus Randall and Caldwell: LACM 31849-2, 242 mm SL, Gulf of Mexico, Middle Grounds, 28° 30′ N, 84° 15′ W, 12, 13 June 1969, C. Swift and party.

Calamus arctifrons Goode and Bean: LACM 31537-36, 137 mm SL, and LACM 31537-38, 159 mm SL, Wakulla Co., 5.5 mi WSW St. Marks Light, 6 Sept. 1969, C. Swift and party.

Diplodus holbrooki (Bean): LACM 31848-2, 123 mm SL, Franklin Co., mouth Alligator Harbor, 4 July 1968, C. Swift and party; LACM 31851-1, 159 mm SL, Franklin Co., off mouth Ochlockonee River, 4 Oct. 1969, J. Wiese, R. Lazor.

Lagodon rhomboides (Linnaeus): LACM 31845-1, 143 mm SL, Bay Co., St. Andrews Bay, 14 Oct. 1967, C. Swift and party, LACM 31848-1, 151 mm SL, Franklin Co., mouth Alligator Harbor, 4 July 1968, C. Swift and party.

Pagrus sedecim Ginsburg: LACM 31738-2, head only (neurocranium 51.8 mm long), Okaloosa Co. ca. 15 mi S Destin, 2 April 1966, R. W. Yerger and class; LACM 31849-1, 292 mm SL, Gulf of Mexico, Middle Grounds, 28° 30′ N, 84° 15′ W, 12, 13 June 1969, C. Swift and party.

Anatomical Abbreviations

The following abbreviations are used in figures 2 to 5:

bo	basioccipital	para	parasphenoid
bs	basisphenoid	pro	prootic
epo	epiotic	pto	pterotic
exo	exoccipital	seth	supraethmoid
fr	frontal	soc	supraoccipital
int	intercalar	spho	sphenotic
leth	lateral ethmoid	vo	vomer
pa	parietal		

Hypsocephalus, new genus

Diagnosis: A hoplopagrine lutjanid distinguished from the living and only other known genus of the subfamily, *Hoplopagrus*, by: 1) a skull which is high and deep rather than elongate; 2) supra- and lateral temporal fossae shallow and flattened rather than deeply excavated; 3) a supraoccipital crest extending anterior to a vertical through the center of the bony orbit rather than forward beyond the anterior edge of this orbit; 4) the globular swelling at the posterior end of the parasphenoid excavated posteriorly rather than a solid protuberance; 5) vomerine teeth in a roundish patch rather than a transverse band; 6) molariform palatine teeth present rather than lacking altogether; 7) two rather than one row of teeth for most of the length of the dentary; 8) three rather than two rows of teeth for most of the length of the premaxillary; and 9) a deeply excavated cavity in the basioccipital broadly confluent with the myodome rather than only narrowly excavated and slightly confluent. Type species *Hypsocephalus atlanticus*. The name *Hypsocephalus* (υψos, high or elevated, + cephalus, head) refers to the high, deep skull and the specific name *atlanticus* refers to the Atlantic Ocean, the general locality of the fossil, in contrast to the eastern Pacific Ocean, the area where the only living relative, *Hoplopagrus*, occurs.

Hypsocephalus atlanticus, new species

Figures 2-7

Holotype: LACM VP 27859, a single neurocranium, 49.4 mm long, with the right posterolateral side broken off, thus the epiotic, exoccipital, pterotic, and intercalar are absent from this side (see below). Other bones found in definite association with, and certainly part of, this one fish are: a left cleithrum about three-fourths complete, the middle half of the right cleithrum, a fragmentary anterior one-third of the right maxillary, the middle two-thirds of the right premaxillary, the anterior one-fifth of the left premaxillary, the middle three-fourths of the right dentary, a small fragment of the anterodorsal edge of the left dentary, the anterior half of the right articular, the distal two-thirds and the anterior and proximal one-fourth of the right hyomandibular, impressions of three anterior premaxillary teeth, about half of the right exoccipital with the articular facet for the atlas vertebrae intact, one complete neural arch and spine with the dorsal one-fifth of an anterior abdominal vertebrae attached, several fragmentary branchiostegal rays imbedded in a small piece of limestone, one dorsal spine pterygiophore, and the posterolateral corner of the skull also imbedded in a limestone block.

Locality: LAV Loc. 7189 Florida, Jackson Co., T: 5N, R: 11W, Sec. 13, 2.7 airline miles NW of Marianna (Figure 1), collected by Brooks and Suzanne Ellwood and Edward M. Renner on 2 April 1970. The skull was taken from Milton's Cave (Figure 1) in the lower member of the Crystal River formation, the uppermost Eocene formation in this north Florida area. The locality is a small, intricate cave, and the skull and associated bones were found in a solution cavity of the cave 13.2 ± 0.5 meters below the surface of the ground.

Diagnosis: As for the genus.

DESCRIPTION

Vomer: The ventral surface of the vomer is roughly circular and covered with stout bluntly pointed teeth (Figure 4). The anteriormost tooth is longest and largest in diameter. It is flanked posterolaterally on each side by a tooth slightly smaller in diameter, and about half as high. Posterior to these three, and partially between the posterior two, is a cluster of six small teeth. A seventh small tooth was present as evidenced by a small empty socket just posterior to the lateral robust tooth on the right side. Ventrally a low, rounded keel on the vomer is continuous with that on the parasphenoid. Laterally a low rounded ridge extends posterodorsally to, and is continuous with, that of the lateral ethmoid. The vomer bears a broadly rounded bridge middorsally as well, and with the ventral and lateral ones, the vomer is diamond shaped in cross section just above the tooth patch. Posterodorsally the dorsal ridge bifurcates narrowly around the narrow rostral fenestra (of Starks, 1926) to meet the supraethmoid.

Comparison: In *Hoplopagrus* the vomerine tooth patch is narrow anteroposteriorly and wider laterally; an anterior transverse row of three or four stout, almost molariform teeth is followed by a row of four to six much smaller teeth similarly proportioned. All the living snapper genera known have villiform vomerine teeth (when they are present), and the vomerine tooth patch assumes a variety of shapes (Gill, 1884; Regan, 1913; Norman, 1966; Anderson, 1967).

Parasphenoid: The anterior half of the parasphenoid bears a wide, thin ventral keel, which is least developed anteriorly at the vomer-parasphenoid articulation (Figure 2). The keel extends further ventrally to the posterior and abruptly ends in 90° angle ventral to the ascending parasphenoid processes articulating with the prootics. Just posterior to the keel, the parasphenoid expands into a globular swelling that is concave posteriorly, and the parasphenoid continues posteriorly as a narrow, dorsoventrally flattened flange ventral to, and articulating dorsally with the basioccipital.

Comparison: The parasphenoid of *Hoplopagrus* is similar to *Hypsocephalus* except that the swollen brace for the upper pharynageals is not as strongly developed. The parasphenoid of *Lutjanus* lacks this swelling, is relatively longer, and is keeled ventrally. In *Ocyurus* a strong, rounded ridge extends laterally and posterodorsally from the posterior end of the parasphenoid along the ventral and anterolateral edge of each otic bulla. In *Ocyurus* the keel on the parasphenoid is very low. In all of the above except *Ocyurus* the parasphenoid is straight, and the ventral edges of the vomerine tooth patch, of the parasphenoid keel, and of the basioccipital lie along a straight line. The ventral surface of the anterior half of the parasphenoid is slightly concave in *Pristipomoides* and *Rhomboplites.* In *Rhomboplites, Pristipomoides,* and *Ocyurus* the longitudinal profile of the parasphenoid is a shallow V. The ventralmost point is at the posterior end of the keel, just ventral to the ascending processes.

Lateral Ethmoid: The lateral ethmoid is essentially rectangular anteroposteriorly. The ventral edge broadly articulates with the parasphenoid, and its anteroventral and posteroventral angles bear short robust pillars which articulate with the palatine. The posterior pillar is shorter and its flat, longitudinally oval facet faces ventrally. The flat oval surface of the anterior pillar faces about equally anteriorly, laterally, and dorsally. The anterior pillar lies on a ridge extending from the lateral corner of the vomer, through the facet, and posterodorsally to the posteromedial portion of the lateral ethmoid where it converges with a thick vertical ridge on the posterior edge of the lateral ethmoid. This vertical ridge narrows ventrally, terminating in the posterior facet. Dorsally it thickens, extends laterally, and its cancellous dorsal surface articulates with the lateral edge of the frontal. A space separates the two lateral ethmoids medially just under the frontals. The lateral ethmoids meet along the middle one-fourth of the vertical distance between the frontals and the parasphenoid. Ventral to this midline contact the lateral ethmoids are separated narrowly to their ventral articulation with the parasphenoid. Ventral to and slightly lateral to the anterior opening of the supraorbital lateral line canal in the frontal, the olfactory canal courses anteriorly from

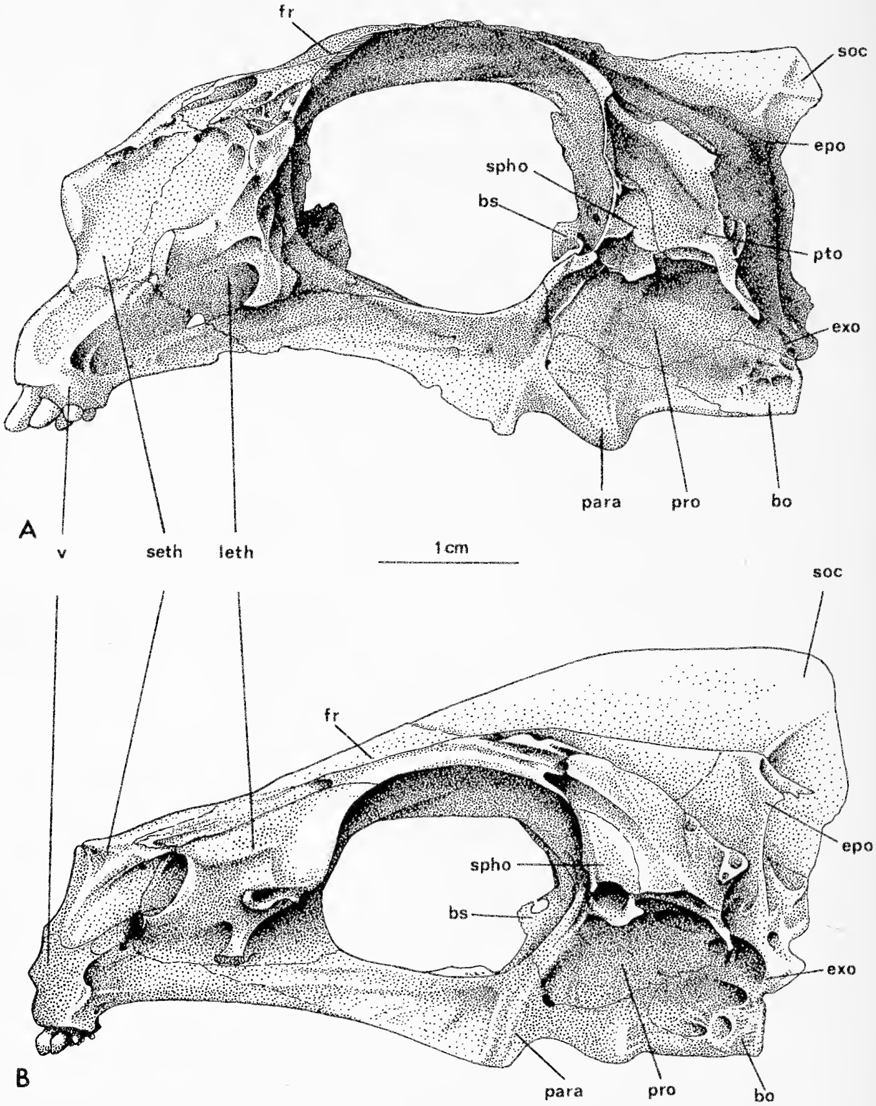


FIGURE 2. Lateral view of the neurocrania. A, *Hypsocephalus atlanticus* (LACMVP 27859); B, *Hoplopagrus guntheri* (LACM 31774-1).

the orbital cavity through the lateral ethmoid. This canal is a vertical oval in cross section, 3 mm high and 1 mm wide.

Comparison: The two facets for articulation with the palatine are similar to *Hypsocephalus* in *Hoplopagrus*, but in the latter both face slightly more laterally. In *Ocyurus* and *Lutjanus* the anterior facet faces anteroventrally and slightly laterally, and the posterior one faces ventrally and slightly anteriorly. The facets are at the ends of ridgelike struts of bone in the above genera. *Rhomboplites* and *Pristipomoides* bear these two facets in the same orientation as in *Hypsocephalus*, but they are only slightly raised from the lateral bone surface. The third facet which receives the medial side of the lachrimal lies slightly more dorsal than the anterior palatine facet and is dorsal, lateral and slightly posterior to the posterior palatine facet in *Hypsocephalus, Hoplopagrus, Ocyurus*, and *Lutjanus*. In *Rhomboplites* and *Pristipomoides* the lachrimal facet is on the same level as the anterior palatine facet, and is above and lateral to the posterior one. *Hoplopagrus* shares with *Hypsocephalus* the strongly developed dorsal and dorsolateral portion of the lateral ethmoids. In *Lutjanus, Ocyurus,* and *Pristipomoides,* this surface faces laterally and slightly anteriorly, meeting about perpendicularly with the lateral edge of the frontals. In *Rhomboplites* the lateral ethmoid faces more dorsally than in *Lutjanus* and *Ocyurus,* but still meets the frontal with an abrupt angle rather than through a continus surface as in the hoplopagrines. The olfactory nerve foramen is large in *Hoplopagrus* (which has an exceptionally large nasal capsule) and about the same relative size as in *Hypsocephalus* in the remaining recent genera.

Supraethmoid: The dorsal surface of the supraethmoid is shaped like a posteriorly directed arrowhead, its posterolateral surfaces bounded by the frontals (Figure 3). The supraethmoid is widest just anterior to the frontals; immediately anterior to this widest point it narrows in width by about one-third. Here the anterolateral transverse edges each bear a short pointed process. A thick median ridge extends anteriorly a short distance and then bends perpendicularly and continues ventrally. The ridge narrows ventrally and the anterior edge flattens out anteroventrally around the rostral fenestra. This thick anterodorsal ridge of the supraethmoid narrows slightly posteroventrally before the lateral surfaces of the bone flare laterally to meet the lateral ethmoids.

Comparison: The dorsal surface of the supraethmoid is similar to *Hypsocephalus* in *Pristipomoides* and is reduced to a small square in *Rhomboplites* and *Ocyurus.* In *Hoplopagrus* it is oblong, gently rounded anteriorly and directed posteriorly between the frontals. It is long and slender in *Lutjanus*, where it is widest between the anterior tips of the frontals and gradually narrows posteriorly. In the recent genera the anterior end of the dorsal surface of the supraethmoid meets at right angles with the vertical, mid-longitudinal ridge of the anterior surface which slopes ventrally and anteriorly. The rostral fenestra is large in *Hoplopagrus* and *Pristipomoides* (as in *Hyposocephalus*), small in *Ocyurus* and *L. synagris*, and absent in *Rhomboplites, L. campechanus*, and *L. griseus*. In *Hoplopagrus* a low ridge is present parallel and lateral to the median ridge. It is absent in *Hypsocephalus* and is absent or only present as a slight suggestion of a raised area in the other recent genera.

Frontal: The frontals are thin and dip medially to produce a shallowly concave interorbital region. The articulation between them extends posteriorly and slightly dorsally from the posterior apex of the supraethmoid to a vertical through the middle of the bony orbit and the beginning of the supraoccipital crest. Each frontal continues posteriorly and laterally of the supraoccipital crest to a vertical between the two facets for articulation of the hyomandibular. Anteriorly, laterally, and ventrally the frontals firmly articulate with the lateral ethmoids, and continue posteriorly to rim the orbit. Along the posterodorsal edge of each orbit they meet the sphenotics, the articulation itself continues

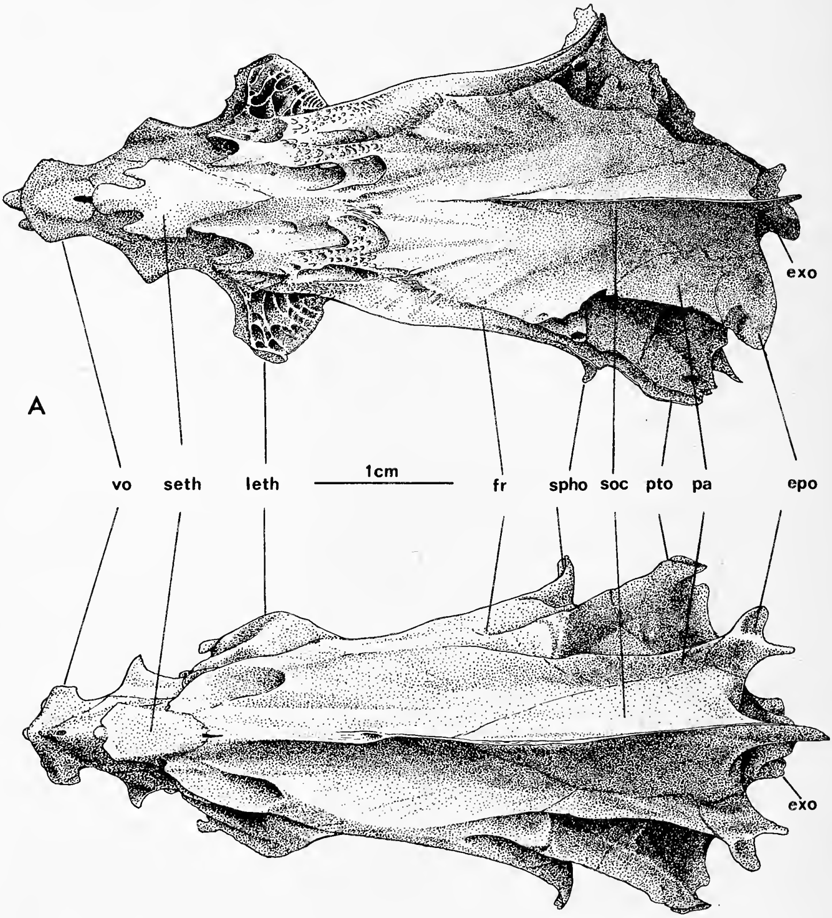


FIGURE 3. Dorsal view of the neurocrania. A, *Hypsocephalus atlanticus* (LACMVP 27859); B, *Hoplopagrus guntheri* (LACM 31774-1).

medially and posteromedially of the dorsal edge of the orbit as a shelf forming the anterolateral edge of the supratemporal fossae. This shelf continues posteriorly and laterally on the pterotic bone.

Comparison: In all the recent lutjanid genera examined except *Pristipomoides* the frontals contribute to the anterior portion of the supraoccipital crest, slightly in *Rhomboplites* and considerably in the remaining genera. In *Pristipomoides* and *Lutjanus apodus* the crest extends anterior to reach the posterior third of the orbit. In *Rhomboplites* and *Lutjanus griseus* the crest reaches only to a vertical line through the anterior third of the orbit diameter. The longitudinal ridge which extends ventrally to meet the pterosphenoid from the medial portion of each frontal is short in *Rhomboplites* and *Ocyurus.* This ridge extends more ventrally in *Hoplopagrus* and *Lutjanus* to form about the dorsal third of the wall separating the braincase from the orbit. The anterior supraorbital canal foramen in the frontal opens over the anterior third of the orbit in *Rhomboplites* and *Lutjanus griseus,* dorsal and slightly medial to the anterior edge of the orbit in *L. synagris* and *L. apodus,* and slightly anterior to the front edge of the orbit in *Pristipomoides, Ocyurus, Hoplopagrus,* and *Hypsocephaus.*

Parietal: Each parietal is largely a flat shelf which extends laterally and slightly dorsally from near the posterodorsal margin of the orbit to the epiotic posteriorly. The shelf forms the ventral and lateral surface of the shallow supratemporal fossa. From the lateral edge of this shelf, the parietal extends ventrally toward the pterotic about as far as it does medially toward the supraoccipital. The vertical, laterally facing portion forms (with the frontal anteriorly and the epiotic posteriorly) the medial boundary of the lateral temporal fossa. This ridge diverges laterally toward the posterior region of the skull. Dorsally the parietal bears a shallow longitudinal trough.

Comparison: Only the parietal of *Rhomboplites* resembles that of *Hypsocephalus,* largely covering the floor of the supratemporal fossae and extending laterally and slightly dorsally into the low ridges extending from the epiotics to the frontals. In *Hoplopagrus, Ocyurus,* and *Lutjanus* these ridges resemble each other and are oriented vertically and slightly laterally. In *Pristipomoides* this ridge is largely restricted to the parietal bone, with a slight contribution from the frontals anteriorly and no involvement of the epiotics posteriorly. The ridges are parallel to the supraoccipital crest in *Rhomboplites, Ocyurus, Lutjanus griseus, L. synagris,* and *L. campechanus.* They diverge slightly laterally to the posterior in *Hoplopagrus, Pristipomoides,* and *L. apodus.*

Epiotic: The dorsal surface of the epiotics inclines slightly posteriorly and slightly laterally. The lateral half of the dorsal surface is shallowly excavated for articulation with the dorsal limb of the posttemporal. The medial half of the dorsal surface is slightly depressed, and there is no trace of a posteriorly directed spine. The epiotic articulates ventrally with the exoccipital via a strong columnar strut directed ventrally and slightly medially and posteriorly. This strut along with that of the exoccipital, forms the posterolateral corner of the temporal region.

Comparison: Just ventromedial to the epiotic facet for receiving the upper limb of the posttemporal, *Hoplopagrus, Ocyurus, Rhomboplites,* and *Lutjanus* bear a posteriorly directed process. This spine is lacking in *Hypsocephalus* and *Pristipomoides.* The facet for the posttemporal faces posteriorly and dorsolaterally in *Ocyurus, Hoplopagrus,* and *Lutjanus* and almost directly dorsally in *Rhomboplites* and *Pristipomoides.*

Prootic: The prootic is gently inflated laterally and dorsally to accommodate the anterior end of the otolith. Posteriorly the prootic articulates with the basioccipital below and the exoccipital above. It joins broadly with the parasphenoid ventrally. A narrow portion directed dorsally and slightly laterally occupies the ventral half of the anterior hyomandibular facet and articulates with the sphenotic dorsally. A short shelf extends laterally from and borders the posteroventral aspect of this facet. Medially the prootics meet as a flat shelf forming the floor of the anterior one-third of the braincase and abut against the basisphenoid anteriorly. Each posterior and vertical edge of this shelf extends anterolaterally from the anterior end of a thin medial process of the basioccipital to form the anteromedial wall of the chamber for the saccular otolith. Anteriorly and dorsally the prootic forms a transverse squarish plate articulating with the basisphenoid ventromedially, the pterosphenoid dorsomedially, and the sphenotic dorsally. Just dorsolateral to the tripartite juncture with the basisphenoid and pterosphenoid the prootic bears a large foramen. The pars jugularis, with its two large foramina, is overlain by a narrow arch which extends ventrally, anteriorly, and medially from the anteroventral corner of the anterior hyomandibular facet, and broadly inserts on the anterolateral edge of the prootic. The shelf bordering the posteroventral edge of the anterior hyomandibular facet bears a thin blade which extends ventrally parallel and posterolateral to this arch. This blade terminates in a free end about half way along the arch. The prootic bears another free ending blade which originates on the medial side of the anterolateral edge of the prootic. It extends dorsally, parallel, and anteromedial to this arch.

Comparison: The arch over the pars jugularis consists of a single pillar of bone in *Rhomboplites, Pristipomoides, Ocyurus,* and *Lutjanus.* In *Hoplopagrus* the two incomplete arches parallel to the main one (as in *Hypsocephalus*) are present but not as extensively developed. In *Hoplopagrus* the pars jugularis is partly bridged over anteriorly by three narrow flat shelves of bone: a ventrolateral projection of the pterosphenoid, a ventromedial extension of the sphenotic and a medial extension from the prootic where it abuts the pterotic anterior to the hyomandibular facet. This arrangement is only present in large *Hoplopagrus.* The posteroventral portion of the prootic is inflated to accommodate the large otolith in *Rhomboplites, Ocyurus, Pristipomoides, Lutjanus synagris,* and *L. campechanus.* In *L. griseus* and *L. apodus* it is only slightly expanded, but more so than in *Hoplopagrus* which has a small otolith, as apparently did *Hypsocephalus.*

Sphenotic: The sphenotic is a flat bone which occupies the middle one-third of the posterior face of the orbit and the dorsal one-half of the anterior hyomandibular facet (Figure 2). The large eye and foreshortened skull leave the sphenotic (and pterotic) with greatest dimensions in a vertical rather than longitudinal direction. The sphenotic articulates with the pterotic posteriorly via a suture proceeding vertically and then anteriorly from the posterior margin of the anterior hyomandibular facet. The sphenotic articulates with the prootic ventrally via the anterior hyomandibular facet and via an articulation extending medially from this facet to the articulation with the pterosphenoid. Dorsally the sphenotic articulates with the frontal.

Comparison: In *Lutjanus griseus, L. campechanus, Ocyurus,* and *Rhomboplites* the sphenotic lies more dorsal and more anterior in the posterodorsal quarter of the orbit. In *Lutjanus synagris, L. apodus, Pristipomoides,* and *Hoplopagrus* it is placed only slightly more dorsal than in *Hypsocephalus.* In all of the recent lutjanid genera examined the sphenotic bears a laterally directed spine which originates on the posterior surface at the anterodorsal corner of the anterior hyomandibular facet. This region is broken on both sides in *Hypsocephalus.*

Pterotic: Like the sphenotic, the pterotic is oriented largely vertically. Its dorsal two-thirds directly posterior to the sphenotic, and the ventral one-third is posterior to as well as slightly ventral to the anterior hyomandibular facet. The pterotic bears the entire posterior hyomanidbular facet. This facet is horizontally elongate, and slightly wider posteriorly. It lies directly posterior to the anterior facet, from which it is slightly separated. The short pointed process of the pterotic just below and lateral to the articular surface for the ventral limb of the posttemporal (on the intercalar) is directed ventrally and only slightly laterally and posteriorly. Just ventral and medial to the posterior hyomandibular facet, a shelf of the pterotic extends medially and slightly ventrally to articulate with the intercalar and exoccipital posteriorly, and the prootic anteriorly. The pterotic occupies the posterolateral edge of the skull and has a ridge which bears the temporal lateral line canal. From this ridge the pterotic dips ventromedially to meet (anterior to posterior) the frontal, parietal, epiotic, and exoccipital, and forms the lateral border and floor of the lateral temporal fossa.

Comparison: The pterotic in *Rhomboplites, Ocyurus, Pristipomoides,* and *Lutjanus* extends almost directly posterior from the dorsal half of the orbit. In these genera the process on the posterior lateral border of pterotic extends largely posteriorly and only slightly laterally and ventrally. In *Hoplopagrus* this spine projects much more ventrally as it does in *Hypsocephalus,* and the pterotic is posterior to the middle half of the orbit in both of these genera as well.

Intercalar: The intercalar is flat and occupies an almost horizontal, ventrally facing surface (Figure 4). It is narrowly pointed laterally just ventral and posterior to the posterolateral spine of the pterotic. The intercalar rapidly widens medially and slightly ventrally to articulate broadly with the prootic anteriorly and exoccipital posteriorly. This articulation lies just dorsolateral to a shallow longitudinal groove marking the dorsal edge of the otic bulla. The transversely oval, concave facet which receives the lower limb of the postemporal faces directly posterior and about three-fourths of the facet lies above the spine of the pterotic just lateral to the facet.

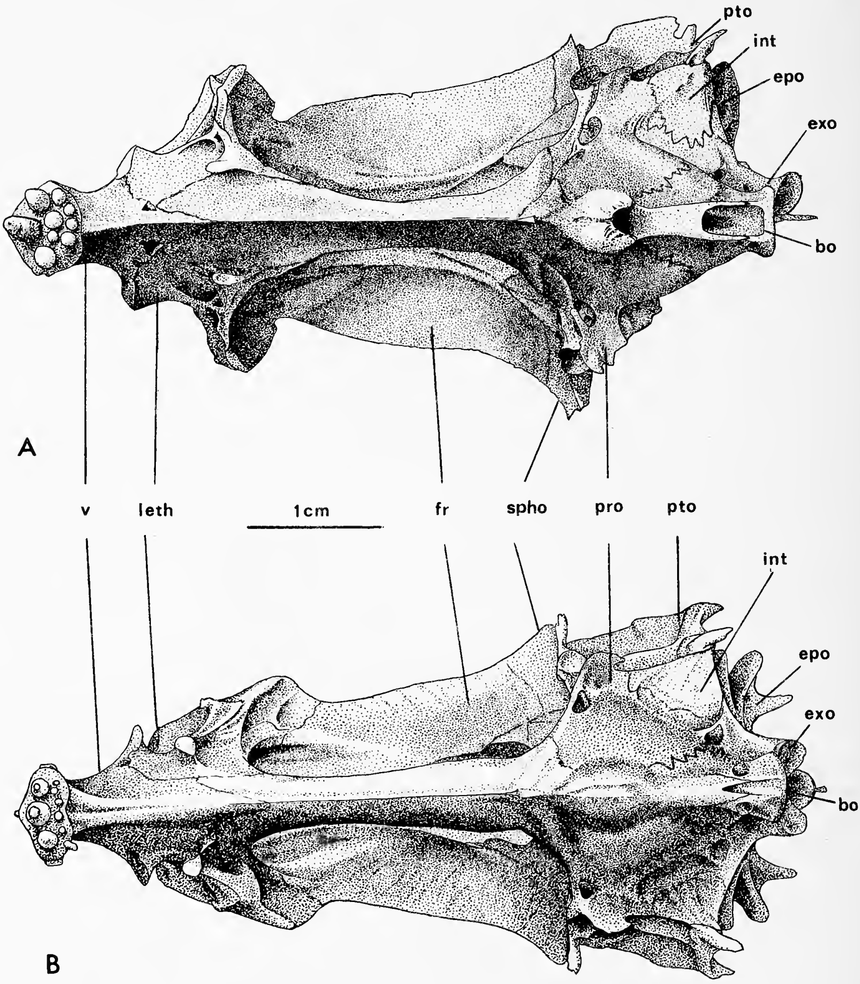


FIGURE 4. Ventral view of the neurocrania. A, *Hypsocephalus atlanticus* (LACMVP 27859); B, *Hoplopagrus guntheri* (LACM 31774-1).

Comparison: The intercalar is roughly trapezoidal in *Lutjanus, Ocyurus,* and *Rhomboplites,* the anterior and posterior edges roughly parallelling each other, and the medial and lateral ones converging anteriorly. The intercalar is quite similar in orientation and shape in *Hypsocephalus* and *Hoplopagrus.* The facet for reception of the postemporal lies entirely above the lateral pterotic process in *Hoplopagrus.* In the other genera examined the facet lies directly medial to the process, and the facet is directed laterally as well as posteriorly rather than just to the posterior. The facet is immediately medial to the process of the pterotic in *Lutjanus, Hoplopagrus,* and *Hypsocephalus,* but is separated by a short, thin, horizontal ridge in *Rhomboplites* and *Ocyurus.* In *Pristipomoides* the facet is posterior as well as medial to, and widely separated from the pterotic process.

Basisphenoid: Only the dorsal half of the basisphenoid is present, assuming the ventral, basal portion was originally possessed. A thin, compressed piece of this basal limb extends anteroventrally. Posterodorsally it is narrowly confluent with the two, dorsolaterally extending wings. From this attachment these two wings spread a short distance, transversely and fanlike, to form a small part of the central anteroventral wall of the braincase. They articulate broadly with the pterosphenoids laterally. Just posterior to the basisphenoid is the large hypophyseal foramen which the ventral and posteroventral tips of each fan virtually encircle before articulating with the two prootics posteriorly. The dorsal tips of the basisphenoid rise only slightly to articulate with the pterosphenoids, and form the ventral border of a large, vertically elongate opening which extends dorsally to the underside of the frontals and lies between the brain and orbital region.

Comparison: The dorsal edge of the basisphenoid in *Hoplopagrus,* as in *Hypsocephalus,* curves dorsally only slightly towards the pterosphenoids. In *Lutjanus, Ocyurus, Pristipomoides,* and *Rhomboplites* the dorsolateral edges of the basisphenoid curve dorsally, entering the ventrolateral as well as the ventral edge of the cavity connecting brain and orbit. The hypophyseal foramen is larger (*Lutjanus apodus*), about the same size (*Pristipomoides, Rhomboplites*), or smaller (*Ocyurus, Hoplopagrus, Lutjanus synagris, L. campecharus, L. griseus*) than in *Hypsocephalus.* The foramen is rounded in *Hypsocephalus* and *Hoplopagrus,* and is transversely oval in the other snapper genera.

A slight projection extends anterodorsally into the orbit from the basal portion of the basisphenoid in *Hoplopagrus.* There is no such projection on the basal portion in *Rhomboplites* and *Pristipomoides,* but a broad flat projection is present in *Lutjanus* and *Ocyurus.*

Pterosphenoid: The two pterosphenoids form much of the anterior wall of the braincase and, much of the lateral border of the large foramen connecting the braincase with the orbital region. About the middle of the medial margin of each bears a short, medially directed point of bone. On the left side a small foramen occurs ventral and slightly lateral to this projection, and another foramen is present dorsolaterally about half way between the tip of the projection and the surface of articulation with the frontal. On the right side the corresponding ventrolateral foramen is lacking, and in the position of the dorsolateral one are two smaller foramina. The pterosphenoid articulates, in a broad arc laterally (dorsal to ventral) with the frontal, sphenotic, prootic, and basisphenoid, respectively.

Comparison: In *Lutjanus, Rhomboplites,* and *Ocyurus* the pterosphenoid occupies about the same relative position as in *Hypsocephalus,* and bears slight (*Lutjanus, Rhomboplites*) to prominent, narrowly pointed medial projections (*Ocyurus*). The pterosphenoids are straight edged medially in *Hoplopagrus,* and lack any medial projections. The pterosphenoids are less extensive in *Hoplopagrus,* where the frontals extend ventrally to occupy the dorsolateral walls of the cavity connecting the brain with the orbit. This cavity is a wide vertical oval in *Hypsocephalus,* only slightly elongated dorsoventrally in *Hoplopagrus,* much elongated dorsoventrally in *Lutjanus* and *Ocyurus,* and narrowly constricted in *Rhomboplites* with a roughly circular opening dorsal and ventral to a narrow interspace. In *Pristipomoides* the pterosphenoids firmly articulate medially for the middle third of the vertical distance between the dorsal edge of the basisphenoid and the underside of the frontals. Thus the orbit and brain cavity are connected by two subequal circular openings occupying the dorsal and ventral one-third of this distance.

Basioccipital: The posterior basioccipital facet is vertical, facing directly posterior. Anterior to this facet the bone is almost a vertical rectangle in cross section, compressed to about two-thirds the facet width. Ventrally it is deeply excavated and this cavitation extends anteriorly above the transverse posterior end of the parasphenoid. Further dorsally and anteriorly this cavity opens widely into the posterior myodome. Laterally the basioccipital forms the ventrolateral wall of the posterior portion of the chamber for the saccular otolith. A thin, compressed, medial extension runs anteriorly and slightly dorsally to articulate with the thick median juncture of the prootics.

Comparison: The whole posterior facet of the basioccipital lies in one plane and faces somewhat posterodorsally in *Lutjanus, Ocyurus,* and *Rhomboplites.* The posterior facet faces posteriorly in *Hoplopagrus.* The anterodorsal portions which enter the otic bulla are somewhat more expanded in *Lutjanus synagris* and *Ocyurus,* but are compressed in *Lutjanus griseus* and *Hoplopagrus. Rhomboplites* and *Pristipomoides* have large otoliths and a widely expanded basioccipital. The basioccipital is only narrowly excavated ventrally in *Lutjanus* and the cavity is not confluent with the posterior myodome. The cavity is small and narrowly confluent in *Hoplopagrus,* and large and confluent in *Ocyurus, Pristipomoides,* and *Rhomboplites.* In *Rhomboplites* the basioccipital is wider (almost square) just anterior to the posterior facet rather than being narrowly compressed and rectangular.

Supraoccipital: The supraoccipital penetrates anteriorly between the frontals to a position slightly behind a vertical through the middle of the orbit. It widens posteriorly and along the posterior edge of the skull occupies the medial half of each supratemporal fossa. The lateral surfaces slope slightly ventrolaterally to the parietal and epiotic. The supraoccipital crest is broken dorsally and is described from photographs taken before it was collected when the crest was more complete. The supraoccipital crest is low, only slightly higher than the dorsal surface of the skull anteriorly. A slight ridge extends posterodorsally from the posterodorsal border of the skull on each side of the crest. About 5 mm along this ridge, another ridge extends from it posteriorly and slightly ventrally.

Comparison: The supraoccipital (in the supraoccipital crest) extends anteriorly to a vertical through the center of the orbit in *Hoplopagrus, Rhomboplites,* and *Ocyurus.* In *Lutjanus* and *Pristipomoides* it extends only to a vertical through the posterior one quarter of the horizontal orbit diameter. The ridge extending posterodorsally from the posterodorsal corner of the skull bears a ventral branch distally in *Hoplopagrus, Rhomboplites,* and *Ocyurus,* but the ventral branch is lacking in *Lutjanus.* In *Rhomboplites, Ocyurus,* and *Hypsocephalus* the main branch extends to the posterodorsal apex of the supraoccipital crest, but in *Lutjanus* and *Pristipomoides* this ridge reaches to a point a little below the apex along the vertical posterior edge of the crest.

Exoccipital: Although the right exoccipital is fragmentary, the left is complete. Clearly both met in the midline over the basioccipital, and the ventral, lateral and at least dorsolateral walls of the foramen magnum were bounded by the exoccipitals (Figure 5). Each flat facet receiving the dorsal portion of the atlas vertebra is a regular transverse oval facing ventromedially. The medial edge terminates a millimeter or two short of the midline and the exoccipital facets did not form a continuous articular surface. From the facet a strong pillar of bone extends anterodorsolaterally and forms the posterolateral corner

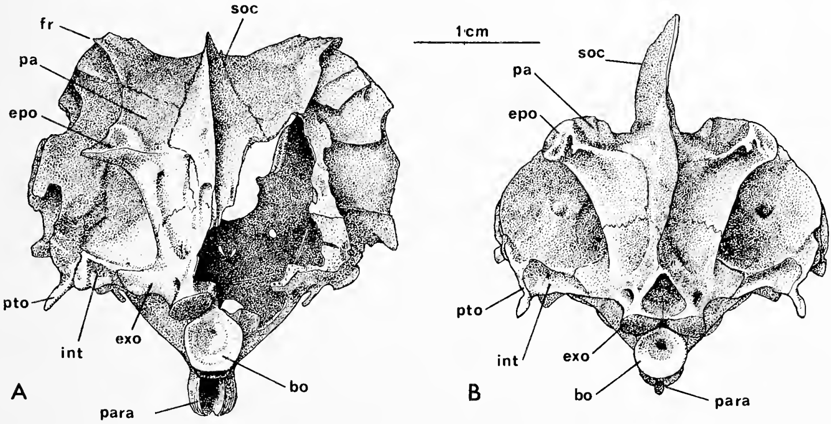


FIGURE 5. Posterior view of the neurocrania. A, *Hypsocephalus atlanticus* (LACMVP 27859); B, *Hoplopagrus guntheri* (LACM 31774-1).

of the skull. The ridges soon bifurcate, one branch extending dorsally and slightly anteriorly to the epiotic, and the other laterally and slightly anterior to the intercalar and pterotic. A foramen is present just dorsolateral to the articular facet for the atlas vertebra, and another larger one pierces the exoccipital just anterior to the pillar of bone which extends laterally towards the pterotic.

Comparison: Medial extensions from, and about half as wide as, the exoccipital facets form a continuous articular surface across the midline in *Ocyurus, Rhomboplites, Pristipomoides,* and *Lutjanus.* These facets have narrowed medial extensions in *Hoplopagrus* but do not meet in the midline. The exoccipitals have greater antero-posterior extent in *Lutjanus* and *Ocyurus* than in *Rhomboplites, Hoplopagrus,* and *Hypsocephalus.*

Dentary: About three-fourths of the right dentary is present, and its medial side is covered with limestone (Figure 6). Only about one-eighth of the left dentary remains. The dentary is robust and bears a lateral row of robust, bluntly pointed teeth about the size of the larger vomerine teeth. These lateral teeth diminish slightly in size posteriorly. An inner row of robust teeth about half the size of the outer teeth is visible on the fragmentary left dentary. This inner row extends backward to at least half the length of the dorsal limb of the dentary. The symphysis is lacking, but the dentaries seem to be oriented as they were in life, and appear to have met via a deep, strong articulation. The dentary rises sharply posteriorly and it appears that the length of the intact dentary is subequal to the vertical distance between the posterior ends.

Comparison: Hypsocephalus and *Hoplopagrus* have an outer row of bluntly pointed robust teeth. In *Hypsocephalus* the nature of the dentition on the anterior ends of the dentaries is unknown. In *Hoplopagrus* two or three larger blunt canines are developed anteriorly in each dentary, and the inner row is restricted to two or three smaller teeth present just behind these canines. In the remaining genera a single row of slender to robust canines is followed by a small number of fine inner teeth restricted to the anterior one-third or less of each dentary.

Articular: Only the anterior one-third of the right articular is present, and it essentially occupies its normal position between the posterior limbs of the dentary (Figure 6). The articular is deep and robust like the dentary.

Comparison: The most that can be seen from the fragmentary articular is that it is relatively deep, at least anteriorly, as are the articulars in the other genera.

Cleithrum: Only a fragment of the left cleithrum is present (Figure 6). More complete and relatively intact cleithra were present in the cave before the skull was collected, and they are described from photographs of two views. Three-fourths of the left cleithrum and the middle third of the right one were present. The upper limb was pointed on the anterodorsal edge. A short distance below it widens perpendicularly backward, so the flat plate of the dorsal limb has a largely horizontal dorsal surface. The posterior edge was about

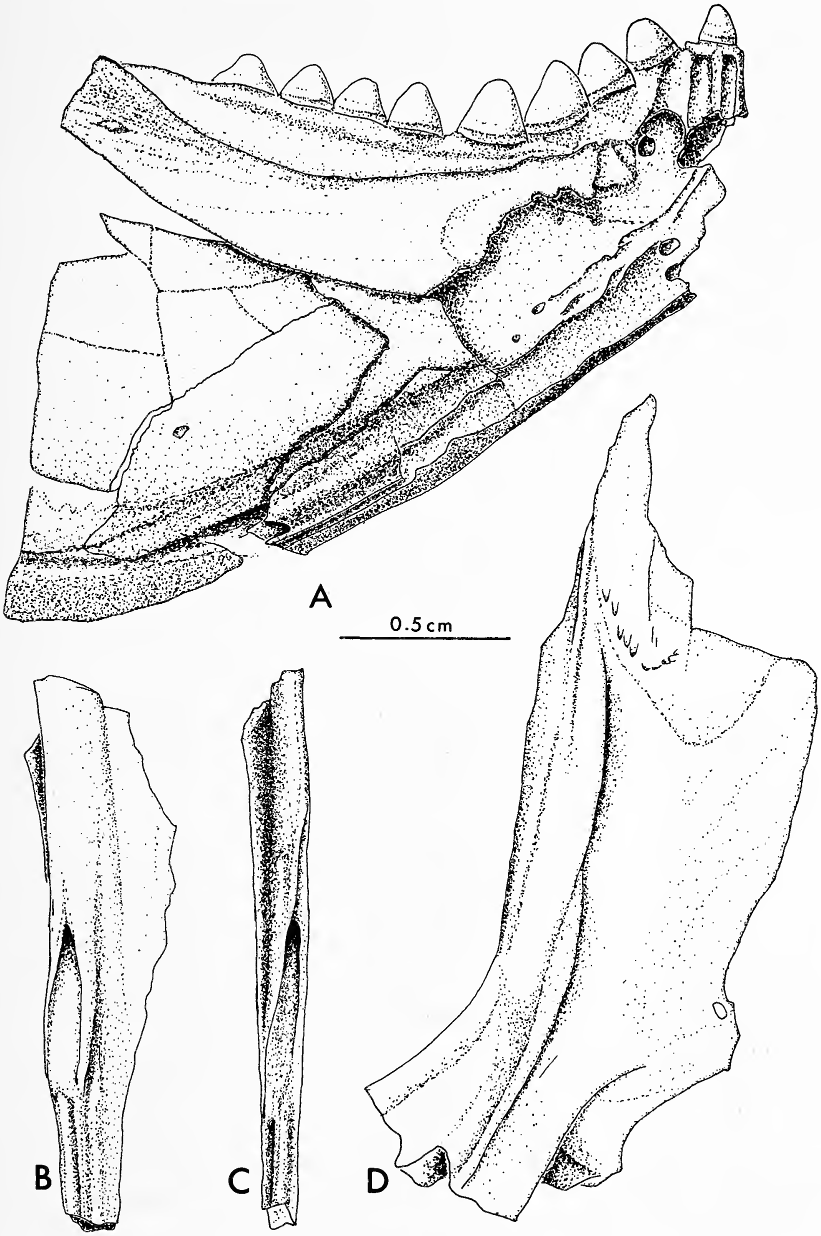


Figure 6. Bones of *Hypsocephalus atlanticus*. A, Lateral view of right dentary and anterior portion of the right articular. B, Lateral view of distal two-thirds of the right hyomandibular. C, Posterior view of B. D, Lateral and slightly anterior view of the fragmentary left cleithrum.

vertical and the dorsal limb is roughly uniform in width below the narrow anterodorsal point. The posteroventral angle of the dorsal limb bears a short, rounded, flat projection just above the position of the coracoid. The anteroventral limb possesses a wide flange laterally. Both ventral limb flanges lack the anterior one-fourth of their extent. A shallow groove is present on the lateral edge and it extends dorsally and anteroventrally about one-half the distance of each limb. The dorsal and posterior edge of the upper limb are broken so the exact shape is not known.

Comparison: The cleithra of recent genera show only minor differences which are not discernible on the fossil.

Hyomandibular: Most of the ventral limb and the anterior third of the proximal articular portion of the right hyomandibular are present. Only the anterior facet which articulates with the skull is present of the three proximal articular surfaces of the hyomandibular. The facet is flat, slightly oval dorsoventrally, and bears a small notch ventrally. From this facet a ridge extends posteriorly and laterally. It runs into a strong, dorsoventral ridge which is directed anterolaterally, and is broken dorsally and ventrally. The anterior flat blade of the hyomandibular extends ventrally a short distance to a transverse break in the bone. The medial ridge leading from the anterior to the posterior articular facet is broken just behind the anterior facet. The thickened posterior edge of the hyomandibular is longitudinally oval in cross section, and is hollow in the distal one-third. The proximal two-thirds is hollow also, and opens out posterolaterally via an elongate oval foramen. Along the posterior edge of the shaft a groove originates near the distal end of this foramen. The groove widens and deepens proximally to the broken end which lies about two-thirds of the estimated total length of the intact bone from the distal end (Figure 6).

Maxillary: Only the ventral half of the anterior third of the maxillary is present (Figure 7 C, D, H). The anterior excavation which accommodates the premaxillary was high and narrow. The ventral edge of the medial side bears a low rounded swelling which articulates laterally with the ascending process of the premaxillary. Dorsal to this swelling extends a low, rounded, vertical ridge, which is about as long as the thickness of the shaft of the maxillary. The shelf extending anterolaterally from the head of the maxillary was thin and does not appear to have been expanded distally.

Comparison: The medial articular surface and ridge dorsal to it are relatively smaller in the fossil than in *Hoplopagrus*. The ridge is sharp rather than rounded in *Hoplopagrus* as well. The ridge is rather sharp edged and much higher and longer in all the other recent snapper genera. The ridge is straight edged in the hoplopagrines and *Rhomboplites* and is a raised semicircle in the other recent genera.

Premaxillary: The premaxillary is dorsoventrally flattened and bears an outer row of enlarged teeth about the same size as those on the dentary and an inner double row of molariform teeth about one-third the size of the outer

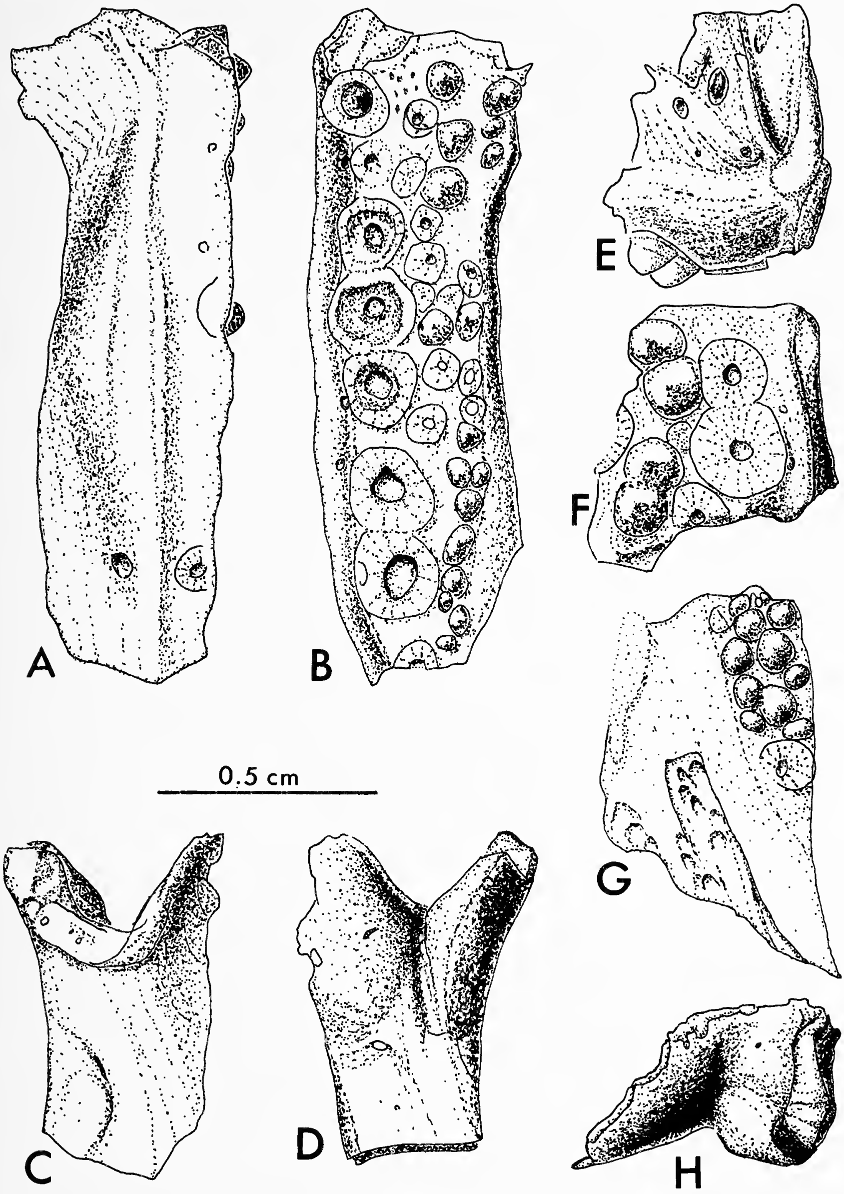


FIGURE 7. Bones of the jaws and palate of *Hypsocephalus atlanticus*. A, Anterior view of anterior two-thirds of right premaxillary. B, Ventral view of A. C, Dorsal view of the head of the right maxillary. D, Ventral view of C. E, Medial view of anterior end of left premaxillary. F, Ventral view of E. G, Ventral view of posterior portion of left palatine. H, Medial view of the head of the right maxillary.

ones (Figure 7 A, B, E, F). The second tooth from the medial end of the bone in the outer row is about twice as large (at least in diameter) as the others. The bases of the two medial teeth are present on the fragmentary anteromedial end of the left premaxillary and most of the shaft is known from the right one. One or two more enlarged teeth may have been present at the anterior end of the premaxillary, but a total of more than three is unlikely.

Comparison: Hoplopagrus consistently has only a single row of smaller inner teeth, and usually has two enlarged canines anteriormost in the outer row of each premaxillary. The other recent snapper genera have a single outer row of canines with the anterior one to five teeth enlarged. The inner ones consist of two to five rows of villiform teeth, usually with more rows anterior and medial and less posterior and lateral.

Palatine: The small posterior fragment of the left palatine bears 12 small molariform teeth (Figure 7 G).

Comparison: This piece could have been from a palatine bone shaped like that of *Lutjanus, Ocyurus, Rhomboplites,* or *Pristipomoides,* but it is too fragmentary to discern the original shape. *Hoplopagrus* lacks palatine teeth and the bone is a narrow shaft without the wide flattened area which bears palatine teeth in other lutjanids.

Dorsal Spine Pterygiophore: The left side of the first dorsal spine pterygiophore and its two dorsal spines are exposed on a small chunk of limestone. The basal two-thirds of the moderately robust spines are present, and articulated with the pterygiophore. The pterygiophore is flat with a low, flat, straight ridge running ventrally from the articulation of the second spine. This ridge lies slightly posterior to a line vertically bisecting the lateral surface of the bone, and is slightly enlarged and rounded just ventral to the second spine base. Just ventral to the first spine, the pterygiophore bears a low, rounded protuberance which extends anterodorsolaterally. The length of the dorsal surface of the pterygiophore is about half the height of this bone; the ventral tip is broken and the height cannot be precisely determined.

Comparison: The lateral ridge below the second dorsal spine base, and the low protuberance below the first spine are of similar configuration in all the other snappers, except possibly that of *Pristipomoides* which was not examined. In the recent snaper genera the depth is two and one-half to four times the length of the dorsal edge, rather than about twice as in *Hypsocephalus.* The first two dorsal spines are slightly compressed, long and slender, and the first spine is just about half the length of the second in the recent snapper genera, and this appears to have been true for the fossil although only the proximal two-thirds to three-fourths of each spine is present.

DISCUSSION

The fossil resembles the living *Hoplopagrus guntheri* more than any other percoid examined. The living and fossil species together appear closest to lutjanids, although they are distinctive in their own right, and also bear some resemblance to sparids and pomadasyids. This conclusion is largely (and necessarily) based on characters in the neurocranium and jaws, the only elements available in the fossil. The nature of the teeth on the premaxillaries, dentaries, vomer, and palatines has been stressed since they are often the only osteological features described for Indo-Pacific percoids (Weber and de Beaufort, 1931, 1936; Gosline and Brock, 1960; Smith, 1961; Marshall, 1964). Detailed search for relationships has been restricted to three families Lutjanidae, Pomadasyidae, and Sparidae. Comparative materials has been listed previously and the following works have also been useful: Gregory (1933); Patterson (1964); and Leccia (1961).

Characters taken together which distinguish the hoplopagrines from other percoids are: 1) robust, conical teeth on the premaxillaries, dentaries, and vomer; 2) a vertical and transverse posterior facet on the basioccipital; 3) articular surfaces of exoccipitals for the atlas vertebrae not continuous across the midline; 4) a ventral, globular swelling on the posterior end of the parasphenoid; 5) a narrow, compressed otic region; 6) a strong, compact dorsal surface of the lateral ethmoids lateral to the anterior ends of the frontals; 7) lateral ethmoid facets for the palatine oriented as in lutjanids (see below); and 8) supraethmoid (not vomer!) convex in profile. Many of these characters are found elsewhere in percoids.

The robust conical teeth occur also among the lutjanids and sparids but show more variation in size in these families. In lutjanids the outer robust teeth are followed by minute villiform teeth, and the vomerine teeth are usually present and villiform. The only exceptions are some species of the lutjanid genus *Lethrinus* which have canines anteriorly and molariform teeth posteriorly (Weber and de Beaufort, 1936). Pomadasyids resemble lutjanids in having strong canines followed by fine villiform teeth, or having all jaw teeth villiform. Sparids all show considerable range of tooth shapes, with canines or incisors anteriorly and conical or molariform teeth posteriorly. The relatively uniform shape, lack of great dimorphism in size, the teeth diminishing in size posteriorly, and the presence of teeth on the vomer in hoplopagrines makes them similar to lutjanids.

The posterior facet of the basioccipital faces posterodorsally in pomadasyids and lutjanids. This facet is transverse and vertical in sparids as it is in hoplopagrines. In sparids the articular surfaces of the exoccipital facets accommodating the atlas vertebrae vary. Those of *Calamus* and *Archosargus* do not meet in the midline like those of hoplopagrines. They meet narrowly in *Lagodon,* and form a wide continuous surface in *Diplodus.* These facets meet through a continuous surface in lutjanids and the pomadasyids *Brachydeutereus, Orthopristis, Anisotremus, Haemulon aurolineatum,* and *H. sciurus.* They fail to meet middorsally in *Haemulon plumieri.* The hoplopagrines most resemble some sparids and some pomadasyids in the relations of the facets for the atlas vertebrae.

No development of a globular swelling at the posterior end of the parasphenoid is apparent in the lutjanids examined or in the pomadasyid *Anisotremus.* The remaining pomadasyids and all the sparids examined have such a swelling moderately to well developed. In contrast to the solid rounded protuberance of the hoplopagrines, the swelling in sparids and pomadasyids is bilateral with a midventral longitudinal groove partially dividing it. The hoplopagrines seem to resemble sparids and pomadasyids rather than lutjanids in possessing this swelling, but since it is differently formed in hoplopagrines it may be independently developed and not indicative of relationship.

All the lutjanids and pomadasyids examined have moderately to greatly inflated otic regions, but the hoplopagrines resemble the sparids examined in having a compressed otic region.

The size and arrangement of the cephalic lateral line system pores in hoplopagrines is within the range of variation seen in the lutjanids and sparids examined. The pomadasyids have distinctive large cephalic canals quite different from those in hoplopagrines.

The lateral ethmoids have a well-developed dorsal surface lateral to the anterior ends of the frontals in sparids and pomadasyids, and this surface is deeply excavated in all of the genera examined in these two families except in *Brachydeutereus* where the upper surface is only a shallow depression. In hoplopagrines this surface is rugose and flat or rounded as it is in lutjanids, although the surface faces largely laterally and slightly anteriorly in lutjanids rather than dorsally.

The orientation and position of the palatine facets on the lateral ethmoids of the hoplopagrines resemble those of all the lutjanids examined, namely one some distance behind the other with the anterior one slightly more dorsal and slightly more lateral than the posterior one. In pomadasyids the vomer and lateral ethmoid are longer and the facets are much closer together. The anterior one is directly anterolateral and slightly dorsal to the posterior one. The anterior facet faces much more laterally than in lutjanids as well. In sparids the anterior facet is strongly developed and faces anteriorly and slightly laterally, and the posterior facet is obsolescent. The supraethmoid is similar in size and shape in hoplopagrines and lutjanids, namely with a flat dorsal surface between the anterior ends of the frontals with a midventral keel anterior to this. The bone is convex dorsally in profile. In the sparids and pomadasyids examined the supraethmoid is concave in profile and is flat or excavated along the middorsal line, apparently to accommodate the long ascending processes of the premaxillaries.

In most of the characters shared by *Hoplopagrus* and *Hypsocephalus* and just discussed, the hoplopagrines resemble the lutjanids. A few characters like the swelling at the posterior end of the parasphenoid and the orientation of the posterior exoccipital facets resemble some sparids and some pomadasyids, but are differently developed or variably developed enough so that they do not seem to be strong indicators of relationship.

The characters in the dentition and ethmoid region of hoplopagrines are probably the strongest evidence of a relationship with the lutjanids. The ethmoid region, maxillaries, and premaxillaries are basically similar and reflect the capability to expand the oral cavity both ventrally and laterally. The lutjanids, including hoplopagrines, are predaceous and have moderately protrusible mouths which also expand laterally, producing a large enough opening to utilize vomerine and palatine teeth which are present in most lutjanids. In both sparids and pomadasyids the mouth is restricted laterally, and the upper jaw is much more protrusible. These fish are largely nibblers and grazers (Randall, 1967), and the restricted lateral movement of smaller mouths has eliminated the need for vomerine or palatine teeth which are uniformly lacking in these two families. Thus, the hoplopagrines are interpreted as lutjanids which have retained the typical larger, expansive mouth, but have specialized to feed on resistant prey by developing strong, robust teeth resembling those of some sparids.

Hypsocephalus is distinctive among lutjanids in possessing two flanges on the prootic, one anterolateral and another posterolateral to the main columnar arch forming the anterolateral wall of the prootic. Sparids typically have two complete arches (Patterson, 1964) and I found this in all the sparids examined except *Lagodon* in which the posterior one is incomplete, resembling the posterior flange of *Hypsocephalus*. All the pomadasyids examined have a single complete arch with an additional free ending posterolateral flange from the shelf under the anterior prootic facet for the hyomandibular. More variation probably exists than has been suspected and this character should be investigated in as many acanthopterygians as possible.

Hypsocephalus is also unique among the lutjanids and sparids examined in lacking a pointed process on the epiotic just medial to the facet for the upper limb of the posttemporal. Among the percoids examined this process is lacking in all the pomadasyids, and the significance of this absence is not known.

The living *Hoplopagrus guntheri* has tubular anterior nostrils, a well-developed knob on the upper interopercle, thick, enlarged, and conical canines on the anterior ends of the dentaries and premaxillaries, conditions which cannot be determined in the fossil. Lutjanids generally possess the interopercular knob, but it is usually less well developed, and the sparids examined lack it. The sparids lack palatine teeth also, and the large canines and tubular nostrils are unique for *Hoplopagrus* among lutjanids and sparids. The lateral ethmoid canal for the olfactory nerve in *Hypsocephalus atlanticus* is about the same size as in other lutjanids, and it apparently did not have a particularly large nasal capsule, as does *Hoplopagrus* (Pfeiffer, 1964).

Lutjanids in general feed largely on crustaceans and fishes, with fishes forming a greater proportion of the diet in larger individuals (Randall, 1967). The strong molariform teeth of *Hoplopagrus* indicates that it eats resistant prey of some kind, as presumably did *Hypsocephalus atlanticus*. Edmund Hobson (personal communication) found *Hoplopagrus* to be nocturnal, and believes that its feeding habits may be similar to a nocturnal Hawaiian sparid, namely *Monotaxis grandoculis* (Forskal). He finds this Hawaiian sparid to feed largely on hermit crabs and sea urchins which move out into the open more at night. Possibly the feeding habits of *Hoplopagrus* are similar, as perhaps were those of the fossil.

The description of the holotype of *Lutjanus avus* W. K. Gregory, 1930 shows that it consisted of a majority of the cranial bones, and they seem to be typical of the genus *Lutjanus*. *Lutjanus avus* had strong outer teeth and fine inner ones on the dentary and premaxillaries, and villiform vomerine teeth. Unfortunately the holotype of *L. avus* could not be found during a thorough search of the Florida Geological Survey Collections in 1957, (Stanley J. Olsen, personal communication), and thus it has not been re-examined.

The holotype of *Lutianus hagari* Jordan and Gilbert, 1919, recently transferred from Stanford University to the California Academy of Sciences, and the counterpart (LACM 1329), were examined and they do not represent a lutjanid as Jordan and Gilbert (1919) believed. The first four or five dorsal spines (11 in all) are longest. The next to the last four are about half the height of the anterior ones. The last spine is a little longer than these four and is very close to the much longer first soft ray, a condition found in percichthids, scorpaenids, percids, and some sciaenids, but not in lutjanids. The anal fin almost certainly had three anal spines, although the anteriormost small spine is difficult to distinguish. The posterior two spines are clearly marked, and the second is about one-third the diameter and about two-thirds the length of the third. A good number of cycloid body scales is present. The scale focus is placed posteriorly and six to nine radii occupy the anterior fields. The skull is badly crushed but at least the dentaries (and probably the premaxillaries) appear to have borne villiform teeth along with small canines.

The arrangement of dorsal spines and the cycloid scales definitely exclude the fossil from the family Lutjanidae. Percichthids (except *Stereolepis*) and percids are extremely unlikely in deep water Miocene deposits from California. All of the characters of the fossil noted above are found in *Stereolepis* and many scorpaenids, and upon thorough study the fossil of *Lutianus hagari* may prove to be one of these.

GEOLOGY AND PALEOECOLOGY

About fourteen and one-half meters of limestones ranging from Oligocene to Eocene in age occur within the measured stratigraphic section at Milton's Cave. The highest beds which outcrop at the surface are the marine Oligocene Marianna limestones about 3.5 meters thick. Under these are upper Eocene limestones which have been extensivly studied (Puri, 1957; Cheetham, 1963). The Ocala group is the uppermost late Eocene bed, and the top of the Ocala group is represented by the Crystal River Formation. The Crystal River Formation is divided into an upper Bumpnose Member and a lower member. The skull of *Hypsocephalus atlanticus* was discovered in this lower member.

The lower member is also comprised of an upper and lower zone. The skull came from the upper zone which is a white to light brown, creamy, generally soft, granular relatively permeable and pure limestone. This zone is quite porous, has been carried into solution over large areas of the cave, and is called the *Operculinoides ocalanus-Asterocyclina* Zone by Puri and Vernon (1964). The two zones of the lower member are hard to distinguish and locally grade into each other.

The *Operculinoides-Asterocyclina* Zone indicates a depositional environment of a continental shelf region between 33 and 66 meters, with salinities from 32 $^{\circ}/_{\circ\circ}$ to 37 $^{\circ}/_{\circ\circ}$ water temperatures of 20°C or more, moderate agitation, and no evidence of reef formation (Cheetham, 1963; Puri and Vernon, 1964). Conditions found today between the continental shelf margin of Florida and the Bahamas Bank seem to be analogous with those which existed in the late Eocene, namely a gently sloping continental shelf bounded on the outside by a depression (Suwanee Straits of Eocene times) beyond which existed a bank (Ocala Bank of Eocene time). In the late Eocene, the mainland was in southern Alabama and Georgia and the highlands of central Florida were occupied by the Ocala Banks.

The specimen of *Hypsocephalus atlanticus* died and was deposited at moderate depths on a mainland shelf. The excellent three dimensional preservation indicated a relatively undisturbed bottom. A fish entombed in a sediment consisting of these fine foraminiferal particles may have been well preserved due to anaerobic bacterial action (Dunkle and Olsen, 1959). During late Eocene time the north Florida area was tropical or subtropical and the sea level was gradually falling (Cheetham, 1963). There was a progressive extinction of endemic forms among the cheilostome bryozoa (Cheetham, 1963), and the line of hoplopagrine snappers may have become extinct in the western Atlantic in this period as well. However, the Miocene, Pliocene, and Pleistocene also saw substantial sea level falls (although at progressively lower levels than the Eocene deposits) which were accompanied by cooling (Tanner, 1968), and the extinction of the hoplopagrines may have taken place at one of these later times. A tropical and subtropical shallow water reef shark genus, *Heterodontus,* was present through Miocene times in the western north Atlantic, but is known today only from the eastern Pacific, Indo-Pacific, eastern Atlantic and the Indian oceans. Both *Heterodontus* and *Hypsocephalus* may have been eliminated at the same time, when conditions in the Caribbean area apparently became unfavorable for warm water forms living about hard substrates at shallow and moderate depths.

ACKNOWLEDGMENTS

We wish to thank the Florida State Cave Club of Florida State University, Tallahassee, particularly members Robert Royal, Eugene Neel, and Edward Renner for assisting the junior author in discovery and collection of the fossil. Their interest and concern for making the specimen available to science is highly commendable. Elizabeth Wing, Robert Christensen, David Cupka, and Jack Rudloe all helped us obtain skeletal material of recent snappers, grunts, and porgies used in this study. An opportunity to collect comparative material of *Hoplopagrus guntheri* in Baja California was afforded by the generosity of the Janss Foundation, Thousand Oaks, California. William Eschmeyer, Lillian Dempster, and Pearl Sonada aided in sorting the old Stanford University collection of fossil fishes now in the California Academy of Sciences. The map of Milton's Cave was drafted by Edward Renner, James Leaird, and the junior author from a Brunton and Tape survey by the Florida State Cave Club made on 5 July 1970. The photographs of the fossil in the cave were made by the junior author. Various editions of the manuscript were typed by Terri Kato, Barbara Savino, and Janet Dock. The excellent drawings of the neurocrania of the fossil and of *Hoplopagrus* were done by Mary Butler, and the remaining illustrations were made by the senior author.

LITERATURE CITED

ANDERSON, W. D. 1967. Field guide to the snappers (Lutjanidae) of the western Atlantic. U.S. Fish Wildl. Ser., Bur. Comm. Fish. Circ. 252, 14 p.

CASIER, E. 1966, Faune Ichthyologique du London Clay. Brit. Mus. Nat. Hist., London. xiv + 496 p., plus a separate Atlas of 68 pl.

CHEETHAM, A. H. 1963. Late Eocene zoogeography of the eastern Gulf Coast region. Geol. Soc. Amer. Mem. 91: xii + 113 p.

DANIL'CHENKO, P. G. 1967. Superorder Teleostei, In: Fundamentals of Paleontology, Vol. XI, Agnatha, Pisces. D. V. Obruchev (Ed), p. 603-712, Israel Program for Scientific Translations, Jerusalem.

DUNKLE, D. H., AND S. J. OLSEN. 1959. Description of a beryciform fish from the Oligocene of Florida. Fla. Geol. Surv. Contrib. Fla. Vert. Paleontol. Pap. No. 3, 20 p.

GILL, T. N. 1862a. On new generic types of fishes. Proc. Acad. Nat. Sci. Phila. 13: 77-78.

————. 1862b. Catalogue of the fishes of lower California in the Smithsonian Institution, collected by J. Xantus. Proc. Acad. Nat. Sci. Phila. 14: 249-262.

————. 1884. The osteological characters of the Lutjaninae. Proc. U.S. Nat. Mus. 7(23): 351-355.

GOSLINE, W. A. AND V. E. BROCK. 1960. Handbook of Hawaiian Fishes. Univ. Hawaii Press, Honolulu. 372 p.

GREGORY, W. K. 1930. A fossil teleost fish of the snapper family (Lutianidae) from the lower Oligocene of Florida. Fla. St. Geol. Surv. Bull. 5:7-17.

————. 1933. Fish Skulls. A study of the evolution of Natural Mechanisms. Trans. Amer. Phil. Soc. 23(2): vii + 481 p.

JORDAN, D. S., AND B. W. EVERMANN. 1898. The fishes of North and Middle America: A descriptive catalog of the species of fish-like vertebrates found in the waters of North America, north of the isthmus of Panama. Bull. U.S. Nat. Mus. 47 (Pt. II), i-xxx, 1241-1936.

JORDAN, D. S., AND J. Z. GILBERT. 1919. Fossil fishes of southern California. Leland Stanford Jr. Univ. Pub. (Univ. Ser.) 38: 1-64.

LECCIA, F. M. 1961. Osteologia comparada en ocho especies de Pomadasyidae (Pisces-Perciformes) del Golfo de Cariaco, Venezuela, y areas adyacentes. Bol. Inst. Ocean. Univ. Oriente. 1(2): 396-473.

LEHMAN, J. -P. 1966. Actinopterygii. In: Traite de Paleontologie. Tome IV, vol. 3, p. 1-242, Jean Piveteau (Ed.) Masson et Cie, Paris, France.

MARSHALL, T. C. 1964. Fishes of the Great Barrier Reef and coastal waters of Queensland. Angus and Robertson, Sydney. xiv + 566 p.

NORMAN, J. R. 1966. A draft synopsis of the Orders, Families, and genera of recent fishes and fish-like vertebrates (excluding Ostariophysi, Scleroparei, Ammodytidae and a few other families, notably Centrarchidae, Percidae and Cichlidae) covering literature up to 1938, and as far as it was available to the author, from 1938 to 1944. Brit. Mus. Nat. Hist., London. 649 p.

PATTERSON, C. 1964. A review of Mesozoic Acanthopterygian fishes, with special reference to those of the English Chalk. Phil. Trans. Roy. Soc. Lond. Ser. B, 247 (739): 213-482.

PFEIFFER, W. 1964. The morphology of the olfactory organ of *Hoplopagrus guentheri*, Gill, 1862. Can. J. Zool. 42(2):235-237.

PURI, H. S. 1957. Stratigraphy and zonation of the Ocala group. Fla. Geol. Surv. Bull. 38. 248 p.

PURI, H. S., AND R. O. VERNON. 1964. Summary of the Geology of Florida and a guidebook to the classic exposures. Fla. Geol. Surv. Spec. Publ. No. 5. ix + 312 p.

RANDALL, J. E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. Miami 5: 665-847.

REGAN, C. T. 1913. The classification of the Percoid fishes. Ann. Mag. Nat. Hist. 8th Ser., 12(17): 111-145

ROMER, A. S. 1966. Vertebrate Paleontology. Univ. Chicago Press, Chicago, Ill. ix + 468 p.

SMITH, J. L. B. 1961. The sea fishes of southern Africa. 4th Ed. Central News Agency, South Africa. xvi + 580 p.

STARKS, E. C. 1926. Bones of the ethmoid region of the fish skull. Stanford Univ. Pub., Univ. Ser., Biol. Sci. 4(3): 139-338.

TANNER, W. F. (Ed.) 1968. Tertiary sea level fluctuations. Paleogeography, Paleoclimatol., Paleoecol. 5: 5-171.

WALFORD, L. 1937. Marine game fishes of the Pacific Coast from Alaska to the Equator. Univ. Calif. Press, Berkeley. xxix + 205 p., 69 pl.

WEBER, M., AND L. F. DE BEAUFORT. 1931. The fishes of the Indo-Australian Archipelago. Vol. VI, Perciformes (continued). E. J. Brill, Leiden. xii + 488 p.

————. 1936. The fishes of the Indo-Australian Archipelago. Vol. VII, Perciformes (continued). E. J. Brill, Leiden. xvi + 607 p.

WEILER, W. 1968. Otolithi Piscium. Fossilium Catalogue 1: Animalia, Pars 117. 196 p.

WOODWARD, A. S. 1901. Catalogue of the fossil fishes in the British Museum Natural History. Pt. IV. Containing the actinopterygian Teleostomi of the suborders Isospondyli (in part), Ostariophysi, Apodes, Percesoces, Hemibranchii, Acanthopterygii and Anacanthini. London. xxxviii + 636 p.

Accepted for publication April 4, 1972

Printed in Los Angeles, California by Continental Graphics

NUMBER 231
JUNE 23, 1972

THE STATUS OF *LEPTODACTYLUS PUMILIO* BOULENGER (AMPHIBIA, LEPTODACTYLIDAE) AND THE DESCRIPTION OF A NEW SPECIES OF *LEPTODACTYLUS* FROM ECUADOR

By W. Ronald Heyer

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.–(1) The 1964 AIBS Style Manual for Biological Journals is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1964 AIBS Style Manual for Biological Journals in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.–Authors will be sent galley proof which should be corrected and returned promptly. Changes in the manuscript after galley proof will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

VIRGINIA D. MILLER
Editor

THE STATUS OF *LEPTODACTYLUS PUMILIO* BOULENGER (AMPHIBIA, LEPTODACTYLIDAE) AND THE DESCRIPTION OF A NEW SPECIES OF *LEPTODACTYLUS* FROM ECUADOR[1]

By W. Ronald Heyer[2]

Abstract: *Leptodactylus pumilio* Boulenger, 1920, is shown to be a junior synonym of *Eleutherodactylus parvus* (Girard). The Pentadactylus species group of *Leptodactylus* is redefined and a new species of this group is described from Amazonian Ecuador. The presence of dorsolateral folds combined with the uniformly black coloration of the posterior surface of the thigh distinguish the new species from the other members of the group. The karyotype of the new species has a diploid number of 22 bi-armed chromosomes with no secondary constrictions. A key to the species of the Pentadactylus group is provided.

Introduction

A preliminary analysis of a cross sectional representation of the genus *Leptodactylus* indicated that the species could be grouped into five species assemblages (Heyer, 1968). I am presently analyzing each of these groups in detail (e.g., Heyer, 1970). As in all long-term projects, data are gathered continuously on all groups. The purpose of this paper is to report two findings that are outside of my current main project. First, examination of the holotype of *Leptodactylus pumilio* indicates a nomenclatural change is necessary. Second, a new species of the Pentadactylus group is described from specimens recently collected in Amazonian Ecuador.

Acknowledgments

Several people have helped in the research and preparation of this report. Alice G. C. Grandison was a gracious hostess during my brief visit to the British Museum (Natural History) (BMNH). Philip A. Silverstone, Natural History Museum of Los Angeles County (LACM), kindly photographed the type of *Leptodactylus pumilio*. Keith A. Berven, Pacific Lutheran University, helped with the field work in Ecuador. Don Johnson, Director of the Summer Institute of Linguistics in Ecuador, allowed us to undertake field work at their institute base camp of Limoncocha during the summer of 1971. John W.

---

[1] Editorial Committee for This Contribution
Robert L. Bezy
Roy W. McDiarmid
Ian R. Straughan

[2] Research Associate, Section of Herpetology, Natural History Museum of Los Angeles County; and Biology Department, Pacific Lutheran University, Tacoma, Washington 98447.

Wright, LACM, aided in the chromosome analysis and reviewed the manuscript. Research support from NSF grant GB-27280 is gratefully acknowledged.

Leptodactylus pumilio

Figure 1

In February of 1969, I had the opportunity to examine the type of *Leptodactylus pumilio* at the British Museum (Natural History). The specimen was originally catalogued as 1914.3.20.7 but has been recatalogued as 1947.2.17.35. The salient features of the type (Fig. 1) are: 1) The sternum has a cartilaginous plate; 2) Fingers III and IV have small disks, the toes have large disks; 3) The finger and toe disks have peripheral grooves, the upper surfaces are undivided; 4) The tympanum is not visible on the left, barely visible on the right; 5) The tarsus is smooth; 6) There is a dark triangular patch under the vent. Members of the genus *Leptodactylus* are characterized in part by having a bony style in the sternum, disks (if present) without peripheral grooves, and (usually) a tarsal fold. The holotype clearly

FIGURE 1. Dorsal (*left*) and ventral (*right*) views of holotype of *Leptodactylus pumilio* (= *Eleutherodactylus parvus*), BMNH 1947.2.17.35, from Teresópolis, Brasil.

is not a member of the genus *Leptodactylus,* but of the genus *Eleutherodactylus.* The holotype was collected in Teresópolis, Brasil, where fortunately, few species of *Eleutherodactylus* occur. The dark seat patch is characteristic of *Eleutherodactylus parvus* (Girard, 1853) and a comparison of the holotype of *L. pumilio* with specimens of *E. parvus* in the collections of the British Museum convinced me that they are conspecific. *Leptodactylus pumilio* Boulenger is thus a junior synonym of *Eleutherodactylus parvus* (Girard).

THE NEW ECUADORIAN SPECIES

During two months of field work in the upper Amazon basin, a series of juvenile frogs of a new species of the genus *Leptodactylus* were collected. With the exception of *Leptodactylus laticeps,* they are the most distinctively colored species of *Leptodactylus* in life. As the species is so distinctive and apparently has not been collected previously, I prefer to describe the new species based on the juvenile specimens rather than await collection of adults.

The new species belongs to the Pentadactylus species group as provisionally defined earlier (Heyer, 1968). The group is in need of thorough revision to determine the status of the *L. pentadactylus* and *L. pentadactylus*-like populations. In addition to the new species described below, the species group consists of: *L. laticeps* Boulenger, 1918; *L. pentadactylus* (Laurenti) 1768 (probably a composite); *L. rhodomystax* Boulenger, 1883; *L. rhodonotus* (Gunther), 1868; *L. rugosus* Noble, 1923; *L. syphax* Bokermann, 1969. Members of this group have noticeable fringes on the toes as juveniles, but the fringes are absent in adults. The adult character state of free toes separates members of the Pentadactylus group from members of the Melanonotus and Ocellatus groups which have extensive toe fringes as adults. Species of the Marmoratus group are small, never exceeding 29 mm SV; species of the Pentadactylus group are large, greater than 60 mm SV. The most distinctive characteristic that separates members of the Pentadactylus group from the Fuscus group is the presence of thumb spines and chest spines (usually) in males of members of the Pentadactylus group. Male members of the Fuscus group lack thumb and chest spines. Members of the Fuscus group are moderate sized, only one species reaching 65 mm SV. Members of the Pentadactylus group have broad, rounded snouts from above, members of the Fuscus group have more pointed snouts.

For the new species I propose the name:

Leptodactylus knudseni, new species

Figure 2

Holotype.—LACM 72117, a juvenile female from Limoncocha, 0° 24′S, 76°37′W, Provincia de Napo, Ecuador. The specimen was collected in a pasture, in a decaying log (15 cm diameter) at 14:38 hrs on 3 August 1970 by Keith A. Berven and W. Ronald Heyer. Elevation 260 m.

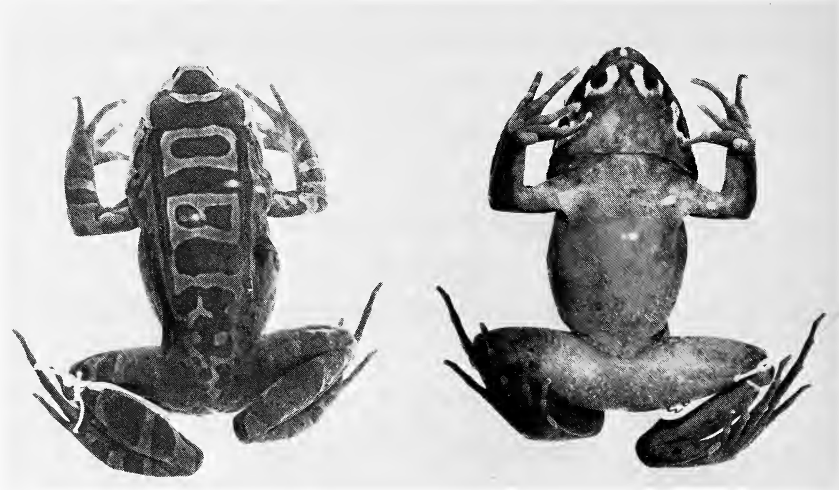


FIGURE 2. Dorsal (*left*) and ventral (*right*) views of paratype of *Leptodactylus knudseni*, LACM 72133, from Limoncocha, Provinica de Napo, Ecuador. Specimen is 62.5 mm SV.

Topoparatypes.—LACM 72118-149 (32 specimens), collected by Keith A. Berven and W. Ronald Heyer between 7 June and 4 August 1971.

Diagnosis.—In life, *Leptodactylus knudseni* is the only member of the Pentadactylus group with prominent chartreuse markings on a black background. In preservative, *L. knudseni* can be recognized by the presence of a pair of dorsolateral folds which differentiates it from *L. laticeps, L. rugosus,* and *L. syphax* all of which lack dorsolateral folds. The posterior surface of the thigh is uniformly black in *L. knudseni,* marbled in *L. pentadactylus* and *rhodonotus,* and distinctly light spotted on a dark background in *L. rhodomystax.*

Description of Holotype.—Snout ovoid from above, rounded in profile; canthus rostralis distinct; loreal concave; tympanum distinct, greatest diameter 5/6 eye diameter; vomerine teeth in two arched series extending posterior to choanae; finger lengths in order of decreasing size III > I > II = III, first finger much longer than second; inner metacarpal tubercle large, ovoid, smaller than heart-shaped outer metacarpal tubercle; dorsal surfaces shagreened, upper surface of tibia scattered with white tipped tubercles; one pair of weak dorsolateral folds extending from eye to sacrum, another pair of folds extending from posterior angle of eye over tympanum to angle of jaw, diffuse gland at angle of jaw; ventral surfaces smooth, belly disk fold distinct; toe tips not expanded; sides of toes with visible fringe, not extensively developed; subarticular tubercles moderately developed; outer metatarsal tubercle distinct, rounded, about two-thirds length of elongate inner metatarsal tubercle, tarsal fold distinct, extending 5/6 length of tarsus; no metatarsal fold; lower surface of tarsus scattered with white tipped tubercles; sole of foot smooth except for three or four white tipped tubercles on outermost edge of sole.

Measurements (in mm).—Snout-vent (SV), 63.2; head length, 22.9; head width, 22.8; interorbital distance. 5.0; greatest diameter of typmanum, 4.8; diameter of eye, 6.1; eye-nostril distance, 5.0; femur, 24.6; tibia, 27.4; foot, 30.8.

Coloration in preservative.—Dorsal surfaces black with light gray patterns, side of head light gray with dark triangles on upper lip, the dark triangle under the eye extending to the eye; the light gray of the side of the head bordering the lower half of the typmanum; tip of snout with light gray stripe bifurcating at nostrils, extending along canthus rostralis, continuous with light stripe on outer edge of eyelid and light interorbital bar; dorsum with light cross bars, breaking down posteriorly; dorsolateral fold dark; upper arm with light cross bars; upper femur and tarsus with irregular light cross bands; upper tibia with light pattern surrounding dark central area; chin bordered with alternating dark and light blotches; venter profused with melanophores scattered with small light dots (visible under magnification, melanophores contracted); bottom of tarsus and sole of foot black; posterior surface of thigh uniform black.

Variation.—The paratypes range in size from 32.8 to 62.5 mm. The variation (minimum-mean-maximum ± 1 standard error) in measurement ratios (expressed as per cent) among the type series is: head length/snout-vent, 36-38.7-40 ± 1.0; head width/snout-vent, 35-38.2-40 ± 1.4; femur/snout-vent, 40-43.0-46 ± 1.4; tibia/snout-vent, 39-43.3-46 ± 1.6; foot/snout-vent, 47-50.3-55 ± 2.0. The color pattern is similar among all the paratypes, the greatest variation occurring in the degree of light marking on the dorsum in the sacral region. In several specimens the melanophores are expanded on the belly, producing a black belly with small light dots.

The color in life of specimen LACM 72118 was typical of other specimens in the type series: posterior surface of thigh jet black; upper surfaces of legs with barely discernible yellowish green cross bands; belly gray with lighter punctations; chin with yellow marks along edge; dorsum with greenish yellow bands enclosing brownish green areas which are black bordered; iris gold-yellow above, rusty gold below; head mostly yellowish green.

Karyotype.—Twenty-four cells were examined from marrow and spleen tissue of specimens 72145, 72147, and 72148. The slides will be deposited in LACM. The terminology used is that defined by Patton (1967). Several chromosomes are borderline in their classification and vary according to their state of contraction. Three pairs of metacentrics (Fig. 3, chromosome pair numbers 1, 4, 9), 4 pairs of submetacentrics (Fig. 3, numbers 2, 5, 10, 11), and 4 pairs of subtelocentrics (Fig. 3, numbers 3, 6, 7, 8) are common. The Fundamental Number is 44; there are no secondary constrictions. An analysis of the karyotypic variation found within the genus is in progress and will be reported on separately. Preliminary results indicate that the karyotype of

L. knudseni is similar to the karyotypes of other members of the Pentadactylus and Ocellatus groups.

Ecology.—Two individuals were taken from a selectively logged secondary forest. The primary forest at Limoncocha is Tropical Moist Forest according to Holdridge's classification (1964). The other specimens were collected in a pasture (Fig. 4). All specimens were taken from under cover during the day: one from bark, five from under boards, 21 from under logs ranging in diameter from 15 to 70 cm, five from within rotten logs ranging in diameter from 15 to 30 cm. Other species of *Leptodactylus* collected in sympatry with *L. knudseni* at Limoncocha were *L. discodactylus, mystaceus, pentadactylus,* and *wagneri.* Further ecological aspects of the five sympatric *Leptodactylus* will be reported in a later paper by Heyer and Bellin.

Etymology.—The new species is named for Dr. Jens W. Knudsen, who was the most important influence in my decision to be a professional biologist, and who continues to encourage my research efforts.

Remarks.—Leptodactylus knudseni raises the number of recognized species from Ecuador to 10. The other nine species as summarized by Heyer and Peters (1971) are: *Leptodactylus discodactylus, hylaedactylus, labrosus,*

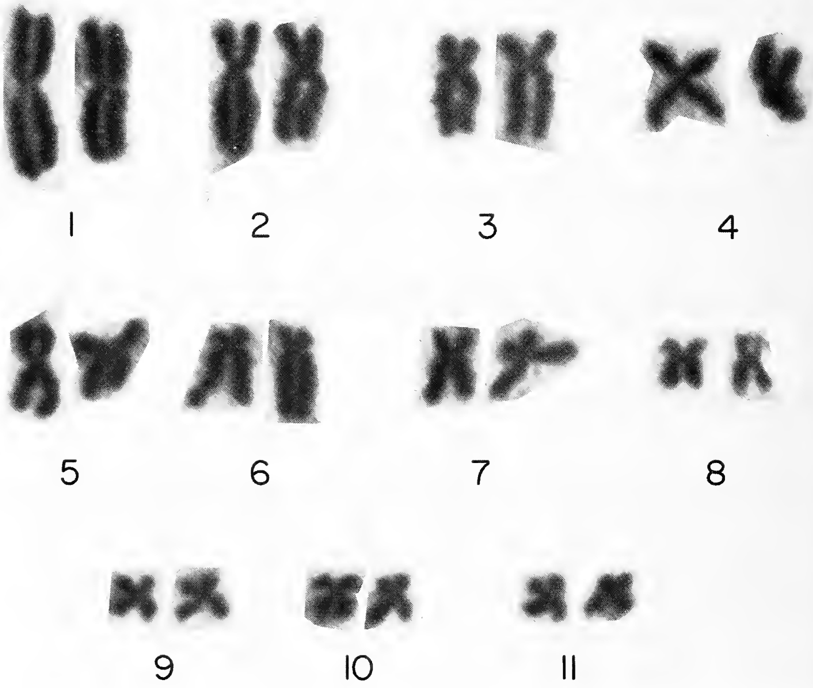


FIGURE 3. Karyotype of *Leptodactylus knudseni.* Marrow and spleen preparation from LACM 72147.

FIGURE 4. Pasture habitat at Limoncocha where most specimens of *Leptodactylus knudseni* were collected. Note selectively logged secondary forest in background.

melanonotus, mystaceus, pentadactylus, rhodomystax, ventrimaculatus, and *wagneri.*

Specimens of *Leptodactylus knudseni* will key out to couplet 5 in Heyer and Peters (1971: 169). The uniformly colored posterior surface of the thigh of *L. knudseni* will separate it from the variously patterned posterior thigh surfaces of *L. mystaceus, hylaedactylus,* and *ventrimaculatus.*

A PRELIMINARY KEY TO THE SPECIES OF THE PENTADACTYLUS GROUP

1A. Dorsal pattern of large discrete dark spots on a lighter background (Argentina) .... *L. laticeps*

1B. Dorsal pattern variable, never with distinct spots 2

  2A. Dorsolateral folds lacking 3

  2B. A pair of dorsolateral folds 4

3A. Dorsum very rugose; males with a single thumb spine (Guayana shield) .... *L. rugosus*

3B. Dorsum warty, not rugose; males with two thumb spines (Brasil, Mato Grosso) .... *L. syphax*

4A. Posterior surface of thigh uniform (Ecuador) .... *L. knudseni*
4B. Posterior surface of thigh patterned 5
5A. Posterior surface of thigh dark with discrete light spots (northern South America) .... *L. rhodomystax*
5B. Posterior surface of thigh marbled, never with distinct light spots 6
6A. Large, adults to 160 mm; males usually with a single thumb spine (widespread) .... *L. pentadactylus*
6B. Moderately large, adults to 80 mm; males with two thumb spines (Peru) .... *L. rhodonotus*

RESUMEN

Se demuestra que *Leptodactylus pumilio* Boulenger, 1920, es un sinónimo menor de *Eleutherodactylus parvus* (Girard). La especie Pentadactylus grupo de *Leptodactylus* es redefinida y una nueva especie de este grupo del Ecuador Amazónico es descrita. La presencia de pliegues dorsolaterales combinada con la uniforme coloración negra de la superficie posterior del muslo, distingue a la nueva especie de los otros miembros del grupo. El cariotipo de la nueva especie tiene un número diploide de 22 cromosomas birrámeos sin constricciones secundarias. Se proporciona una clave para las especies del grupo Pentadactylus.

LITERATURE CITED

BOULENGER, G. A. 1920. Descriptions of two new frogs from Brazil. Ann. Mag. Nat. Hist. 9(5):122-124.

GIRARD, C. F. 1853. Descriptions of new species of reptiles, collected by the U.S. Exploring Expedition, under the command of Capt. Charles Wilkes, U.S.N. Second part.--Including the species of batrachians, exotic to North America. Proc. Acad. Nat. Sci. Phila. 6:420-424.

HEYER, W. R. 1968. Biosystematic studies on the frog genus *Leptodactylus*. Ph.D. Dissertation, Univ. So. Calif. 234 p.

————. 1970. Studies on frogs of the genus *Leptodactylus* (Amphibia, Leptodactylidae). VI. Biosystematics of the Melanonotus group. Los Angeles Co. Mus., Contrib. Sci. 191:1-48.

————, AND J. A. PETERS. 1971. The frog genus *Leptodactylus* in Ecuador. Proc. Biol. Soc. Wash. 84(19):163-170.

HOLDRIDGE, L. R. 1964. Life zone ecology. Tropical Science Center, San Jose, Costa Rica. 124 p.

PATTON, J. L. 1967. Chromosome studies of certain pocket mice, genus *Perognathus* (Rodentia: Heteromyidae). J. Mammal. 48:27-37.

Accepted for publication April 17, 1972

Printed in Los Angeles, California by Continental Graph

NUMBER 232
OCTOBER 17, 1972

PRELIMINARY REPORT ON LATE CRETACEOUS MAMMALS FROM THE EL GALLO FORMATION, BAJA CALIFORNIA DEL NORTE, MEXICO

By JASON A. LILLEGRAVEN

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1972 CBE Style Manual, third edition (AIBS) is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1972 CBE Style Manual, third edition (AIBS) in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Any changes or alterations, other than typographical corrections, will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

PRELIMINARY REPORT ON LATE CRETACEOUS MAMMALS FROM THE EL GALLO FORMATION, BAJA CALIFORNIA DEL NORTE, MEXICO[1]

By JASON A. LILLEGRAVEN[2]

ABSTRACT: A preliminary study of the mammalian fossils from the late Campanian (Late Cretaceous) "El Gallo Formation" west of El Rosario, Baja California del Norte, Mexico suggests the presence of *Mesodma, cf. M. formosa* (Ectypodontidae, Multituberculata), *?Stygimys* sp., species probably new (Eucosmodontidae, Multituberculata), *Pediomys* sp., species probably new (Pediomyidae, Marsupialia), and a new genus of indefinite familial affinities (Insectivora). The sample provides the first knowledge of Mesozoic mammals from the west coast of North America. Despite taxonomic differences from the distant and better known mammalian local faunas of the Rocky Mountain region, the composition of the El Gallo assemblage is basically similar to taxa found in the Western Interior and does not suggest a profound endemism.

INTRODUCTION

Prior to the beginning of the present study, Mesozoic mammals from North America were unknown from rocks west of the Rocky Mountains. Field workers in the summer of 1968 under the direction of Dr. William J. Morris discovered remains of multituberculate mammals in the "El Gallo Formation," Baja California del Norte, Mexico (Fig. 1). Fossils of therian mammals were discovered in the summer of 1970 by members of another field party working under my supervision. The present paper is a preliminary report to the scientific community of these significant finds. Hopefully, future collecting and study will result in a monographic treatment of the potentially extremely important mammalian local fauna.

The "El Gallo Formation" is thought to be middle to late Campanian in age (see Morris, 1967: 1539). An unpublished potassium-argon date of approximately 73 million years is now available from a tuff in the lower one-third of the "formation" (Morris, personal communication). Although principally nonmarine in origin, a small number of marine interbeds are known. Rocks are well exposed in deeply dissected badlands and dip approximately 10° regularly to the northeast. Only a small percentage of the exposed

---

[1] EDITORIAL COMMITTEE FOR THIS CONTRIBUTION
William A. Clemens
Richard C. Fox
David P. Whistler

[2] Research Associate, Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County; and Department of Zoology, San Diego State University, San Diego, California 92115.

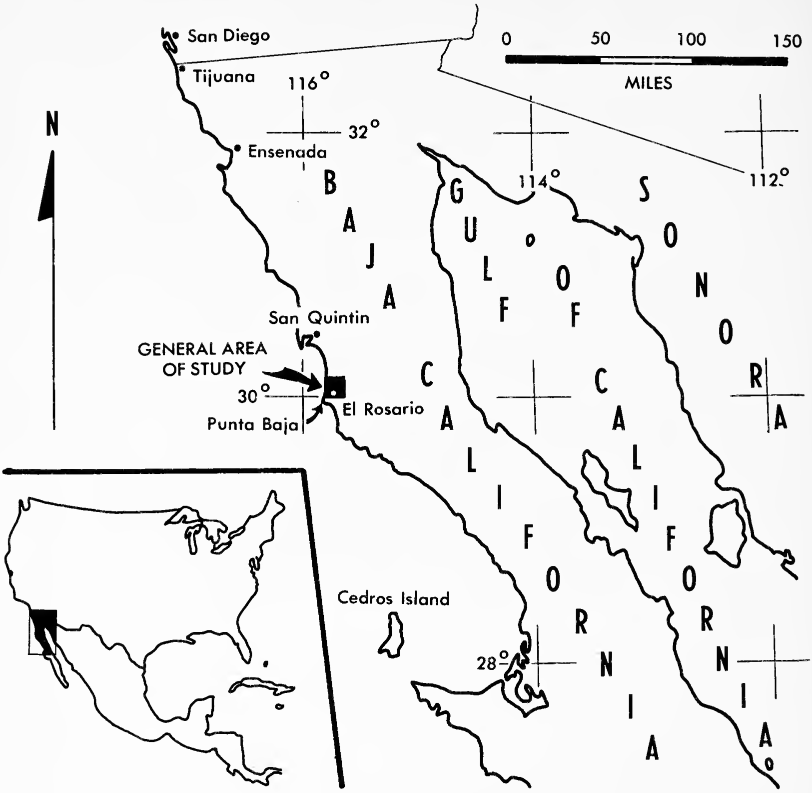


FIGURE 1. General locality maps.

area is accessible to motor vehicles. Depositional facies shift from dominantly conglomeratic near the basement source area approximately six miles to the east of the fossiliferous area to complex but generally finer clastic facies in the west. Petrified wood is common throughout. The "El Gallo Formation" was proposed by Kilmer in his unpublished Ph.D. dissertation (1963). No description or type section has ever been published, nor is the dissertation available through the microfilm services. Thus, until described in publication form, the unit must be considered informally.

LOCALITIES

Known fish-, amphibian-, lizard-, and dinosaur-bearing localities from the "El Gallo Formation" are numerous and are recorded in the files of the Vertebrate Paleontology Section, Natural History Museum of Los Angeles County. Although dinosaur bones may be expected in nearly any sedimentary rock in the area, it is interesting and important to note that all small-vertebrate localities discovered to date are in gray to black silty claystone beds. For unknown reasons, fossils of microvertebrates are rare in the paler and coarser-textured rocks.

Fossil mammals have been discovered at three localities at various stratigraphic levels, all of which are located within the middle one-third of the formation, well above the dated tuff. Because there are no surveyed maps of the area, localities were plotted on aerial photographs and described in field notes augmented by Polaroid photos. These are also on file in the Natural History Museum of Los Angeles County. The numbers of the mammal-bearing localities are: LAV-7170, LAV-7171, LAV-7172.

METHODS

Known productive layers were quarried by breaking rocks into walnut-sized or smaller pieces while looking for freshly exposed bones. Bone-bearing clods were wrapped for later preparation in the laboratory. The others lacking exposed bones were dropped into burlap bags and carried to a soaking-tub at camp. Rocks were soaked 24 hours in kerosene, which was then siphoned off and replaced by water. The extent of breakdown of the rocks was then dramatic, for it was practically nonexistent after soaking only in water. The resultant mud was scooped into a table height large stacked screen-box system. The upper seive was of standard gauge window screening, and the lower of 40 wires per inch bronze wire cloth. A small pump carried brackish water from a lagoon via a hose to above the mud, and gentle spraying washed away all but a concentrate of rocks and skeletal fragments. The concentrate was air dried on long burlap strips and sorted for fossils at a later time. Although considerable care to avoid breakage of the fossils was exercised through all stages of the washing process, I feel the "washing table" technique used is less desirable than others. It is necessary to scoop the fossil-bearing mud from the soaking-tub onto the screens, and even the gentlest of water spraying is damaging to small delicate bones and teeth. I feel that the quarry matrix should be soaked, washed, and dried in the same screen box and that during washing the fossil-bearing mud should be agitated gently while completely submerged in water.

All measurements (which follow the citation of individual teeth in the various "Referred or available specimens" sections) are in millimeters and were made with an EPOI Shopscope at San Diego State University using the orientations specified by Lillegraven (1969: 16). Abbreviations of measurements are as follows:

A-P	Antero-posterior length	Post-W	Posterior width
W	Greatest width	W-Tri	Width of trigonid
Ant-W	Anterior width	W-Tal	Width of talonid

The abbreviation LACM is used throughout the descriptions to indicate specimens cataloged in the Natural History Museum of Los Angeles County (Vertebrate Paleontology).

SYSTEMATIC DESCRIPTIONS

Class Mammalia

Subclass Allotheria

Order Multituberculata

Family Ectypodontidae Sloan and Van Valen, 1965

[original name emended, Van Valen and Sloan, 1966]

Genus *Mesodma* Jepsen, 1940

Mesodma, cf. ***M. formosa*** (Marsh), 1889b

Holotype: Yale Peabody Museum 11812, left P_4 (Marsh, 1889b, pl. 8, fig. 36-39).

Referred specimens: LACM 27588, M^1 fragment (W 1.21); LACM 27589, M^2 (A-P 1.33, W 1.33); LACM 27590, M_2 (A-P 1.38, W 1.26).

Localities: LAV-7170 and LAV-7171.

Distribution of Mesodma formosa: Upper part of Edmonton Formation, Alberta; Hell Creek Formation, Montana, and South Dakota; type Lance Formation, Wyoming; possibly Kirtland and Fruitland Formations, New Mexico (see list, Fassett and Hinds, 1971: 19); "El Gallo Formation," Baja California del Norte.

Comments: The three specimens here identified as *Mesodma formosa* cannot be distinguished from specimens of that taxon from Upper Cretaceous deposits of the Rocky Mountain region. The size ranges and descriptions follow closely and, until more evidence is forthcoming, I feel no new names should be defined despite the differences in ages of deposits. Because of the lack of equivalent dental elements, comparison is impossible with *M. senecta* (see Fox, 1971a).

Family Eucosmodontidae (Jepsen, 1940)

Genus *Stygimys* Sloan and Van Valen, 1965

?Stygimys sp.

Referred specimens: LACM 27591, M^2 (A-P 1.96, W 1.70) (Figure 2, A., B., C.); LACM 27592, I_1.

Localities: LAV-7170 and LAV-7172.

Distribution of genus: Hell Creek Formation, Montana; various lower and middle Paleocene localities, Rocky Mountain region; "El Gallo Formation," Baja California del Norte.

Comments: The M^2 here referred to *?Stygimys* sp. (Fig. 2) is strikingly similar in overall morphology with specimens (e.g., LACM 27593) of *Stygimys kuszmauli* from the Bug Creek Anthills Local Fauna of the Hell Creek Formation, Montana (Sloan and Van Valen, 1965). However, distinct differences do exist in that the El Gallo specimen is significantly smaller than

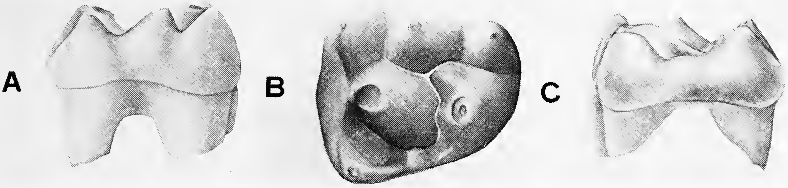


FIGURE 2. A.-C. ?*Stygimys* sp., species probably new, LACM 27591 (LAV-7170) right M^2: A. lingual view; B. occlusal view; C. labial view. Approximately 13X.

the Hell Creek material (the latter are approximately A-P 2.6, W 2.3). Also, the El Gallo specimen has smoother cusp sides with much less ornamentation than the usual Hell Creek M^2's referred to *Stygimys.* The greater epi- and inter-cusp ornamentation on the Hell Creek specimens is quite possibly a specialization advanced from the primitive condition.

Additional, but admittedly weak, evidence suggesting the assignment of the M^2 to *Stygimys,* or at least the Taeniolabidoidea, is a fragmentary lower incisor from Locality LAV-7172 of the "El Gallo Formation" showing a distinct rodentlike eucosmodontid enamel distribution. *Stygimys* and *Catopsalis* are the only known North American Cretaceous genera possessing the eucosmodontid-type incisor enamel pattern (see Sloan and Van Valen, 1965:224). Eucosmodontid multituberculate teeth have recently been recovered from the Upper Cretaceous Kirtland and Fruitland formations of New Mexico (see list, Fassett and Hinds, 1971: 19).

Although I consider the El Gallo specimen to be distinct at least at the specific level from previously described material, I believe it would be wise to refrain from adding a new name to the taxonomic literature until a larger sample is available to allow the writing of a secure diagnosis.

Additional Multituberculate Teeth

Four other multituberculate teeth have been recovered that should be mentioned but are, in my opinion, unidentifiable generically at the present time. LACM 27594 (LAV-7172) is an isolated P^3 (A-P 1.19, W 1.02) with four cusps. It resembles in basic structure the P^3 of *Mesodma formosa* illustrated by Lillegraven (1969:22, Fig. 8, *2*) but is proportionately shorter anteroposteriorly. Two P_4's (LACM 27595 from LAV-7170 and 27596 from LAV-7172) are represented by the posterior halves only, and no possibility exists for making serration counts or lobe descriptions. Finally, a fragmentary questionable lower right incisor tip (LACM 27597 from LAV-7172) has been recovered. Little can be said about it except that it lacks a eucosmodontid enamel pattern but has a deep longitudinal trough along what I interpret to be the dorsolateral surface of the tooth.

Subclass Theria
Infraclass Metatheria
Order Marsupialia
Family Pediomyidae Clemens, 1966
Genus *Pediomys* Marsh, 1889a

Pediomys sp.

Only available specimen: LACM 27598, M^1 (A-P 1.67 [est.], Ant-W 1.44, Post-W 1.61) (Figure 3, A., B.).

Locality: LAV-7172.

Distribution of genus: "El Gallo Formation," Baja California del Norte; Oldman (unpublished) and Milk River formations, Alberta; Judith River Formation, Montana (in press, A. Sahni); upper part of Edmonton Formation, Alberta; Hell Creek Formation, Montana and South Dakota; Lance Formation, Wyoming; North Horn Formation, Utah; possibly Kirtland and Fruitland Formations, New Mexico (see list, Fassett and Hinds, 1971:19).

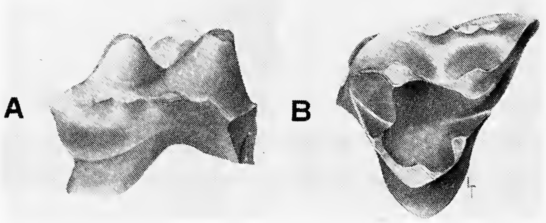


FIGURE 3. A.-B. *Pediomys* sp., species probably new, LACM 27598 (LAV-7172), left M^1: A. labial view; B. occlusal view. Approximately 17X.

Comments: The M^1 (Figure 3) almost certainly represents a heretofore undescribed small species of the genus *Pediomys*. The overall morphology most closely resembles the teeth of *P. elegans* (see Clemens, 1966), but a series of significant differences exist. The transverse measurements of LACM 27598 are proportionately less than in any other pediomyid save *P. exiguus* of the Milk River Formation of Alberta (see Fox, 1971b). As in most specimens of *P. elegans,* stylar cusp B and the stylar shelf labial to the paracone are lacking, but, in contrast, stylar cusp C in LACM 27598 is slightly larger and more robust than stylar cusp D. Stylar cusp D in LACM 27598 is long, low, and anteroposteriorly twinned, giving the appearance of beading. Wear facets are observed both on stylar cusps C and D. Unfortunately, the anterolabial corner of LACM 27598 is broken away. Lingual cingula are lacking. Details of the protocone, conules, paracone, and metacone of LACM 27598 are similar to those of the teeth of *P. elegans* (see Clemens, 1966:37). Wear facets are illustrated in Figure 3 and indicate strong shearing function along the postmetacrista in the usual therian manner. The tooth is strongly three-rooted and shows numerous differences from teeth identified as marsupial DP^3's (e.g., Clemens, 1966, fig. 30 and Lillegraven, 1969, fig. 23, *5*). I believe the tooth to be part of the molar series.

Although the size and general proportions of LACM 27598 are near those of specimens of *Pediomys exiguus,* I believe different species are represented. *P. exiguus* possesses a stylar cusp B, although reduced, usually lacks a stylar cusp C, and has an undivided bladelike stylar cusp D (Fox, 1971b:153).

I can see no serious objections to allying the species represented by LACM 27598 closely with *Pediomys elegans.* I would not unite them as the same species because significant differences in morphology, in geochronologic age, and in geographic location exist. On the other hand, the probable new species is known from only a single upper molar, and I consider it prudent to wait until the hypodigm increases before entering a new specific name into the taxonomic literature.

Infraclass Eutheria
Order Insectivora
Family indefinite
New genus

Available specimens: LACM 27599, M_2 (A-P 2.57, W-Tri 1.58, W-Tal 1.65) (Figure 4, A., B., C.); LACM 27600, mandibular fragment with talonid of M_1 (W-Tal 1.48), M_2 (A-P 2.29, W-Tri 1.50, W-Tal 1.46 [est.]), M_3 (A-P 2.43, W-Tri 1.45, W-Tal 1.33) (Figure 5, A., B., C.).

Locality: LAV-7172.

Distribution: Known only from "El Gallo Formation," Baja California del Norte.

Descriptions: LACM 27599 (Figure 4) is tentatively considered to be M_2 and is essentially unworn. The tooth is fairly robust in general construction with a moderately high crowned trigonid. The protoconid is considerably higher than the metaconid. The paraconid is low, somewhat anteriorly-projecting, and anteroposteriorly compressed. The paraconid is well separated

FIGURE 4. A.-C. Insectivora, family indefinite, new genus, LACM 27599 (LAV-7172), right M_2: A. labial view; B. occlusal view; C. lingual view. Approximately 10X.

from the metaconid and is labial to it. A short, weak cingulum is present at the anterior base of the protoconid. The talonid is slightly wider than the trigonid and the talonid cusps are well defined and separated. The talonid basin is deeply concave. The hypoconulid is close to the entoconid but cannot be strictly said to be twinned with it. The hypoconid is the highest talonid cusp, the hypoconulid the lowest. A cingulum descends steeply from the labial edge of the hypoconulid lateroventrally to the posterolabial base of the hypoconid. The cristid obliqua meets the posterior midline of the base of the protoconid.

LACM 27600 (Figure 5) is a mandibular fragment with a last molar and two preceding molars. These are tentatively identified as M_{1-3}. All three teeth are severely worn and M_1 is represented only by the posterior margin of the talonid. Cusps are distinguishable as individual units only on M_3 but the general cusp arrangement appears to have been similar to that on LACM 27599. Cingula on the available parts of all three teeth are as on LACM 27599.

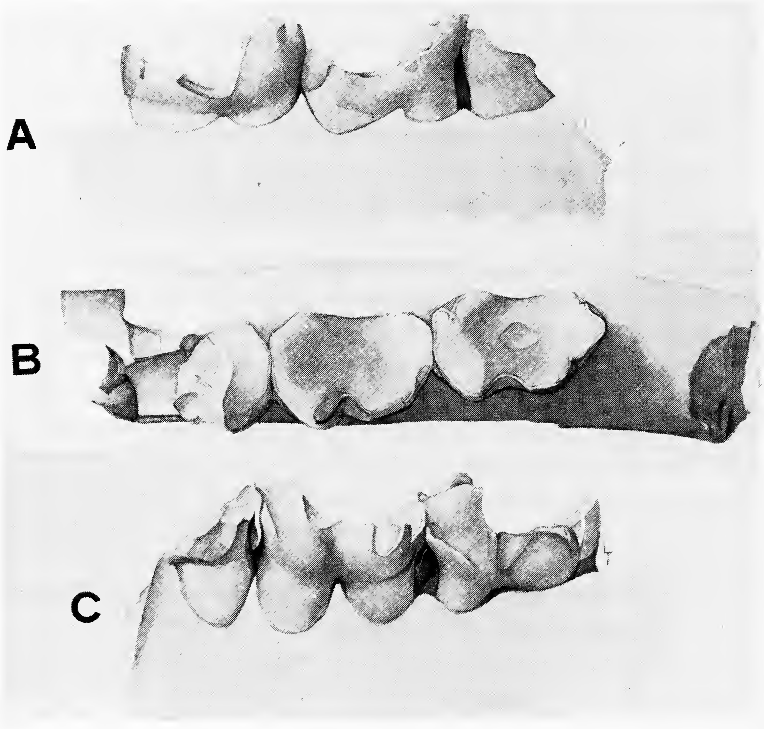


FIGURE 5. A.-C. Insectivora, family indefinite, new genus, LACM 27600 (LAV-7172), left mandibular fragment with M_{1-3}: A. lingual view; B. occlusal view; C. labial view. Approximately 9X.

The hypoconulid of the M_3 is more strongly produced posteriorly than in any other Cretaceous therian known to me, and the proportional width of the talonid of the M_3 is considerably greater than in most Cretaceous therians.

Comments: LACM 27599 and 27600 are identified as eutherian because: (1) the paraconid is proportionately small and labially placed; (2) the hypoconulid on the M_3 is strongly produced posteriorly; (3) the hypoconulid is not closely twinned with the entoconid. The combination of these features is common among placental mammals but rare among marsupials. The significance of the position of the hypoconulid (criterion "3" above) is not completely certain. As stated in the description, it is not as closely twinned with the entoconid as in most Mesozoic marsupials, yet is nearer the entoconid than in most Cretaceous eutherians yet described.

The affinity of the new species at lower categorical levels is uncertain. I placed the species in the Order Insectivora as an act of conservatism. Familial relationships are totally obscure. The specimens suggest somewhat greater similarity with molars of Late Cretaceous palaeoryctid taxa (e.g., *Cimolestes magnus,* see Lillegraven, 1969) than with other known Cretaceous groups, but evidence is insufficient to warrant even a tentative familial assignment. Considerable similarity in general form and size also exists with the "Champ-Garimond tooth" discovered in Upper Cretaceous rocks of France (Ledoux et al., 1966). The identification of that specimen, however, has also yet to be determined (see McKenna, 1969:228). No striking resemblances have been recognized with described Asiatic Cretaceous eutherians (e.g., see Kielan-Jaworowska, 1968) or the one upper molar described by Fox (1970) from the Milk River Formation of Alberta, Canada. Although a strongly developed hypoconulid on the M_3 is a feature common to most early primates, the El Gallo specimens have unusually broad and elongated talonids, paraconids well separated from the metaconids, and other features decidedly different from the most primitive known primates.

Both specimens are very tentatively referred to the same genus, and perhaps they even represent the same species. The specimens are unquestionably representative of a previously unknown genus. However, because of the scanty material at hand, I have declined to name the taxon. Despite any nomenclatorial inconvenience that may be caused, I feel it prudent to wait until adequate reference material becomes available from future field work.

DISCUSSION

The known El Gallo specimens give a tantalizing but misty first glimpse of the Late Cretaceous mammalian fauna of the West Coast of North America. Although all but one of the species discovered so far are probably new, most of the genera seem referable to those well known from the Rocky Mountain region. The El Gallo peri-Pacific Late Cretaceous collection represents ecological, geographical, and temporal settings previously unsampled. One would thus expect taxonomic differences from the distant and better known

Rocky Mountain assemblages and, indeed, they have been found. However, the known assemblage of El Gallo mammals does not suggest great and profound endemism of the Late Cretaceous fauna of Baja California. At the present stage of our knowledge, I see no particular reason to suggest geographic isolation of the peninsula from the remainder of the continent.

ACKNOWLEDGMENTS

The entire project was visualized, implemented, and supervised by Dr. William J. Morris, Department of Geology, Occidental College. Field and laboratory support was generously given by the Vertebrate Paleontology Section, Natural History Museum of Los Angeles County and by a continuing grant from the National Geographic Society. Dr. Ismael Ferrusquia V. of the Instituto de Geologia, Universidad Nacional Autonoma de Mexico participated in the field work in the summer of 1970, personally found the therian mandible, and contributed in many ways to the success of the summer. Dr. Ferrusquia is currently pursuing further investigations on the El Gallo fauna of small vertebrates. The devoted efforts and friendship of the family of Sr. Pedro Fonseca of El Rosario are deeply appreciated. A number of field assistants added greatly to the success of the expeditions. Principal among these were Messrs. Alan Tabrum, Gregg Franz, Richard Bergreen, and Bruce Burns. Illustrations for the paper were prepared by Miss Linda Thompson.

Thanks also go to Drs. Donald E. Savage and William A. Clemens, Jr. of the University of California, Berkeley, and to Dr. Richard C. Fox of the University of Alberta for reading the manuscript and suggesting changes. My wife, Bernice Ann Lillegraven, was helpful in many aspects of the preparation of the manuscript.

Most importantly, the governments of Mexico and Baja California and the citizens of El Rosario are gratefully acknowledged for their generous and concerned interest shown in the project.

RESUMEN

Un estudio preliminar de los aprovechables fósiles de mamíferos de la "formación El Gallo" del último Campaniano (último Cretáceo) al oueste de El Rosario, Baja California del Norte, México, sugiere la presencia de *Mesodma, cf. M. formosa* (Ectypodontidae, Multituberculata), ?*Stygimys* sp., especie probablemente nueva (Eucosmodontidae, Multituberculata), *Pediomys* sp., especie probablemente nueva (Pediomyidae, Marsupialia), y uno género nuevo de incierto afinidad de la familia (Insectívora). Esta muestra representa el primero conocimiento de los mamíferos de la Secundaria de la costa oeste de Norte América. A despecho de las diferencias taxonómicas de las distantes y más conocidas faunas de mamíferos de la región de Montañas Roqueñas, la composición de la colección de El Gallo es fundamentalmente semejante a taxa que es hallada an el interior del oeste y no sugiere una endemia profunda.

LITERATURE CITED

CLEMENS, W. A., JR. 1966. Fossil mammals of the type Lance Formation, Wyoming. Part II. Marsupialia. Univ. Calif. Publ. Geol. Sci. 62. *vi*+ 122 p.

FASSETT, J. E., AND J. S. HINDS. 1971. Geology and fuel resources of the Fruitland Formation and Kirtland Shale of the San Juan Basin, New Mexico and Colorado. U. S. Geol. Surv. Prof. Pap. 676. 76 p.

FOX, R. C. 1970. Eutherian mammal from the early Campanian (Late Cretaceous) of Alberta, Canada. Nature 227:630-631.

________. 1971a. Early Campanian multituberculates (Mammalia: Allotheria) from the Upper Milk River Formation, Alberta. Canadian J. Earth Sci. 8: 916-938.

________. 1971b. Marsupial mammals from the early Campanian Milk River Formation, Alberta, Canada. *In* (D. M. Kermack and K. A. Kermack, eds.) *Early Mammals,* Zool. J. Linnean Soc. 50, Suppl. 1: 145-164.

JEPSEN, G. L. 1940. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming. Am. Philos. Soc., Proc. 83: 217-340.

KIELAN-JAWOROWSKA, Z. 1968. Results of the Polish-Mongolian Palaeontological Expeditions, Part I. Preliminary data on the Upper Cretaceous eutherian mammals from Bayn Dzak, Gobi Desert. Palaeontologia Polonica 19: 171-191.

KILMER, F. H. 1963. Cretaceous and Cenozoic stratigraphy and paleontology, El Rosario area, Baja California, Mexico. Unpublished Ph.D. dissertation, Univ. Calif., Berkeley.

LEDOUX, J.-C., J.-L. HARTENBERGER, J. MICHAUX, J. SUDRE, and L. THALER. 1966. Découverte d'un mammifère dans le Crétacé supérieur a dinosaures de Champ-Garimond près de Fons (Gard). Comptes rendus des séances de l'Académie des Sciences, Paris 262: 1925-1928.

LILLEGRAVEN, J. A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. Univ. Kansas. Paleontol. Contrib., Art. 50 (Vertebrata 12). 122 p.

MARSH, O. C. 1889a. Discovery of Cretaceous Mammalia: Am. J. Sci., ser. 3, 38: 81-92.

________. 1889b. Discovery of Cretaceous Mammalia, Part 2. Am. J. Sci., ser. 3, 38: 177-180.

MCKENNA, M. C. 1969. The origin and early differentiation of therian mammals. Ann. N. Y. Acad. Sci. 167: 217-240.

MORRIS, W. J. 1967. Baja California: Late Cretaceous dinosaurs. Science 155: 1539-1541.

SLOAN, R. E., and L. VAN VALEN. 1965. Cretaceous mammals from Montana. Science 148: 220-227.

VAN VALEN, L., and R. E. SLOAN. 1966. The extinction of the multituberculates. Syst. Zool. 15: 261-278.

Accepted for publication April 4, 1972

Printed in Los Angeles, California, by Anderson, Ritchie and Simon

NUMBER 233
OCTOBER 17, 1972

A NEW GENUS OF CYPRINODONTID FISH FROM NUEVO LEON, MEXICO

By Robert Rush Miller and Vladimir Walters

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1972 CBE Style Manual, third edition (AIBS) is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1972 CBE Style Manual, third edition (AIBS) in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Any changes or alterations, other than typographical corrections, will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

VIRGINIA D. MILLER
Editor

A NEW GENUS OF CYPRINODONTID FISH FROM NUEVO LEON, MEXICO[1]

By ROBERT RUSH MILLER[2] AND VLADIMIR WALTERS[3]

ABSTRACT: *Megupsilon aporus,* a new genus and species of cyprinodontid fish related to *Cyprinodon,* is described from a large series of individuals from an interior basin in Nuevo León, México. It is unique in having a huge Y-chromosome in the male and in the sexually dimorphic chromosome number (male $2n=47$, female 48), as well as in lacking pores in the cephalic sensory canal system, possessing two distinctive behavioral traits (jaw-nudge and opercular rotation) not developed in *Cyprinodon,* and having blackened scales on the side in the nuptial male which also lacks a black terminal band on the caudal fin. *Megupsilon* inhabits shallower water than does the species of *Cyprinodon* with which it is sympatric. It also has a much shorter gut than *Cyprinodon* and is carnivorous, whereas the local *Cyprinodon* is herbivorous. The new genus is a relict, representing an earlier invasion of the basin than does the species of *Cyprinodon.*

INTRODUCTION

Cyprinodontoid fishes comprise nearly one-third of the known freshwater fish fauna of México (approximately 115 of 390 species). Of these, the autochthonous Goodeidae and the Cyprinodontidae together have about as many species as do the Poeciliidae, whereas the fourth family of the group, the Anablepidae, is monotypic. The novelty described here is the third known endemic Mexican genus of the Cyprinodontidae (*Garmanella* Hubbs, 1936 and *Cualac* Miller, 1956 are the other two); its discovery further emphasizes the richness and diversity of the continental fish fauna of México. The new genus is distinguished from all other members of the family karyotyped thus far by the very large Y-chromosome in the male and the sexually dimorphic chromosome number (Uyeno and Miller, 1971). It is confined to a single, spring-fed pond on a high, endorheic plateau in Nuevo León, northeastern México.

---

[1] EDITORIAL COMMITTEE FOR THIS CONTRIBUTION
Robert J. Lavenberg
Robert K. Liu
Camm Swift

[2] Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104.

[3] Department of Zoology, University of California, Los Angeles, California; and Research Associate in Ichthyology, Natural History Museum of Los Angeles County, Los Angeles, California 90007.

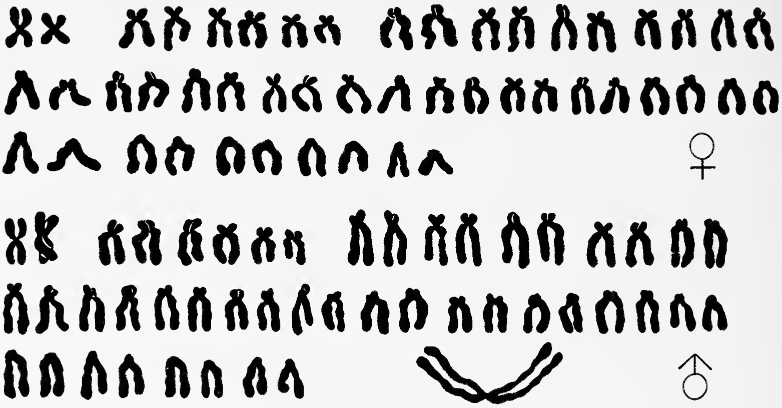


FIGURE 1. Karyotype of *Megupsilon aporus.*

Megupsilon, new genus
Figures 1-4

Type species. Megupsilon aporus, new species.

Diagnosis. A *Cyprinodon*-like killifish with uniserial tricuspid jaw teeth from which it is distinguished by having: (1) a huge Y-chromosome in the male (unique for cyprinodontoids) and a sexually dimorphic diploid chromosome

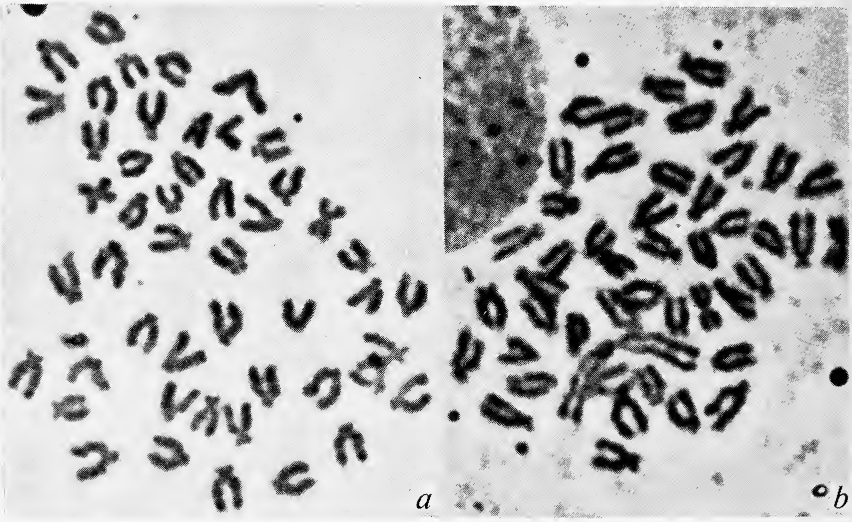


FIGURE 2. Photomicrographs of somatic chromosome complements of *a,* female (2n = 48) and *b,* male (2n = 47), of *Megupsilon aporus* x 1900.

number, 47 in the male and 48 in the female (Figs. 1-2); (2) the cephalic sensory canal system represented by exposed neuromasts only (no trace of canals or pores); (3) two distinctive behavioral traits (see below); (4) blackened scales on the side between dorsal and anal fins in the male (Fig. 3); and (5) nuptial male without black terminal border on caudal fin. In addition, the following combination of characters separates this genus from all others having tricuspid teeth that comprise the North American subfamily Cyprinodontinae (for diagnosis, see Uyeno and Miller, 1962: 528): entire preorbital region scaleless; pelvic fins and girdle lacking; intestine of adult usually shorter than body length; gill rakers few (10-13); anal fin of female about as large as her dorsal fin (Fig. 3). The pelvic fins and girdle are lacking also in *Cyprinodon diabolis* and in the Old World species *Aphanius (Tellia) apodus,* and the development of squamation in the preorbital region is variable in *Cyprinodon* and lacking in *Floridichthys.*

Relationships. The new genus is obviously closest to *Cyprinodon* with which it shares many traits, e.g., tricuspid teeth, body shape, size and position of fins, squamation, and osteological characters. It has diverged sufficiently

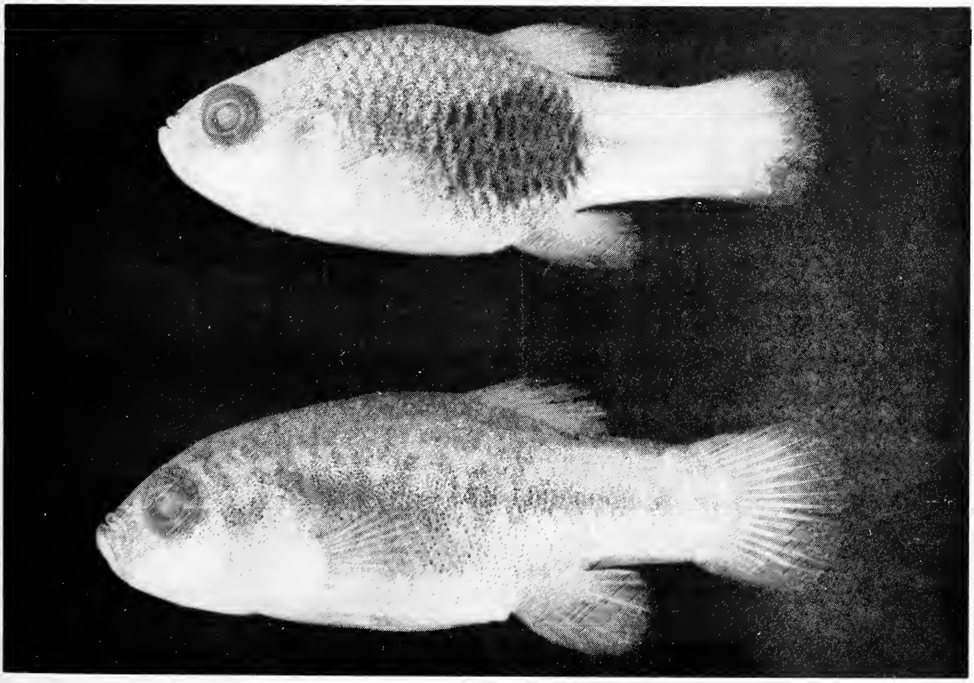


FIGURE 3. Paratypes (UMMZ 189020) of *Megupsilon aporus. Above,* male, 24 mm SL.; *below,* female, 27.5 mm SL. Photo by Louis P. Martonyi.

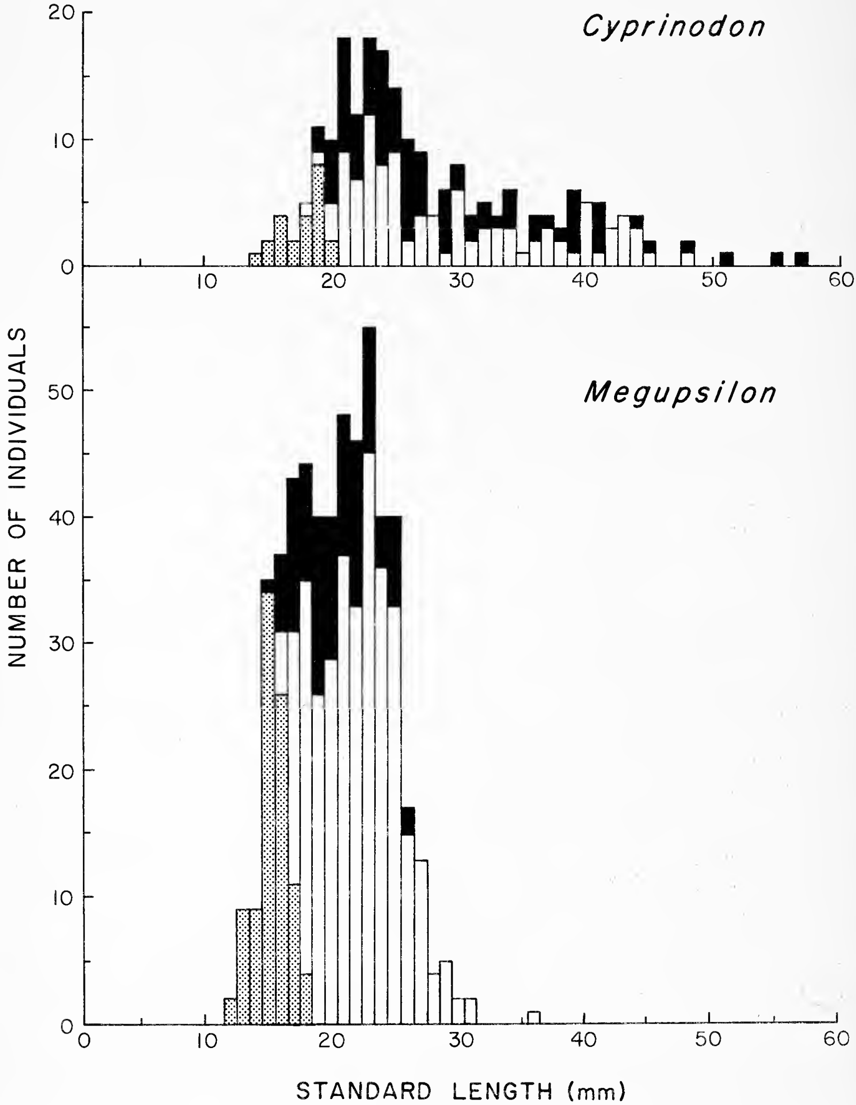


FIGURE 4. Size frequency of 216 *Cyprinodon* sp., UMMZ 189021, and 533 *Megupsilon aporus,* UMMZ 189020, from El Potosí, all collected 25 March 1968. Stipple, immatures; black, males; clear, females.

that it is behaviorally and reproductively incompatible with *Cyprinodon* and both premating and postmating isolating mechanisms prevent its hybridization with that genus. Robert K. Liu (personal communication, 1970) has observed two traits, jaw-nudge and opercular rotation, found in no species of *Cyprinodon* tested and has failed to obtain hybrids in forced matings between the two genera.

Etymology. The generic name is from the Greek prefix *μεγα* (mega-), from *μεγασσ* (megas) meaning big, great, and *υψιλον* (upsilon), name of the Greek letter Υ (*υ*), in reference to the huge Y-chromosome; gender is neuter. The specific trivial, *aporus,* is from the Latin, meaning without pores, in reference to the lack of pores in the sensory cephalic canal system. We are indebted to Carl L. Hubbs for proposing the generic name.

The material used in the following description is deposited in The University of Michigan Museum of Zoology (UMMZ), University of California, Los Angeles (UCLA), and the Natural History Museum of Los Angeles County (LACM).

Megupsilon aporus, new species

Figures 1-3

Types. Holotype, a breeding male, UMMZ 189018, 21.4 mm SL, collected by R. R. Miller and H. L. Huddle at El Potosí, Nuevo León, México, 25 March 1968. Allotype, an adult female, UMMZ 189019, 26.6 mm SL, taken with the holotype. Paratopotypes: UMMZ 189017, an adult male, 19 mm SL, collected by Miller and Huddle at the type locality, 23 February 1961; UMMZ 189020, 510 juvenile to adult (including a male and female cleared and stained), 12-36 mm SL, taken with the holotype; LACM 32147-1, 25 juvenile to adult, 11-28 mm SL, (ex UMMZ 189020); UCLA, W68-21, 124 juvenile to adult, 13-28 mm SL, collected by Vladimir Walters and John Bleck at the type locality, 15 February 1968.

Additional Material (not designated as paratypes). UCLA, W68-74, 151 juvenile to adult, 7-31 mm SL, collected by Vladimir Walters and Bruce J. Turner at the type locality, 29 June 1968. Food studies were performed on 60 of these specimens.

Diagnosis. See generic diagnosis (genus is monotypic).

Description. The generic diagnosis of this species includes most of the important specific characters. Form and pigmentation are portrayed in Figure 3 and other diagnostic features appear in Figures 1 and 2. Proportional measurements are given in Table 1. Methods of counting and measuring are those used by Miller (1948: 9-13). The last two closely approximated rays in both dorsal and anal fins are counted as a single ray.

Dorsal rays: 9(10), 10(29), 11(11), $\bar{x}$ 10.02, all rays branched in 4 fish, the first one unbranched in 44, and the first two rays unbranched in 2; anal rays: 9(4), 10(39), 11(7), $\bar{x}$ 10.06, all rays branched in 35, the first ray unbranched in 15; pectoral rays (both fins): 13(15), 14(60), 15(25), $\bar{x}$ 14.10;

Table 1
Proportional measurements, in thousandths of standard length, of *Megupsilon aporus*.
Data for the holotype and allotype are included with the 20 adults.

			10 Males		10 Females	
Measurement	Holotype ♂	Allotype ♀	Range	Average	Range	Average
Standard length, mm	21.4	26.6	21.1-27.1	24.0	23.0-31.8	25.7
Predorsal length	626	616	598-628	616	598-616	610
Anal origin to caudal base	397	380	391-419	404	366-393	378
Body, greatest depth	421	410	415-459	434	388-428	408
Greatest width	210	218	210-234	221	211-234	225
Head length	369	357	346-369	358	343-370	358
Depth	350	320	327-350	340	311-336	325
Width	234	241	234-253	245	232-263	248
Caudal peduncle length	257	248	257-289	272	244-263	252
Least depth	206	199	194-222	208	180-199	191
Interorbital, least bony width	93	86	93-103	98	82-95	89
Preorbital width	33	34	30-37	34	29-38	33
Opercle length	117	120	103-119	113	111-126	118
Snout length	84	83	81-96	87	76-87	82
Orbit length	107	105	106-114	110	97-114	107
Mouth width	112	120	107-122	116	109-135	123
Upper jaw length	126	128	118-134	128	120-138	130
Mandible length	126	124	114-131	124	117-134	126
Dorsal fin, basal length	178	177	175-203	186	148-181	168
Depressed length	285	278	268-303	284	236-278	260
Anal fin, basal length	140	132	122-144	133	118-138	129
Depressed length	271	244	244-271	254	239-268	250
Middle caudal rays, length	233	229	214-236	227	214-244	225
Pectoral fin length	215	192	188-215	199	182-210	193

caudal rays: 16(1), 17(5), 18(31), 19(10), 20(3), $\bar{x}$ 18.18. The holotype has dorsal i,9, anal 0,10, pectorals 15-15, and caudal 18.

Scales in lateral series: 24(8), 25(41), 26(1), $\bar{x}$ 24.86; scales between dorsal and anal fins: 10(25), 11(24), 12(1), $\bar{x}$ 10.52; scales around caudal peduncle: 14?(1), 15(4), 16(44), $\bar{x}$ 15.88; scales around body: 26(2), 27(3), 28(28), 29(3), 30(12), 31(0), 32(2), $\bar{x}$ 28.56; predorsal scales: 18(4), 19(14), 20(14), 21(12), 22(6), $\bar{x}$ 20.04. The holotype has 25 lateral scales, 10 between dorsal and anal, 16 around peduncle, 28 around body, and 22 predorsal.

Vertebral counts (including hypural complex), taken from radiographs, are: 25(8), 26(50), 27(3), $\bar{x}$ 25.92; of these the precaudal vertebrae number 11(42), 12(15) and the caudal vertebrae 13(1), 14(20), 15(33), 16(3). Holotype 11 + 15 = 26.

Gill rakers: 10(8), 11(24), 12(14), 13(4), $\bar{x}$ 11.28. Holotype, 11. All gill rakers on the outer part of the first arch were counted, without distinction between upper and lower limbs.

The branchiostegals numbered 4 in 6 specimens and 5 in 34; only one fish had the formula 4-4. In the typical count, 4 branchiostegals insert on the ceratohyal and 1 on the epihyal.

Coloration and Dimorphism. The life colors of the new genus were noted in both field and laboratory; the sexes show marked dichromatism (typical also of *Cyprinodon*): nuptial males have steel blue iridescence on the back and sides anterior to the blackened area that lies between the dorsal and anal fins; the caudal peduncle, however, has a golden bronze sheen, seen also on top of the head, and the caudal fin is watery orange, with no trace of the terminal black border typical of *Cyprinodon;* the dorsal and anal fins are chalky bluish white, the base of the dorsal orange. There is a conspicuous, vertical black bar on the eye above and below the pupil that disappears on preservation. There is also an orange spot on the posterior part of the opercle, noted only in the male. Adult females are golden olivaceous over the entire body and have a weak and often interrupted midlateral stripe, from the upper angle of the gill opening to the base of the caudal fin, that is no wider than three-fourths the diameter of the eye; rarely there is a tendency to develop several teardrop-shaped extensions from this stripe toward the anal fin.

The male differs most notably from the female in having the side of the body heavily blackened between the tip of the extended pectoral fin and the bases of the dorsal and anal fins (Fig. 3); this mark varies in development, apparently being most intense and expansive in alpha males. Neither young nor adult possess a dorsal ocellus, found in most species of *Cyprinodon*. The anal fin of the female is as large as or larger than her dorsal fin, whereas in the male the dorsal fin is larger than the anal fin (as typical for both sexes of *Cyprinodon*).

As shown in Table 1, there is marked sexual dimorphism in the measurement of anal origin to caudal base, head depth, caudal peduncle length, least depth of caudal peduncle, least bony width of interorbital, basal length of dorsal fin, and depressed length of dorsal fin. Except for the interorbital measurement, sexual dimorphism is similar in *Cyprinodon*. In addition, males of *Cyprinodon* have notably longer anal fins than do females, whereas these fins are virtually the same length in both sexes of *Megupsilon*. The functional significance of this difference may be related to breeding behavior.

Individuals of the new genus are small, attaining a maximum standard length of only 36 mm (1 female); males are smaller than females and may mature at 15 mm SL (Fig. 4). The smaller male size may be correlated with the absence of territorial behavior in this genus (see below). The sympatric species

FIGURE 5. Spring-fed pond at El Potosí, type locality of *Megupsilon aporus.* View northeast, 23 February 1961 (from Kodachrome by R. R. Miller).

of *Cyprinodon* at El Potosí reaches a larger size and the two sexes are not significantly different in their maximum lengths.

Discussion. Megupsilon is known only from a spring-fed pond (Fig. 5) near the northern edge of the small settlement of El Potosí, 95 airline km due south of Monterrey, on the west side (rain shadow) of the Sierra Madre Oriental, in Nuevo León. The elevation is about 1,880 m, and the highest adjacent mountains (Cerro Potosí) are about 3,640 m. The pond lies in the endorheic basin named La Hediondilla, which is a high, arid plateau extending northward for about 65 km and southward some 50 km from Potosí. We were told that the pond is the only permanent water in the entire basin, which is lowest toward the southeast. At high level, the pond covers somewhat more than 1 hectare and, in places along its eastern side, is 3.5 to 4 m deep. Its water is very clear though easily roiled because of the firm clay that overlies a limestone base. Vegetation is abundant, particularly *Ceratophyllum* which forms dense masses in the southeastern sector; *Potamogeton* is restricted to water deeper than about 1 m, and unidentified "grasses" are restricted to water shallower than about 1 m; floating masses of green and blue-green algae (unidentified) occur among the "grasses" and *Ceratophyllum; Nasturtium* is also present.

An abrupt limestone cliff (Fig. 5) is at the northeastern edge of the pond. The water is moderately alkaline (pH 7.2-7.4, indicator strips) and moderately

TABLE 2
Temperature Measurements[a]

Date	Time	Temperature (° C)
23 Feb. 1961	1630	20.6 air, 19.4 water
14 Feb. 1968	2230	18.9 water
15 Feb. 1968	1000	20.0 water
25 Mar. 1968	1100	17.8 air, 18.0 water
28 June 1968	1545	26.0 water
28 June 1968	2235	16.5 air, 17.0 water

[a]Water temperatures taken 5 cm below the surface, at the south end of the pond.

hard (DH 11-15, approximately 197-269 ppm as CaO). Air and water temperatures are summarized in Table 2.

Each year, starting in July, the pond level is lowered about 1 m as water is pumped out to irrigate the corn fields, according to the residents. This considerably reduces the surface area of the pond. The pond slowly refills, and by October covers the area shown in the photograph; water level then remains stable until the following summer. The commemorative plaque on the wall of the pumphouse states that this structure was dedicated in 1955 and, according to the residents, the partial dam which parallels the limestone cliff and serves to delimit the deeper portion of the pond from the shallower areas was built in 1960. The annual man-caused changes in the level of the pond may have enabled "grasses" to colonize those pond areas which become dry land in summer.

On 23 February 1961 Miller and Huddle collected a single *Megupsilon* and 315 *Cyprinodon* whereas subsequent collections made in Feburary, March and June, 1968, revealed that *Megupsilon* was 2 or 3 times more abundant than *Cyprinodon*. The 1968 collections indicate that *Megupsilon* predominates in the grassy areas of the pond and in the *Ceratophyllum* whereas the *Cyprinodon,* especially the adults, inhabits water deeper than 1 m. It appears to us that yearly pumping of the pond has resulted in an increase in *Megupsilon* habitat and a decrease in *Cyprinodon* habitat. During pluvial times (Wisconsin glaciation), when the now restricted pond probably formed a sizable marsh and lake, the habitat suitable for *Megupsilon* would have been extensive.

One other species of fish, the goldfish *(Carassius auratus),* is present in the pond. Most were greenish bronze but one bright golden one was noted in 1961 and a number of golden individuals were seen in 1968; the brightly-colored goldfish were confined to the deepest part of the pond and were large, perhaps the original propagules. A dwarf species of crayfish, *Cambarellus alvarezi* Villalobos (1952), is endemic to this pond.

Mr. Robert J. Naiman, while a graduate student at UCLA, measured gut length and studied dietary preferences of the 2 cyprinodontids of El Potosí (Tables 3-4). *Megupsilon* has a much shorter digestive tract than does *Cyprinodon:*

Species	$\bar{x}$ Gut Length (as % SL)	Range	N	Size Range
Megupsilon adults	88%	53-130%	55,	16-33 mm SL
Cyprinodon adults	211%	137-348%	36,	27-54 mm SL
Megupsilon juveniles	78%	53-100%	5,	13-15 mm SL
Cyprinodon juveniles	112%	90-133%	14,	10-16 mm SL

Mr. Naiman's data indicate that *Megupsilon* is carnivorous and feeds mainly on larval chironomids whereas *Cyprinodon* is herbivorous and feeds mainly on filamentous algae. The average adult *Megupsilon* contains 3.96 times more animals than does the average adult *Cyprinodon,* and *Megupsilon* juveniles, on the average, contain 4.32 times more animals than do *Cyprinodon* juveniles. On the other hand *Cyprinodon* adults ingest considerably more plant matter than does *Megupsilon;* the mean fullness value (filamentous algae plus vascular plants) for *Cyprinodon* is 22.07 times that for *Megupsilon* and since an adult *Cyprinodon* gut is 4.3 times the length of an adult *Megupsilon* gut ($\bar{x}$ gut length in adults is 86.5 mm vs. 20.3 mm, respectively) *Cyprinodon* must ingest about 100 times more plant matter than does *Megupsilon.* Both species were found to contain appreciable amounts of unicellular algae such as diatoms and desmids but no attempt was made to estimate quantities.

When Walters and Bleck arrived at the pond on 14 February 1968, *Megupsilon* was observed to be actively swimming about at 2230 hrs. No

TABLE 3
Feeding Preferences of the El Potosí Cyprinodontids[a]

Food Category	*Megupsilon aporus,* juveniles[b]		*Cyprinodon* sp., juveniles[c]	
	Mdn No./Fish	$\bar{x}$ No./Fish	Mdn No./Fish	$\bar{x}$ No./Fish
Chironomid larvae	11.0	11.8	0.50	1.21
Other insects plus arachnids	0.3	1.2	0.14	0.50
Copepods *(Cyclops)*	0.3	4.6	0.14	2.50
Larger crustaceans	0.1	0.2	0.00	0.00
Eggs (cyprinodont?)	0.1	0.4	0.00	0.00
Insect eggs	0.1	not counted	0.00	0.00
Filamentous algae	0.1[d]	0.5[d]	9.0[d]	7.4[d]
Vascular plants	0.0[d]	0.0[d]	0.04[d]	0.29[d]

[a] Fishes collected by seining at 0900-1000, 29 June 1968.

[b] N = 5, 13-15 mm SL; 100% with food in gut; no helminth parasites found.

[c] N = 14, 10-16 mm SL; 92.9% with food in gut; no helminth parasites found.

[d] Fullness values. For plant matter, the fullness of the gut was estimated on an arbitrary scale of 0 (gut devoid of algae/vascular plants) to 10 (gut stuffed with algae/vascular plants).

TABLE 4

Feeding Preferences of the El Potosí Cyprinodontids[a]

Food Category	*Megupsilon aporus*, adults[b] Mdn No./Fish	 $\bar{x}$ No./Fish	*Cyprinodon* sp., adults[c] Mdn No./Fish	 $\bar{x}$ No./Fish
Chironomid larvae	9.00	15.71	0.93	4.47
Other insects plus arachnids	2.45	2.25	0.40	1.28
Copepods *(Cyclops)*	0.58	4.58	0.01	0.03
Larger crustaceans	1.13	2.87	0.08	0.56
Eggs (cyprinodont?)	0.22	1.20	0.10	0.39
Gastropods	0.03	0.07	0.00	0.00
Filamentous algae	0.15[d]	0.40[d]	9.64[d]	8.90[d]
Vascular plants	0.02[d]	0.04[d]	0.19[d]	0.81[d]

[a] Fishes collected by seining between 0900-1000, 29 June 1968.

[b] N=55; 20 males, 35 females, 16-33 mm SL; 100% with food in gut; 60.0% with helminth parasites.

[c] N=36; 12 males, 24 females, 27-54 mm SL; 100% with food in gut; 63.9% with helminth parasites.

[d] Fullness values. For plant matter, the fullness of the gut was estimated on an arbitrary scale of 0 (gut devoid of algae/vascular plants) to 10 (gut stuffed with algae/vascular plants).

reproductive activity was noted then or the following morning, which was marked by light rain and overcast sky. Walters and Turner noted that *Cyprinodon* males were maintaining territories in deep water on June 28-29, but such behavior was not observed for *Megupsilon.*

The two killifishes are endemic to the El Potosí pond today. The pond undoubtedly represents the last remnant of a larger body of water which may have filled much of La Hediondilla during Pleistocene pluvial periods. At some past Pleistocene time, the hypothetical lake must have had a drainage connection to the north or northwest to permit entry by the ancestor of the El Potosí *Cyprinodon.* Although this form has not been studied, it appears to belong to the group of species allied to *Cyprinodon eximius* Girard, which today occurs in isolated drainages and in the Rio Conchos basin, of northern México, as well as in certain Rio Grande tributaries in Texas.

The population of *Megupsilon aporus* can only be regarded as relict and representative of a much earlier cyprinodontine invasion of the Mexican Plateau. That it is most closely related to *Cyprinodon* is indicated by the many shared morphological characters. Another relict cyprinodontine, *Cualac tessellatus* Miller, inhabits a warm spring area (La Media Luna) near Rio Verde in San Luis Potosí.

On the morning of 6 July 1972 Walters revisited the spring pond, accompanied by Robert E. Brown, Jr., Richard Haas, Robert K. Liu, and Sylvia H. Walters. Conditions had changed since the last visit. The pump has been inoperable for several years and the spring's flow is now tapped year-round by sluices. Since pond area is now fairly constant there has been a change in the aquatic vegetation. *Ceratophyllum demersum,* restricted to the area of the pump house in 1968, now covers most of the pond with a thick mat; in shallower areas this vegetation was moribund but in fruit, possibly reflecting elevated summer water temperatures. Wide-angle Infrared Ektachrome photographs, taken with a Wratten 12 filter from the hillside about 25 feet above the spring, show the moribund areas as white to pale pink vs. red for healthy areas. In cooler areas the *Ceratophyllum* is partially overlain by *Ranunculus* sp. Grasses are diminished.

Water temperatures, measured between 9 AM and 12 noon with a YSI telethermometer at several scattered locations, were 22-23°C (surface), 16-19°C (shallow depths), and 18°C at the deepest point. Oxygen content, measured at the same times with a Hach Kit, ranged from 4.5-7.5±/0.5 mg/1 = 2.8-5.2 ml/1; the lower readings were taken in shade, near *Ceratophyllum.* Four minnow traps, baited with chicken liver and placed in deep water below the *Ceratophyllum* mat for 90 minutes and then in shallow water in the *Ceratophyllum* mat for 90 minutes yielded several hundred *Cyprinodon* sp., 8 *Megupsilon aporus,* and 2 dwarf crayfish. The trapping results were surprising, in view of the dietary differences between the two fishes as indicated by earlier gut analyses.

Megupsilon aporus was seen to be abundant immediately below and in the *Ceratophyllum* mat. *Cyprinodon* sp. abounded in open water, from the surface to the deepest part of the spring; territorial males were tightly packed in shallow water along the western side of the pond. Crayfish abounded in the *Ceratophyllum.* The goldfish population seemed unchanged. No specimens were preserved; all trapped fish were released.

ACKNOWLEDGMENTS

We are indebted to Robert K. Liu for allowing us to publish his observations on the behavior of *Megupsilon,* and to Robert J. Naiman for the data on gut length and food preferences. Our colleague, Teruya Uyeno, prepared the chromosomes. Biólogo Juan Luis Cifuentes L., Dirección General de Pescas e Industrias Conexas, kindly issued permits for collecting in México. Field work by the senior author was supported by NSF grant GB-6272X and that by the junior author by University of California Faculty Research Grant No. 1780; laboratory studies were supported by NSF GB 8212 (to The University of Michigan Museum of Zoology for Research in Systematic and Evolutionary Biology).

RESUMEN

Megupsilon aporus, un nuevo genero y especie de la familia Cyprinodontidae mas cercamente relacionado a *Cyprinodon,* se describe de un estanque aislado en Nuevo León México. Solamente otro pez, una especie de *Cyprinodon,* es indigeno del mismo manantial. Este nuevo genero se distingue por medio de su dimorfismo sexual en numero de cromosomas, $2n = 47$ en el macho y $2n = 48$ en la hembra, y el macho tambien con una enorme cromosoma Y. Ademas *Megupsilon* solamente tiene neuromastos expuestos (carece canales o poros) en el sistema canal sensorio cefalico, sin aletas o ceñidor pelviano, el intestino del adulto mas corto que el largo del cuerpo, pocos rastrillos branquiales (10-13), el macho nupcial sin margen negra terminal en la aleta caudal pero con una region enegredida en el lado entre las aletas dorsal y anal, y la aleta anal de la hembra aproximadamenta tan grande como su aleta dorsal. Enseña dos caracteristicas de comportamiento que no se encuentran en *Cyprinodon* y no es territorial. Es carnivoro y prefiere agua mas o menos poco profunda. El nuevo genero es una reliquia representando una invasion mas temprana que la del especie simpatrica de *Cyprinodon.*

LITERATURE CITED

MILLER, R. R. 1948. The cyprinodont fishes of the Death Valley system of eastern California and southwestern Nevada. Univ. Mich. Mus. Zool., Misc. Publ. 68: 1-155.

UYENO, T., AND R. R. MILLER. 1962. *Empetrichthys erdisi,* a Pliocene cyprinodontid fish from California, with remarks on the Fundulinae and Cyprinodontinae. Copeia 1962 (3): 519-531.

———. 1971. Multiple sex chromosomes in a Mexican cyprinodontid fish. Nature 231: 452-453.

VILLALOBOS, A. 1952. Estudios de los cambarinos Mexicanos. X. Una nueva especie del genero *Cambarellus* del estado de Nuevo León. Anal. Inst. Biol. 22 (2): 525-532.

Accepted for publication April 5, 1972

Printed in Los Angeles, California, by Anderson, Ritchie and Simon

NUMBER 234
OCTOBER 30, 1972

INDO-WEST PACIFIC FISHES FROM THE GULF OF CHIRIQUI, PANAMA

By RICHARD H. ROSENBLATT,
JOHN E. McCOSKER,
and IRA RUBINOFF

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1972 CBE Style Manual, third edition (AIBS) is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1972 CBE Style Manual, third edition (AIBS) in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Any changes or alterations, other than typographical corrections, will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

INDO-WEST PACIFIC FISHES FROM THE GULF OF CHIRIQUI, PANAMA[1]

By Richard H. Rosenblatt[2], John E. McCosker[2], and Ira Rubinoff[3]

Abstract: Recent collections indicate the presence of a number of Indo-west Pacific fishes in the Gulf of Chiriqui. The Gulf of Chiriqui is not subject to seasonal upwelling as is the adjacent Gulf of Panama, and supports a relatively rich development of hermatypic corals. Twenty-four percent (40) of the reef fish species collected there also occur in the Indo-west Pacific, and of them, nine were previously unrecorded at or near the American mainland: *Myripristis murdjan, Ctenochaetus cyanoguttatus, Gymnothorax flavimarginatus, G. buroensis, G. undulatus, Enchelynassa canina, Uropterygius tigrinus, Malacanthus hoedti,* and *Hemipteronotus taeniourus.* The last six are heretofore unreported from the eastern Pacific, although none is restricted to the Gulf of Chiriqui.

Eastern Pacific records of the following Indo-west Pacific species are regarded as invalid, being based either on misidentification or mislabelings: *Brachysomophis crocodilinus, Gymnothorax chilospilus, Callechelys marmoratus, Myrichthys maculosus, Myripristis berndti, Lutjanus kasmira, Runula tapeinosoma, Abudefduf saxatilis vaigiensis,* and *Antennatus bigibbus.*

The ranges of the eastern Pacific endemic species *Gymnothorax castaneus, Petrotyx hopkinsi,* and *Paraclinus altivelis* are extended to Panama. *Xyrichthys panamensis* Fowler 1944, is synonymized with *Hemipteronotus pavoninus* (Valenciennes, 1839).

Many of the transpacific migrants are localized and limited in their eastern Pacific distributions. Some are seemingly closely associated with the development of hermatypic corals. There is no evidence that any are displacing eastern Pacific endemnic species.

The number of new records in the Gulf of Chiriqui collections reflects the inadequacy of current knowledge of the distribution of the fishes of the eastern tropical Pacific.

INTRODUCTION

Recent collecting efforts by the Scripps Institution of Oceanography and the Smithsonian Tropical Research Institute in the Gulf of Chiriqui, western Panama, have disclosed the presence of a large number of Indo-west Pacific species adjacent to or along the continental coastline in the eastern tropical

---

[1] Review Committee for this Contribution
William A. Bussing
Robert J. Lavenberg
C. Richard Robins
James C. Tyler

[2] Contribution from the Scripps Institution of Oceanography, University of California at San Diego, La Jolla, California 92037

[3] Smithsonian Tropical Research Institute, P.O. 2072, Balboa, Canal Zone

Pacific. Our results are interesting in that many fishes of Indo-west Pacific origin which have previously been reported only from the oceanic Galapagos, Revillagigedo, Cocos, and Clipperton islands are maintaining populations in the coral reef communities in the Gulf of Chiriqui.

The Gulf of Chiriqui lies west of the Gulf of Panama and is not subject to the seasonal upwelling conditions which profoundly affect the fauna of Panama Bay and the Perlas Islands (Schaefer et al., 1958; Forsbergh, 1969). Pacific coastal waters west of the Azuero Peninsula, therefore, present a warmer and more stable thermal regime (Renner, 1963) which facilitates extensive development of certain hermatypic corals (Glynn, in press). The presence of extensive *Pocillopora* bank reefs (Fig. 1) to depths of 10-15 meters provides a habitat similar, but not identical, to that of the islands of the central Pacific. These reefs, in contrast to well-developed Caribbean or Indo-Pacific formations, comprise relatively few species of *Pocillopora,* possibly three or four. Associated with them, however, are several species of *Porites, Pavona,* and the hydrocoral *Millepora* which contribute to the habitat diversity, to which the increased Indo-west Pacific components in the vertebrate and invertebrate fauna may be related. The structure and extent of coral reef development in the Gulf of Chiriqui is discussed in Glynn et al. (in press). Notable Indo-west Pacific invertebrates in the Gulf of Chiriqui include the crown of thorns starfish, *Acanthaster* cf. *planci,* the painted shrimp *Hymenocera picta,* and the fire corals *Millepora intricata* and *M. platyphylla* (Glynn, in press). Eastern Pacific records for *Hymenocera* and *Millepora* are based on specimens from the Gulf of Chiriqui, these forms being as yet unreported from Clipperton, Galapagos, and the Revillagigedo islands. A similar restricted distribution pattern also exists for certain fishes.

COLLECTIONS

The eastern Gulf of Chiriqui contains seven major island groups. The largest is Coiba which is ca. 30 km in length. The outermost island, Montuosa, is 60 km from the mainland and separated by a channel 80 m deep. We have either collected at or made observations using SCUBA at each island group and several mainland localities (Fig. 2) on three separate occasions, during March and September of 1970 and April of 1971. More than 30 days were spent in the field while aboard the vessels R/V *Alpha Helix,* R/V *Tethys,* and USN LST *Traverse County.* A collection of fishes made by C. H. Birkeland and T. Spight at Isla Viradores Sur, Costa Rica (10°34′50″N, 85°43′30″W), is included in this study. Accessory material from other Pacific island and Gulf of California localities was provided through the extensive collecting efforts of the Scripps Institute of Oceanography (SIO), and the University of California at Los Angeles (UCLA). Fishes discussed in this paper are presently housed at SIO, UCLA, the Smithsonian Tropical Research Institute (STRI), the University of Miami Marine Laboratory (UMML), the Harvard Museum of Comparative Zoology (MCZ), the Universidad de Costa Rica (UCR), and the California Academy of Sciences (CAS). In this study we refer to the offshore

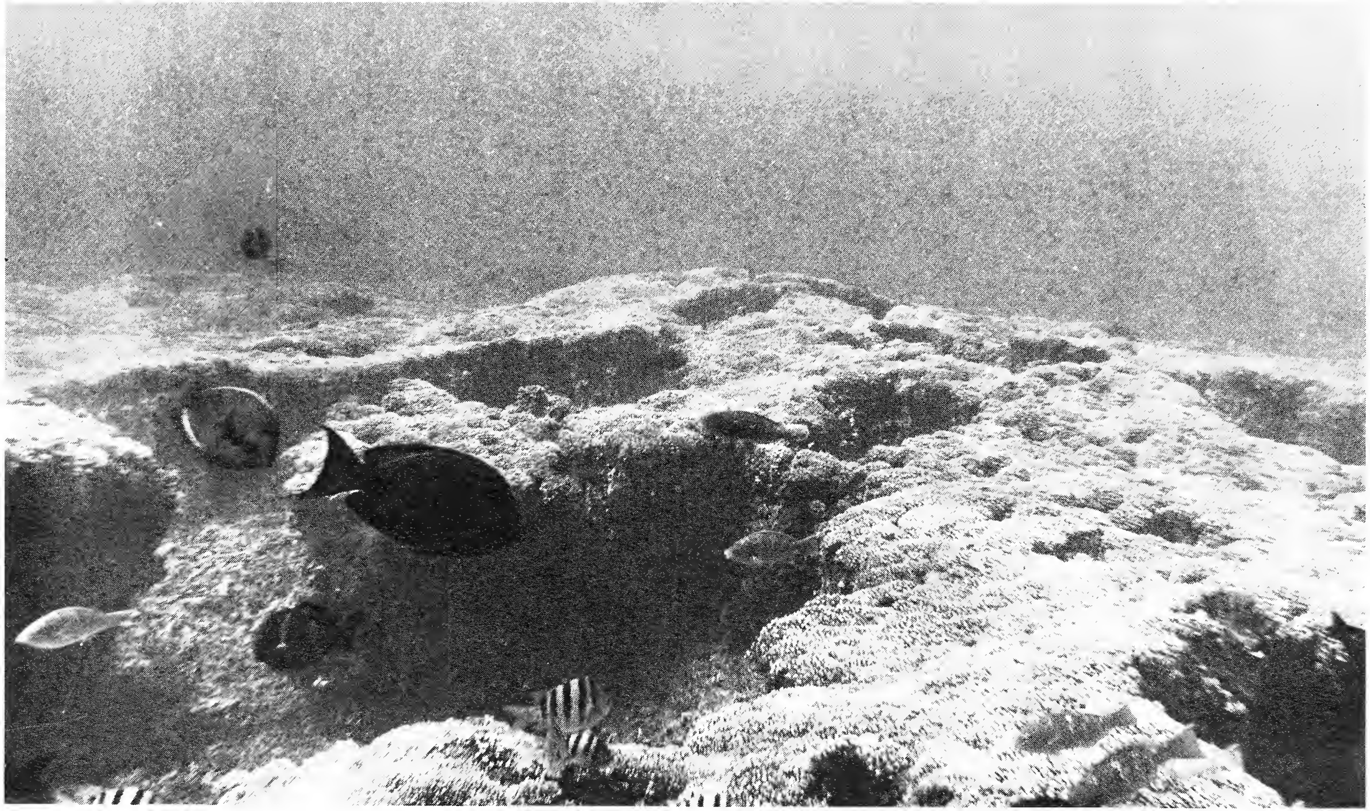


Figure 1. Shallow water (ca. 7 m) *Pocillopora* bank reef at a small island SE of Isla Cavada, Islas Secas. *Ctenochaetus cyanoguttatus*, *Scarus ghobban*, and *Abudefduf troschelii* in foreground. Photo by Peter W. Glynn, 24 March, 1971.

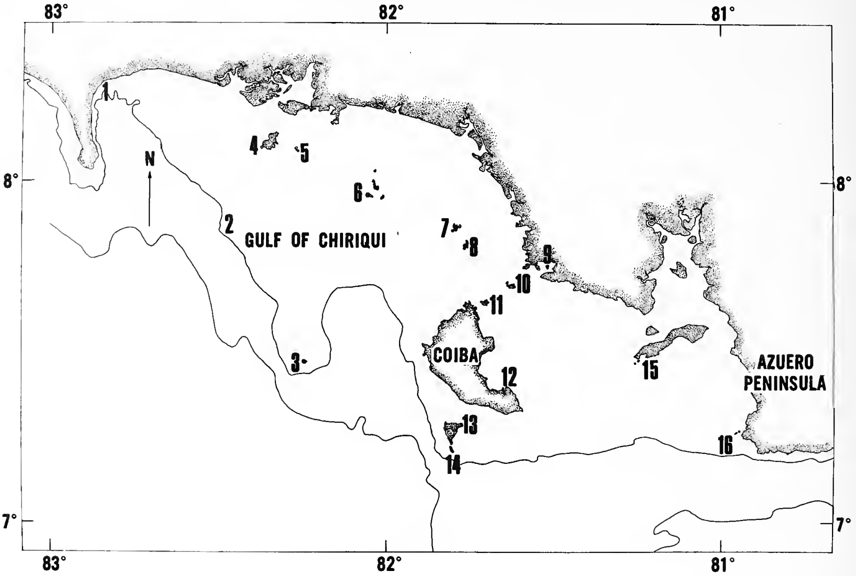


FIGURE 2. Major collection localities in the Gulf of Chiriquí, Panamá. 100 and 1000 fathom contours taken from hydrographic chart H.O. 1018 (1968 edition). 1, Puerto Armuelles; 2, Islas Ladrones; 3, Isla Montuosa; 4, Isla Parida; 5, Isla Balaños and Isla Berraco; 6, Islas Secas; 7, Isla Brincanco and 8, Isla Uva, Islas Contreras; 9, Bahía Honda; 10, Isla Canal de Afuera; 11, Isla Ranchería; 12, Isla Coiba, Bahía de Las Damas; 13, Isla Jicaron; 14, Isla Jicarita; 15, Isla Cebaco; 16, Islas Naranjas.

islands of the eastern Pacific ocean. These include: Isla del Coco, Clipperton Island, Islas de Revillagigedo, and Islas Galapagos.

GULF OF CHIRIQUI FISHES

We have discovered nine Indo-west Pacific fish species previously unrecorded at or near the American mainland. Six species are first reported from the eastern Pacific in this paper. The Indo-west Pacific fishes of the Gulf of Chiriqui can be placed in two categories (Table 1) based on their distribution, and most likely, their dependence upon the coral reef habitat. These categories are arbitrary in some cases, but for the most part the distinction is rather clear cut.

The fishes that are part of the coral reef community of the gulf island groups include 165 species; of these we find that 40 (24 percent) also occur in the Indo-west Pacific region. This high percentage is comparable only to the Clipperton fish fauna, and is probably associated with the extensive coral development at both localities.

Other fishes collected in the Gulf of Chiriqui represent range extensions for the eastern tropical Pacific. A single specimen of *Paraclinus altivelis*

TABLE 1

Eastern Pacific distributions of Indo-west Pacific and circumtropical shorefish species. * Indicates species found in the Gulf of Chiriqui.
† Indicates circumtropical species.

I. Broadly distributed in eastern tropical Pacific

†*_Aetobatus narinari_ (Euphrasen)
Chanos chanos (Forsskål)
†_Albula vulpes_ (Linnaeus)
*_Euleptorhamphus viridis_ (Van Hasselt)
†_Ablennes hians_ (Valenciennes)
*_Kuhlia taeniura_ (Cuvier)
†*_Priacanthus cruentatus_ (Lacépède)
†*_Mugil cephalus_ Linnaeus
*_Alectis ciliaris_ (Bloch)
*_Gnathanodon speciosus_ (Forsskål)
*_Scarus ghobban_ Forsskål
*_S. rubroviolaceous_ Bleeker
*_Sectator ocyurus_ (Jordan and Gilbert)
*_Oxycirrhites typus_ Bleeker
*_Cirrhitichthys oxycephalus_ (Bleeker)
*_Doryrhamplus melanopleura_ (Bleeker)
*_Acanthurus xanthopterus_ (Valenciennes)
*_Fistularia petimba_ Lacépède
†_Canthidermis maculatus_ (Bloch)
Chilomycterus affinis (Günther)
†*_Diodon holacanthus_ Linnaeus
†*_D. hystrix_ Linnaeus
*_Arothron hispidus_ (Linnaeus)
*_A. meleagris_ (Bloch and Schneider)
*_Ostracion meleagris_ Shaw

II. Limited to offshore islands and/or certain mainland localities

*_Triaenodon obesus_ (Rüppell)
*_Echidna nebulosa_ (Ahl)
*_E. zebra_ (Shaw)
*_Gymnothorax buroensis_ (Bleeker)
*_G. flavimarginatus_ (Rüppell)
G. pictus (Ahl)
*_G. undulatus_ (Lacépède)
*_Enchelynassa canina_ (Quoy and Gaimard)
*_Uropterygius tigrinus_ (Lesson)
Holotrachys lima (Valenciennes)
*_Myripristis murdjan_ (Forsskål)
Aphareus furcatus (Lacépède)
*_Malacanthus hoedti_ Bleeker
*_Caranx melampygus_ Cuvier
Forcipiger flavissimus Jordan and McGregor
*_Hemipteronotus pavoninus_ (Valenciennes)
*_H. taeniourus_ (Lacépède)
*_Thalassoma lutescens_ (Lay and Bennett)
Calotomus spinidens (Quoy and Gaimard)
*_Aulostomus chinensis_ (Linnaeus)
*_Acanthurus triostegus_ Linnaeus
*_A. glaucopareius_ Cuvier
*_Ctenochaetus cyanoguttatus_ Randall
*_Zanclus canescens_ (Linnaeus)
Antennarius drombus Jordan and Evermann
†_Xanthichthys ringens_ (Linnaeus)
†*_Melichthys niger_ (Bloch)
†*_Alutera scripta_ (Osbeck)
Canthigaster amboinensis (Bleeker)

(Lockington), previously known only from deep water in the Gulf of California (Rosenblatt and Parr, 1969), was collected in ten m at Isla Canal de Afuera (SIO 71-52). Numerous specimens of *Gymnothorax castaneus* Jordan and Gilbert (which we regard as distinct from *G. dovii* Günther) were collected at several Gulf of Chiriqui and Panama Bay locations and represent a southern extension from the previously known range in Mexico. A single specimen of the brotulid *Petrotyx hopkinsi* Heller and Snodgrass from Isla Uva (SIO 70-135) extends the recorded range of the species from the Galapagos Islands, although it has also been taken between Cape San Lucas and Espiritu Santo Island, Lower California (SIO material). The collections also include a new species of chaenopsid (Stephens and Rosenblatt, MS) and a new species of dactyloscopid, both of which are distinctively different from known genera.

TRANSPACIFIC SHORE FISHES

Briggs (1961, 1964) has listed 62 transpacific shore fishes. His list includes certain records that our studies indicate are invalid for various reasons. These are discussed below:

Brachysomophis crocodilinus (Bennett). The eastern Pacific occurrence of this species rests on a report by Günther (1870) of a single specimen listed as "Galapagos Islands. From the Haslar Collection." Incorrect provenances of Haslar Hospital collection material has already led to several zoogeographic improbabilities (Kresja, 1960). In light of this, and lacking other records, we remove *B. crocodilinus* from the fauna of the eastern Pacific.

Gymnothorax chilospilus Bleeker. Herre's (1936) record of this species from Eden Island Galapagos, was based on a small specimen of *Muraena lentiginosa* Jenyns. We have examined Herre's specimen (SU 24399, now at CAS) and compared it with other material of *M. lentiginosa.* Herre's record of *Gymnothorax undulatus* (Lacépède), also based on *M. lentiginosa,* is discussed later in this paper.

Callechelys marmoratus (Bleeker). Fowler's (1932) record of this species from Charles Island, Galapagos, pertains to the recently described eastern Pacific species *C. galapagensis* McCosker and Rosenblatt, 1972.

Myrichthys maculosus (Cuvier). Fowler's (1938) record of *M. maculosus* from Narborough Island, Galapagos is referable to *M. tigrinus* Girard, an eastern Pacific endemic. The two nominal species are identical in external appearance. However, eastern Pacific populations have a significantly lower number of vertebrae than central and western Pacific material (McCosker, in preparation).

Myripristis berndti Jordan and Evermann. Although Greenfield (1965) did not place Briggs' (1964) record of *M. berndti* in the synonymy of *M. murdjan* (Forsskål) he does include the three Cocos Island specimens recorded by Briggs in his material of *M. murdjan.*

Lutjanus kasmira (Forsskål). The eastern Pacific endemic *L. viridis* Valenciennes is very similar to the Indo-west Pacific *L. kasmira.* Seale (1940) regarded the two as synonymous in recording *L. kasmira* from the Galapagos and Cocos islands. However, Jordan and Evermann (1898) had noted morphological differences between *L. kasmira* and *L. viridis* and regarded the latter as distinct. Our material indicates differences in color pattern between the two species. In *L. viridis* there are five distinct blue stripes, the lowest behind the pectoral base; in *L. kasmira* this band is absent. The upper three stripes in *L. viridis* are almost horizontal, contacting the dorsal profile at the base of the ninth dorsal spine, between the ninth and tenth dorsal soft rays, and the anterior one-third of the caudal peduncle respectively. In *L. kasmira* the corresponding points are the sixth dorsal spine, the fifth or sixth dorsal soft ray, and the end of the soft dorsal. Also in *L. viridis* the fourth stripe runs forward below the eye to the upper lip, rather than ending at the preopercular margin. Seale's (1940) record then should be considered a misidentification of *L. viridis,* and *L. kasmira* removed from the eastern Pacific list.

Runula tapeinosoma (Bleeker). Clark's (1936) Galapagos record of *Petroscirtes tapeinosoma* was without doubt based on a specimen of the wide ranging eastern Pacific *Plagiotremus azaleus* (Jordan and Bollman).

Abudefduf saxatilis vaigiensis (Quoy and Gaimard). The taxonomy of the *Abudefduf saxatilis* species complex is confused. The Atlantic, Indo-west Pacific, and eastern Pacific populations have been considered to represent distinct species or subspecies (*A. saxatilis* (Linnaeus), *A. vaigiensis* and *A. troschelii* (Gill) respectively) or sometimes united under the oldest name, *A. saxatilis.* Herre's listing of Galapagos material with specimens from the western Pacific under the name *A. saxatilis* is insufficient reason to establish the presence of the Indo-west Pacific form at that locality.

Scarops jordani (Jenkins) and *Scarus rubroviolaceus* Bleeker. These nominal species have recently (Rosenblatt and Hobson, 1969) been shown to be synonymous. The older name is *S. rubroviolaceus.*

Amanses carolae (Jordan and McGregor). This species has been shown by Randall (1964) to be synonymous with *Cantherines dumerilii* (Hollard), known from east Africa, the Seychelles, Lord Howe Island, the central Pacific and Hawaii.

Antennatus bigibbus (Lacépède). The specimen on which the Revillagigedo Island record was based (BC 57-160) was included by Rosenblatt (1963) in his material of the eastern Pacific endemic *Antennatus strigatus* (Gill). *A. bigibbus* has not yet been taken in the eastern Pacific.

Our findings, in general, agree with the concept of the eastern Pacific barrier to shorefish distribution as proposed by Ekman (1953) and amplified by Briggs (1961, 1964). Most of the Indo-Pacific elements in western Panama possess larval stages adapted to long distance pelagic transport, or juveniles and adults which may be able to accompany floating debris across the equatorial Pacific using the north equatorial current system (Hubbs and Rosenblatt, 1961).

The often mentioned but poorly understood phenomenon of offshore insular confinement in the eastern Pacific (Snodgrass and Heller 1905; Briggs, 1961, 1967; McCosker, 1971; Rosenblatt and Walker, 1963) deserves further mention. It is important to note that Indo-west Pacific migrants are not only confined to the offshore islands, but are also usually less abundant than the congeneric species of the indigenous fauna. An example is the sympatric association of the squirrelfishes *Myripristis murdjan* and *M. leiognathus* Valenciennes. The former, an Indo-Pacific emigrant, is, in the Gulf of Chiriqui, always found with, but less abundant than, the latter, a widespread eastern Pacific species. The same situation seems to pertain at Clipperton Island, except that the abundant eastern Pacific endemic there is *M. clarionensis*. A similar picture is also found in the Indo-Pacific morays in the eastern Pacific, except at Clipperton Island.

The evidence that the direction of movement across the Pacific has been from west to east has been presented by Briggs (1961) and Hubbs and Rosenblatt (1961). More recent findings have done little to alter their conclusions. It is, however, difficult to argue a west Pacific origin for *Sectator ocyurus*. The species has been recorded only from Hawaii and the Marquesas, on the fringes of the area, and might have crossed from east to west.

Briggs (1961, 1967, 1969, 1970) has in part ascribed the greater success of the Indo-west Pacific species in crossing the eastern Pacific barrier to their status as "dominant species." He (1967: 575) has stated that "It seems clear that the unusually stable ecosystems and high level of competition (in the Indo-west Pacific region) provide the proper environment for the evolution of dominant species that can successfully invade the other regions."

Inherent in this argument is the concept that competition between species leads to an increase in general "fitness" and the ability to compete in a new habitat with different competitors. This might be true if competition (overlap of requirement(s) for resource(s) in short supply) inevitably led to the extinction of all competitors but one, leaving a generalist occupying a broad niche. However, the widespread phenomenon of character displacement (Brown and Wilson, 1956) indicates that a more common result of competitive interaction is coexistence, with competition reduced by narrowing of niche breadth. Competition thus is more likely to produce specialists than generalists. The richness of the Indo-west Pacific fauna, especially in sympatric congeneric species, indicates that competitive interactions have had the latter result. For example Chave (in press) has carefully studied partitioning of the environment by six species of *Apogon* in Hawaii. Although all six occur together, there are differences in substrate preference, time of feeding, position in the water column while feeding, and food organisms taken. Her observations indicate that resources are partitioned in such a way as to reduce competition. Hobson's (1968) observations on *Apogon retrosella*, an eastern Pacific endemic which overlaps in part of its range with a single congener, *A. parri*, indicate much less restriction in several of these parameters. It is found over rocks as well as over sand patches at night, and feeds benthically as well as in midwater. Although it is difficult to predict the results of invasions (MacArthur and Wilson, 1967, Chap. 5), there is no a priori reason to suppose that any one of the Hawaiian species of *Apogon*, each with a narrow range of substrate and food preferences, would be able to replace *A. retrosella* if introduced into the habitat of that species.

The data indeed indicate that eastward migrants have not displaced eastern Pacific endemics. As our previous discussion has shown, a large number of eastward migrants are limited in their eastern Pacific distributions. The Muraenidae are instructive in this regard. There are 15 endemic species of muraenids, distributed among six genera, in the eastern tropical Pacific. As might be expected from their pelagic larval stage, the muraenids are represented by more species of migrants than any other family. Seven species distributed among four genera have crossed the east Pacific barrier. However, none of these is widespread and abundant along the mainland coast.

The success of Indo-west Pacific forms in colonizing the eastern Pacific seems to be related to several factors, among them the ability to survive in the coral-poor, more variable environment of the eastern Pacific, as well as to the presence of endemic competitors. The idea that these species are behaving as "competitively dominant species" is unwarranted, and not supported by evidence.

The paradox that the major equatorial currents flow from east to west but the major faunal movements have been from west to east is more apparent than real. The North Equatorial Current is relatively weak to the east. Movement of water from the mainland of Central America is not strongly unidirectional and more a drift than a current for much of the year (Wyrtki, 1965). In addition a considerable part of the north equatorial current is derived from the California Current, which would not be carrying tropical elements. The South Equatorial Current, which is strong and consistent near its eastern source, originates from the cold Peru Current which flows along the South American coast, where the fauna is essentially temperate (Myers, 1941; Ekman, 1953; Morrow, 1957). It is not surprising that these currents have not been major highways for tropical shore-fish dispersal.

The present impoverishment of the coral reef habitat in the eastern tropical Pacific appears to be limiting the diversity of corallophilic fishes and other inshore faunal elements (as Emerson, 1967, has suggested for the Panamic molluscan fauna). The presence of a suitable reef habitat may be a key to the success of Indo-west Pacific elements in the Gulf of Chiriqui. A similar association of Indo-west Pacific fishes with notable coral development has been described for Isla Jaltemba, Nayarit, Mexico by Greenfield et al. (1970), and an association between coral and certain eastern Pacific scarids has been demonstrated by Rosenblatt and Hobson (1969: 438). As was pointed out in the latter paper, the causative factors in this relationship are not clear. It may be that hermatypic corals and the associated fishes have similar requirements with respect to the physical environment. For example, *Myripristis murdjan* would seem by its distribution to be a strongly corallophilic form. However, it is a nocturnal planktivore which seemingly utilizes coral only as a shelter during the day. Additionally, Indo-west Pacific species form a conspicuous component of the fish fauna at the region of Cape San Lucas, lower California, an area of much poorer coral development than the Gulf of Chiriqui. The interrelationships between the biotic and physical factors in determining these associations clearly can only be elucidated by detailed studies.

In conclusion, we suggest that our findings of this large number of Indo-west Pacific species in western Panama is representative of the poor state of knowledge of fish distribution throughout western Central America, (Rosenblatt and Rubinoff, 1972), and may require reevaluation of the role of distance in maintaining the geographic isolation of many species of shore fishes with vagile embryonic or larval stages.

ANNOTATED LIST OF INDO-WEST PACIFIC REEF-ASSOCIATED FISHES IN THE GULF OF CHIRIQUI

Hemirhamphidae

1. *Euleptorhamphus viridis* (Van Hasselt) — Indo-Pacific, widespread in the eastern Pacific.

Muraenidae

2. *Echidna zebra* (Shaw) — known from the Indo-west Pacific and Hawaii; in the eastern Pacific, from Isla del Carmen to Cabo San Lucas, Isla Jaltemba Mexico, Clipperton Island, nearshore island localities from Costa Rica (UCR 14-38), the Gulf of Chiriqui, and the Perlas Archipelago.

3. *Echidna nebulosa* (Ahl) — known from the Indo-west Pacific and Hawaii; and the eastern Pacific from Bahia Muertos (SIO 61-253), Bahia San Lucas (SIO 67-136), and Manzanillo (UCLA 56-232), Mexico, Cocos Island, the Gulf of Chiriqui, and the Gulf of Panama.

4. *Gymnothorax buroensis* (Bleeker) — known from the Indo-west Pacific and Hawaii. In the eastern Pacific, from Clipperton Island (UCLA 58-289), Cocos Island, Isla del Caño and Isla Murciélago, Costa Rica (UCR 423-58 and 382-29), and a single specimen (SIO 71-48) collected in 10 meters in a *Pocillopora* bank reef at Islas Secas, Gulf of Chiriqui. New record for the eastern Pacific.

5. *Gymnothorax flavimarginatus* (Rüppell) — abundant in Indo-west Pacific and Hawaii, and offshore eastern Pacific islands of Clipperton, Cocos, and Isla del Caño, Costa Rica (UCR 423-125). Observed and photographed, but not collected at Islas Secas and Islas Contreras, Gulf of Chiriqui.

6. *Gymnothorax undulatus* (Lacépède) — Indo-west Pacific and Hawaii. In the eastern Pacific, known only from Isla del Caño, Costa Rica (UCR 423-59) and the Gulf of Chiriqui. We have collected and/or observed this species

at Islas Naranjas, Islas Contreras (SIO 70-135, SIO 71-40), Islas Secas (SIO 70-136, SIO 70-140), and Isla Coiba (MCZ 44103). New record for the eastern Pacific. Galapagos listings for this species are based on Herre's misidentification of a juvenile *Muraena lentiginosa* (SU 24382).

7. *Enchelynassa canina* (Quoy and Gaimard) — Indo-west Pacific and Hawaii. In the eastern Pacific known from Clipperton Island (SIO 59-12, UCLA 56-240) and Isla Montuosa, Gulf of Chiriqui (SIO 70-358). New record for the eastern Pacific.

8. *Uropterygius tigrinus* (Lesson) — Hawaii, Johnston, and the Society Islands. In the eastern Pacific, from Isla Espiritu Santo, Gulf of California (SIO 61-276), Isla Clarion, Islas de Revillagigedo (UCLA 55-131), and Islas Contreras, Gulf of Chiriqui (SIO 70-135, SIO 71-40). New record for the eastern Pacific.

Holocentridae

9. *Myripristis murdjan* (Forsskål) — Red Sea and Indo-west Pacific; eastern Pacific from the major islands groups, nearshore island localities from Costa Rica, and the Gulf of Chiriqui.

Kuhliidae

10. *Kuhlia taeniura* (Cuvier) — Indian Ocean to central Pacific. In the eastern Pacific, from Cape San Lucas to Colombia. Observed at Isla Montuosa and other localities in the Gulf of Chiriqui. The name *K. arge* Jordan and Bollman is available for the eastern Pacific population. In the absence of a critical study we tentatively regard it as conspecific with the western Pacific form.

Priacanthidae

11. *Priacanthus cruentatus* (Lacépède) — Pantropical; in the eastern Pacific, from Cabo San Lucas, Isla Jaltemba, and Islas Tres Marias, Mexico, the major offshore islands, Panama Bay, and the Gulf of Chiriqui.

Mugilidae

12. *Mugil cephalus* Linnaeus — Cosmopolitan in warm seas; in the eastern Pacific from Monterey, California, to Chile.

Branchiostegidae

13. *Malacanthus hoedti* Bleeker — Indian and tropical Pacific Oceans. This species, a new record for the eastern Pacific, was observed and collected at numerous localities in the Gulf of Chiriqui (SIO 70-138, SIO 71-42, SIO 71-53) where it is a common associate of the sand bottom and contiguous reef community at depths of 10-25 meters. The finding of *Malacanthus* initiated a search for additional material in existing collections; as a result of this inspection we now know that *M. hoedti* in the eastern Pacific ranges from Costa Rica

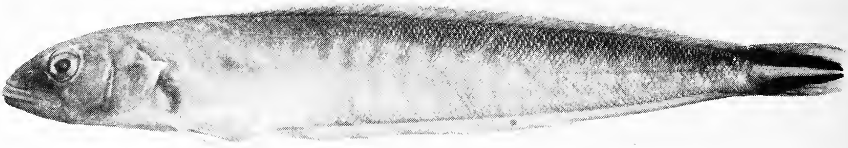


FIGURE 3. *Malacanthus hoedti.* A 244 mm individual from Isla Cavada, Islas Secas (SIO 70-138).

(Isla Viradores Sur, sight record) to Gorgona Island, Colombia (Argosy 27, now at UMML). In the Gulf of Chiriqui we have observed *M. hoedti* at numerous stations, both near the mainland (Bahia Honda) and at several island groups (Islas Naranjas, Brincanco, Uva, and Canal de Afuera). *M. hoedti* was encountered in pairs (not known to be male-female pairs in that the sexes are not externally distinguishable) at all localities. When approached by a diver, the fish would retreat into a burrow head-first. The burrow entrances were at the edges of large rocks, and the shallow burrows run beneath the rocks and terminate in an enlargement. We have compared our material with a series from Hawaii (CAS 24823) and a single specimen from the Caroline Islands (CAS 24824). All agree in morphology, number of vertebrae, and coloration, especially in the distinctively banded caudal (compare Fig. 3 with Berry, 1958, Fig. 7). There are, however, differences in the mean numbers of dorsal and anal rays (Table 2). The differences are significant at the $P \leq .05$ level but not at $P \leq .01$. Differences of this magnitude could indicate separation of the

TABLE 2

Total dorsal and anal rays in *Malacanthus hoedti.* Data for Central Pacific material include counts from Berry (1958).

Total dorsal rays

	54	55	56	57	58	59	60	61	62	$\bar{X}$	95% Conf. interval
E. Pacific	1	1	2	1	3					56.5	± 1.3
Cent. Pacific			1	1	2	-	4	2	1	59.4	± 1.2

Total anal rays

	48	49	50	51	52	53	54	$\bar{X}$	95% Conf. interval
E. Pacific	2	-	3	3				49.9	± 1.0
Cent. Pacific			2	2	3	3	1	51.9	± 0.9

populations at the specific or subspecific level. However, there is broad overlap of the ranges of the dorsal and anal counts. More importantly, our concept of *M. hoedti* (sensu stricto) is based on the Hawaiian population (10 of 11 specimens). Until adequate samples from throughout the entire range of the species are available, it would be premature to give formal taxonomic recognition to differences between the Hawaiian and eastern Pacific populations.

Carangidae

14. *Alectis ciliaris* (Bloch) — Indo-west Pacific and Hawaii, widespread in eastern Pacific. Observed and taken at several localities in the Gulf of Chiriqui.

15. *Caranx melampygus* Cuvier — Indo-west Pacific and Hawaii; in the eastern Pacific, from the major offshore islands and the Cape San Lucas region of Baja California. Observed and photographed over the reefs at several localities in the Gulf of Chiriqui.

16. *Gnathanodon speciosus* (Forsskål) — Indo-west Pacific and Hawaii, and widespread in the eastern tropical Pacific. Observed and collected at numerous localities in the Gulf of Chiriqui (SIO 70-136).

Labridae

17. *Hemipteronotus pavoninus* (Valenciennes) — Indo-west Pacific and Hawaii; in the eastern Pacific, known from Cabo San Lucas, Baja California, several island localities in the Gulf of Chiriqui, and Isla Pedro Gonzalez, Archipielago de las Perlas (as *Xyrichthys panamensis* Fowler, 1944). We follow Randall (1965) in placing *Iniistius* and *Xyrichthys* in the synonymy of *Hemipteronotus*.

18. *Hemipteronotus taeniourus* (Lacépède) — Indo-west Pacific and Hawaii; in the eastern Pacific, from Punta Pescadero, Gulf of California (SIO 59-225, SIO 61-252), the Gulf of Chiriqui, and the Archipielago de las Perlas. New record for the eastern Pacific.

19. *Thalassoma lutescens* (Lay and Bennett) — Indo-west Pacific; in the eastern Pacific from San Jose del Cabo (SIO 61-237), the Gulf of Chiriqui, and the major offshore island groups.

Scaridae

20. *Scarus ghobban* Forsskål — Red Sea and Indian Ocean to eastern Pacific. In Panama, common in the Gulf of Chiriqui and the Archipielago de las Perlas.

21. *Scarus rubroviolaceus* Bleeker — East Africa to central Pacific and Hawaii; in eastern Pacific, at the major offshore island groups, Cabo San Lucas, and in Panama, in the Gulf of Chiriqui and the Archipielago de las Perlas.

Kyphosidae

22. *Sectator ocyurus* (Jordan and Gilbert — Randall (1961) notes that this

species is a senior synonym of *S. azureus* Jordan and Evermann from Hawaii. Known from Hawaii and the Society Islands in the Indo-west Pacific, and in the eastern Pacific, from Cabo San Lucas to Costa Rica, the Gulfs of Chiriqui and Panama, and Isla La Plata, Ecuador.

Cirrhitidae

23. *Cirrhitichthys oxycephalus* Bleeker — Red Sea and Indo-west Pacific; in the eastern Pacific it extends from the Gulf of California to Colombia, and the major offshore islands.

24. *Oxycirrhites typus* Bleeker — Randall (1963) and Morris and Morris (1967) have discussed the range and synonymy of this species, now known from the Indo-west Pacific and Hawaii, and in the eastern Pacific from Los Frailes, Baja California to Isla Gorgona, Colombia. We have observed it in relatively shallow water (15-20 m) associated with the gorgonian *Lophogorgia* cf. *alba,* at Isla Coiba in the Gulf of Chiriqui, Isla Taboguilla in Panama Bay, and Isla Viradores Sur, Costa Rica.

Syngnathidae

25. *Doryrhamphus melanopleura* (Bleeker) — Indo-west Pacific; widespread and common in the eastern Pacific from the Gulf of California to Panama.

Fistulariidae

26. *Fistularia petimba* Lacépède — Indo-west Pacific; in the eastern Pacific from the Gulf of California to Panama.

Aulostomatidae

27. *Aulostomus chinensis* Smith and Swain — Indo-west Pacific; in the eastern Pacific from Clipperton, Revillagigedo, and Cocos Islands, and Islas Contreras in the Gulf of Chiriqui.

Acanthuridae

28. *Acanthurus triostegus* (Linnaeus) — Indo-west Pacific and Hawaii; in the eastern Pacific from Cabo San Lucas, Isla Jaltemba, and Islas Tres Marias, Mexico, to the Gulf of Chiriqui and the offshore island groups.

29. *Acanthurus glaucopareius* Cuvier — Indo-west Pacific and Hawaii; in the eastern Pacific from the major offshore islands (except the Galapagos), Isla Jaltemba, Isla Viradores, and the Gulf of Chiriqui.

30. *Acanthurus xanthopterus* Valenciennes — Indo-west Pacific and Hawaii; in the eastern Pacific, from the Gulf of California to Panama. This is the only surgeonfish species observed at the Perlas Archipelago.

31. *Ctenochaetus cyanoguttatus* Randall/Briggs (1961:554) lists the distribution as "Cocos Island. Line Islands to the Marquesas and west to Aldabra in the western Indian Ocean." This species has been collected in the Gulf of Chiriqui (SIO 71-40), at Isla del Caño, Costa Rica (UCR 423), and photographed at Isla Viradores, Costa Rica.

32. *Zanclus canescens* (Linnaeus) — Widespread in the Indo-west Pacific; in the eastern Pacific from Las Frailes, Gulf of California (SIO 61-243), Isla Jaltemba, Islas Tres Marias, the Gulf of Chiriqui, and the offshore islands.

Diodontidae

33. *Diodon holacanthus* Linnaeus — Circumtropical; widespread in the eastern tropical Pacific.

34. *Diodon hystrix* Linnaeus — Circumtropical; widespread in the eastern tropical Pacific.

Tetraodontidae

35. *Arothron hispidus* (Linnaeus) — Indo-west Pacific and Hawaii; in eastern Pacific from Cabo San Lucas to Panama and the offshore islands.

36. *Arothron meleagris* (Bloch and Schneider) — Indo-west Pacific and Hawaii; in the eastern Pacific it ranges from Cabo San Lucas to Ecuador and the offshore islands. Recent evidence (Tyler, Randall, and McCosker, in preparation) indicates that the polychromatic *A. setosus* (Smith) is conspecific with the wide ranging Indo-Pacific species *A. meleagris.*

Balistidae

37. *Melichthys niger* (Bloch) — A circumtropical species usually associated with oceanic islands (Berry and Baldwin, 1968). This species is present at the offshore islands within the Gulf of Chiriqui (Isla Ladrones and Isla Montuosa) where it replaces *Sufflamen verres* (Gilbert and Starks) on the reef.

38. *Alutera scripta* (Osbeck) — A circumtropical species. In the eastern Pacific, at the offshore islands and Cabo San Lucas. In Panama, it is infrequently seen in the Gulf of Chiriqui and the Archipeilago de las Perlas.

Ostraciontidae

39. *Ostracion meleagris* Shaw — Indo-west Pacific and Hawaii; in the eastern Pacific from Cabo San Lucas, Bahia Banderas, Isla Jaltemba, the offshore islands, and the Gulf of Chiriqui.

RESUMEN

Las colecciones recientes nos indican la presencia de un número de especies de peces del Indo Pacífico Occidental en el Golfo de Chiriquí. El veinticuatro por ciento (40) de las especies de peces de arrecifes también se encuentran en el mar Indo Pacífico Occidental. El Golfo de Chiriquí está fuera del efecto de afloramiento, como si lo está el Golfo de Panamá; siendo así relativamente más rico en el desarrollo de corales hermatípicos.

Nueve de las especies del Indo Pacífico Occidental que no han sido registrado en o cerca del continente Americano fueron colectadas: *Myripristis murdjan, Ctenochaetus cyanoguttatus, Gymnothorax flavimarginatus, G. buroensis, G. undulatus, Enchelynassa canina, Uropterygius tigrinus, Malacanthus hoedti,* y *Hemipteronotus taeniourus.* Las ultimas seis de las especies

mencionadas no han sido reportadas como del Pacífico Oriental; aunque ninguna se encuentra confinada al Golfo de Chiriquí.

Los datos de las siguientes especies del Pacífico Oriental son clasificados como nulos, basándose en el hecho de que no han sido correctamente identificados o erróneamente registrados: *Brachysomophis crocodilinus, Gymnothorax chilospilus, Callechelys marmoratus, Myrichthys maculosus, Myripristis berndti, Lutjanus kasmira, Runula tapeinosoma, Abudefduf saxatilis vaigiensis* y *Antennatus bigibbus.*

La distribución de las siguientes especies endémicas del Pacífico Oriental *Gymnothorax castaneus, Petrotyx hopkinsi,* y *Paraclinus altivelis* se ha extendido hasta Panamá. *Xyrichthys panamensis* Fowler, 1944, es sinónimo con *Hemipteronotus pavoninus* (Valenciennes, 1839).

Muchos de los migratorios transpacífico están restringidos y limitados en su distribución Pacífico Oriental. Algunos se encuentran aparentemente en estrecha relación asociados con el desarrollo de corales hermatípicos. No existe evidencia que nos indique que dichas especies estén desplazando especies endémicas del Pacífico Oriental.

El número de especies encontradas por primera vez en el Golfo de Chiriquí refleja el poco conocimiento en lo que se refiere a la distribución de los peces del Pacífico trópico oriental.

ACKNOWLEDGMENTS

We thank C. H. Birkeland, T. F. Dana, P. W. Glynn, S. McCosker, and A. Rodaniche for field assistance, W. N. Eschmeyer (CAS), C. R. Robins (UMML), and B. W. Walker (UCLA) for permission to examine and use material in their care, The National Science Foundation (GB 4408), The Smithsonian Tropical Research Institute, and the U. S. Armed Forces Southern Command (Rodman Naval Station) for shiptime, and P. W. Glynn for his critical reading of a draft of this manuscript. Special thanks are due B. W. Walker, W. Baldwin, and K. S. Norris for information regarding fish distribution in the eastern tropical Pacific, and W. A. Bussing (UCR) who has allowed us to cite unpublished Costa Rican records from his collections. Much of this work was completed during the tenure of J. McCosker as a pre-doctoral fellow with the STRI, whose support is gratefully acknowledged. These studies would not have been possible without the continued cooperation of Lt. Col. R. D. Paredes and Sr. J. L. Obarrio of the Republic of Panama.

LITERATURE CITED

BERRY, F. H. 1958. A new species of fish from the western North Atlantic, *Dikellorhynchus tropidolepis,* and relationships of the genera *Dikellorhynchus* and *Malacanthus.* Copeia (2):116-125.

________, AND W. J. BALDWIN. 1966. Triggerfishes (Balistidae) of the eastern Pacific, Proc. Cal. Acad. Sci. 34(9):429-474.

BRIGGS, J. C. 1961. The East Pacific Barrier and the distribution of shore fishes. Evol. 15:545-554.

________. 1964. Additional transpacific shore fishes. Copeia (4):706-708.

________. 1967. Relationship of the tropical shelf regions. Stud. Trop. Oceanogr. Miami 5:569-578.

________. 1969. The sea-level Panama Canal: potential biological catastrophe. BioScience 19(1):44-47.

________. 1970. Tropical shelf zoogeography. Proc. Calif. Acad. Sci., 4th Ser., 38(7): 131-138.

BROWN, W. L. AND E. O. WILSON. 1956. Character displacement. System. Zool. 5: 49-64.

CHAVE, E. H. 1973. Ecological separation of six species of Hawaiian cardinalfishes. Copeia (*in press*).

CLARK, H. W. 1936. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 29. New and noteworthy fishes. Proc. Calif. Acad. Sci., fourth ser., 21(29):383-396.

EKMAN, S. 1953. Zoogeography of the sea. Sidgwick and Jackson, London. 417 p.

EMERSON, W. K. 1967. Indo-Pacific faunal elements in the tropical eastern Pacific, with special reference to the mollusks. "Venus," Jap. J. Malacol: 25(3):85-93.

FORSBERGH, E. D. 1969. On the climatology, oceanography and fisheries of the Panama Bight. Bull. Inter-Amer. Trop. Tuna Comm. 14(2):49-385.

FOWLER, H. W. 1932. The fishes obtained by the Pinchot South Seas Expedition of 1929, with descriptions of one new genus and three new species. Proc. U.S. Nat. Mus. 80(6):1-16.

________. 1938. The fishes of the George Vanderbilt South Pacific Expedition, 1937. Monogr. Acad. Nat. Sci. Phila. no. 2. 349 p.

________. 1944. Results of the Fifth George Vanderbilt Expedition (1941). Monogr. Acad. Nat. Sci. Phila. no. 6:57-529.

GLYNN, P. W. In Press. Observations on the ecology of the Caribbean and Pacific coasts of Panama. The Panamic Biota: some observations prior to a sea-level canal. Sym. Biol. Soc. Wash.

________, R. H. STEWART AND J. E. MCCOSKER. In Press. Pacific coral reefs of Panama: structure, distribution, and predators. Geol. Rundschau.

GREENFIELD, D. W. 1965. Systematics and zoogeography of *Myripristis* in the eastern tropical Pacific. Calif. Fish and Game 51(4):229-247.

________, D. HENSLEY, J. W. WILEY, AND S. T. ROSS. 1970. The Isla Jaltemba coral formation and its zoogeographical significance. Copeia (1):180-181.

GÜNTHER. A. 1870. Catalogue of the fishes in the British Museum Vol. VIII, Catalogue of the Physostomi. London, Taylor and Francis. 549 p.

HERRE, A. W. C. T. 1936. Fishes of the Crane Pacific Expedition. Publ. Field, Mus. Nat. Hist., Zool. ser. 21. 472 p.

HOBSON, E. S. 1968. Predatory behavior of some fishes in the Gulf of California. U.S. Dept. Interior, Bureau Sport Fish. and Wildlife, Res. Report 73. 92 p.

HUBBS, C. L. AND R. H. ROSENBLATT. 1961. Effects of the equatorial currents of the Pacific on the distribution of fishes and other marine animals. Tenth Pac. Sci. Cong., Abst. of Symposium Papers: 340-341.

JORDAN, D. S. AND B. W. EVERMANN. 1898. The fishes of North and Middle America: A descriptive catalogue . . . Panama. Part II. Bull. no. 47, U.S. Nat. Mus. 1241-1936.

KRESJA, R. J. 1960. The eastern, tropical Pacific fishes of the genus *Blenniolus,* including a new island endemic. Copeia (4):322-336.

MACARTHUR, R. H. AND E. O. WILSON. 1967. The theory of Island Biogeography. Princeton University Press. 203 p.

MCCOSKER, J. E. 1971. A new species of *Parapercis* (Pisces: Mugiloididae) from the Juan Fernández Islands. Copeia (4):682-686.

________, AND R. H. ROSENBLATT. 1972. Eastern Pacific snake-eels of the genus *Callechelys* (Apodes: Ophicthidae). Trans. San Diego Soc. Nat. Hist. 17(2): 15-24.

MORRIS, R. A. AND D. E. MORRIS. 1967. A rare hawkfish *Oxycirrhites typus* Bleeker found in Hawaii. Ichthyologica 39(2):71-72.

MORROW, J. E. 1957. Shore and pelagic fishes from Peru, with new records and the description of a new species of *Sphoeroides.* Bull. Bingham Oceanogr. Coll. 16(2):1-55.

MYERS, G. S. 1941. The fish fauna of the Pacific ocean, with especial reference to zoogeographical regions and distribution as they effect the international aspects of the fisheries. Proc. 6th Pac. Sci. Congr. 3, 1939:201-210.

RANDALL, J. E. 1961. A record of the kyphosid fish *Sectator ocyurus* (=*azureus*) from the Society Islands. Copeia (3):357-358.

________. 1963. Review of the hawkfishes (family Cirrhitidae). Proc. U.S.N.M. 114(3472):389-451.

________. 1964. A revision of the filefish genera *Amanses* and *Cantherhines.* Copeia (2):331-361.

________.1965. A review of the razorfish genus *Hemipteronotus* (Labridae) of the Atlantic Ocean. Copeia (4):487-501.

RENNER, J. A. 1963. Sea surface temperature monthly average and anomaly charts eastern tropical Pacific ocean, 1947-58. U.S. Fish and Wildlife Serv. Spec. Rept., Fish. No. 442. 57 p.

ROSENBLATT, R. H. 1963. Differential growth of the ilicium and second dorsal spine of *Antennatus strigatus* (Gill) and its bearing on the validity of *A. reticularis* (Gilbert). Copeia (2):462-464.

________, AND E. S. HOBSON. 1969. Parrotfishes (Scaridae) of the eastern Pacific, with a generic rearrangement of the Scarinae. Copeia (3):434-453.

________, AND T. D. PARR. 1969. The Pacific species of the clinid fish genus *Paraclinus.* Copeia (1):1-20.

________, AND I. RUBINOFF. 1972. *Pythonichthys asodes,* a new heterenchelyid eel from the Gulf of Panama, Bull. Mar. Sci. 22(2):355-364.

________, AND B. W. WALKER. 1963. The marine shore fishes of the Galapagos Islands. Occ. Pap. Calif. Acad. Sci. 44:97-106.

SCHAEFER, M. B., Y. M. M. BISHOP, AND G. V. HOWARD. 1958. Some aspects of upwelling in the Gulf of Panama. Inter-Amer. Trop. Tuna Comm., Bull. 3(2): 77-132.

SEALE, A. 1940. Report on fishes from Allan Hancock Expeditions in the California Academy of Sciences. Allan Hancock Pacific Exped. 9(1):1-46.

SNODGRASS, R. E. AND E. HELLER. 1905. Shore fishes of the Revillagigedo, Clipperton, Cocos and Galapagos Islands. Proc. Washington Acad. Sci. 6:333-427.

WYRIKI, K. 1965. Surface currents of the eastern tropical Pacific ocean. Bull. Inter-Amer. Trop. Tuna Comm. 9(5):271-304.

Accepted for publication September 14, 1972

NUMBER 235
DECEMBER 29, 1972

REVIEW OF THE INSECTIVORA FROM THE EARLY MIOCENE SHARPS FORMATION OF SOUTH DAKOTA

By J. H. HUTCHISON

CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM • LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Natural History Museum of Los Angeles County. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

INSTRUCTIONS FOR AUTHORS

Manuscripts for CONTRIBUTIONS IN SCIENCE may be in any field of Life or Earth Sciences. Acceptance of papers will be determined by the amount and character of new information. Although priority will be given to manuscripts by staff members, or to papers dealing largely with specimens in the collections of the Museum, other technical papers will be considered. All manuscripts must be recommended for consideration by the curator in charge of the proper section or by the editorial board. Manuscripts must conform to those specifications listed below and will be examined for suitability by an Editorial Committee including review by competent specialists outside the Museum.

Authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that the primary type has become the property of a scientific institution of their choice and cited by name.

MANUSCRIPT FORM.—(1) The 1972 CBE Style Manual, third edition (AIBS) is to be followed in preparation of copy. (2) Double space entire manuscript. (3) Footnotes should be avoided if possible. Acknowledgments as footnotes will not be accepted. (4) Place all tables on separate pages. (5) Figure legends and unavoidable footnotes must be typed on separate sheets. Several of one kind may be placed on a sheet. (6) An abstract must be included for all papers. This will be published at the head of each paper. (7) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. Summaries will be published at the end of the paper. (8) A diagnosis must accompany any newly proposed taxon. (9) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in the proper proportions for reduction to CONTRIBUTIONS page size. Consult the 1972 CBE Style Manual, third edition (AIBS) in preparing illustration and legend copy for style. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Original illustrations and art work will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proof which should be corrected and returned promptly. Any changes or alterations, other than typographical corrections, will be billed to the author. Unless otherwise requested, page proof also will be sent to the author. One hundred copies of each paper will be given free to each author or divided equally among multiple authors. Orders for additional copies must be sent to the Editor at the time corrected galley proof is returned. Appropriate order forms will be included with the galley proof.

Virginia D. Miller
Editor

REVIEW OF THE INSECTIVORA FROM THE EARLY MIOCENE SHARPS FORMATION OF SOUTH DAKOTA[1]

By J. H. HUTCHISON[2]

ABSTRACT: Five of the seven reported insectivore taxa from the Sharps Formation (early Arikareean) of South Dakota are considered valid: *Ocajila makpiyahe, Proscalops evelynae, Quadrodens wilsoni, Domnina greeni, D. dakotensis.* One additional genus of shrew, *Trimylus,* is added to the fauna. *Quadrodens* is the senior synonym of *Palaeoscalopus* and is regarded as a talpid.

INTRODUCTION

In two papers covering the early Miocene (early Arikareean) vertebrate faunas from the Sharps Formation of the Wounded Knee area of southwestern South Dakota, Macdonald (1963, 1970) described six new species and three new genera of insectivores. A survey of the more recent paper and subsequent examination of the figured material indicates a need for some taxonomic revision and re-allocation of several of his specimens.

METHODS

Measurements were made with a Gaertner measuring microscope and are given to the nearest hundredth of a millimeter (mm). Length of lower teeth equals the maximum possible length of parallel planes normal to a best fit line along the lingual margin of the tooth, with entoconid perpendicular to plane of view. Width equals the maximum width between parallel planes parallel to the length line. All specimens are conserved in either the Museum of Geology, South Dakota School of Mines and Technology (SDSM) or the Natural History Museum of Los Angeles County (LACM).

SYSTEMATICS

FAMILY Erinaceidae Fischer von Waldheim, 1817
SUBFAMILY Galericinae Pomel, 1848
TRIBE Echinosoricini (Cabrara, 1925) Gill, 1872
GENUS *Ocajila* Macdonald, 1963
Ocajila makpiyahe Macdonald, 1963

Macdonald (1963) initially described *Ocajila makpiyahe* on a single dentary fragment with M_2-M_3, but he made no subfamily assignment of the

---

[1] REVIEW COMMITTEE FOR THIS CONTRIBUTION
William A. Clemens
Jason A. Lillegraven
David P. Whistler

[2] Museum of Paleontology, University of California, Berkeley, California 94720

genus. Van Valen (1967: 262) placed *Ocajila* in the tribe Echinosoricini and suggested that the type jaw "may represent the otherwise unknown lower dentition of *Brachyerix* but is more probably a synonym of the echinosoricine *Lanthanotherium*." The lower dentition of *Brachyerix* has subsequently been identified (Rich and Rich, 1971) and is quite unlike *Ocajila*. The reduction of the paralophid and low profile of the molars support the placement in the Echinosoricini and close relationship with *Lanthanotherium*.

Subsequently Macdonald (1970) referred two new specimens to *Ocajila makpiyahe*, one of which he figured. He stated (p. 19) that "the M_1 of LACM 9380 represents the first record of this tooth. It is an enlarged version of M_2 with no significant variations in the pattern." LACM 9380 is referable to the soricid species *Trimylus* (see below). The second referred specimen (LACM 9491) is referable to *O. makpiyahe* but contributes no new information.

FAMILY Talpidae Fischer von Waldheim, 1817
SUBFAMILY Proscalopinae K. M. Reed, 1961
GENUS *Proscalops* Matthew, 1901
Arctoryctes Matthew, 1907

Before any discussion of the evolutionary position of *Proscalops evelynae* from the Sharps Formation is undertaken, the probable stratigraphic position of the types of the named species of *Proscalops* needs clarification. The type localities of *P. tertius* K. M. Reed, 1961, *P. terrenus* (Matthew, 1907), and *P. secundus* Matthew, 1909 lack precise data as to location or formation or both. However, study of isolated teeth (to be published elsewhere) from known formations in South Dakota and adjacent states provides a reference to which the probable chronostratigraphic position of those type specimens may be determined. K. M. Reed (1961) states that *P. tertius* came from the " "White River fm.," possibly Brule, "Badlands, South Dakota." " The presence of *Oligoscalops* in the lower member (Scenic Member) of the Brule Formation (K. M. Reed, 1961, and unpublished) and the slightly more advanced character of *P. evelynae* from the Sharps Formation which overlies the Brule Formation indicate that *P. tertius* is probably from the Poleslide member of the Brule Formation. This assumption is strengthened by a specimen of the P^4-M^1, LACM 1493 from locality 1990, from the Poleslide Member in the Wounded Knee area that is essentially identical with *P. tertius;* however, the possibility that the type of *P. tertius* is from the lower part of the Sharps Formation or is conspecific with *P. evelynae* (see below) cannot be objectively ruled out with the present small sample sizes.

Macdonald (1963, 1970) has concluded that the type skull of *P. secundus* may have come from the upper portion of the Monroe Creek Formation or the lower Harrison Formation. Although lack of lower teeth of this type prohibit a refined interpretation of its evolutionary stage, Macdonald's conclusion is in agreement with the supposed position of *P. secundus* in the biostratigraphic series that has been based upon upper molar and premolar

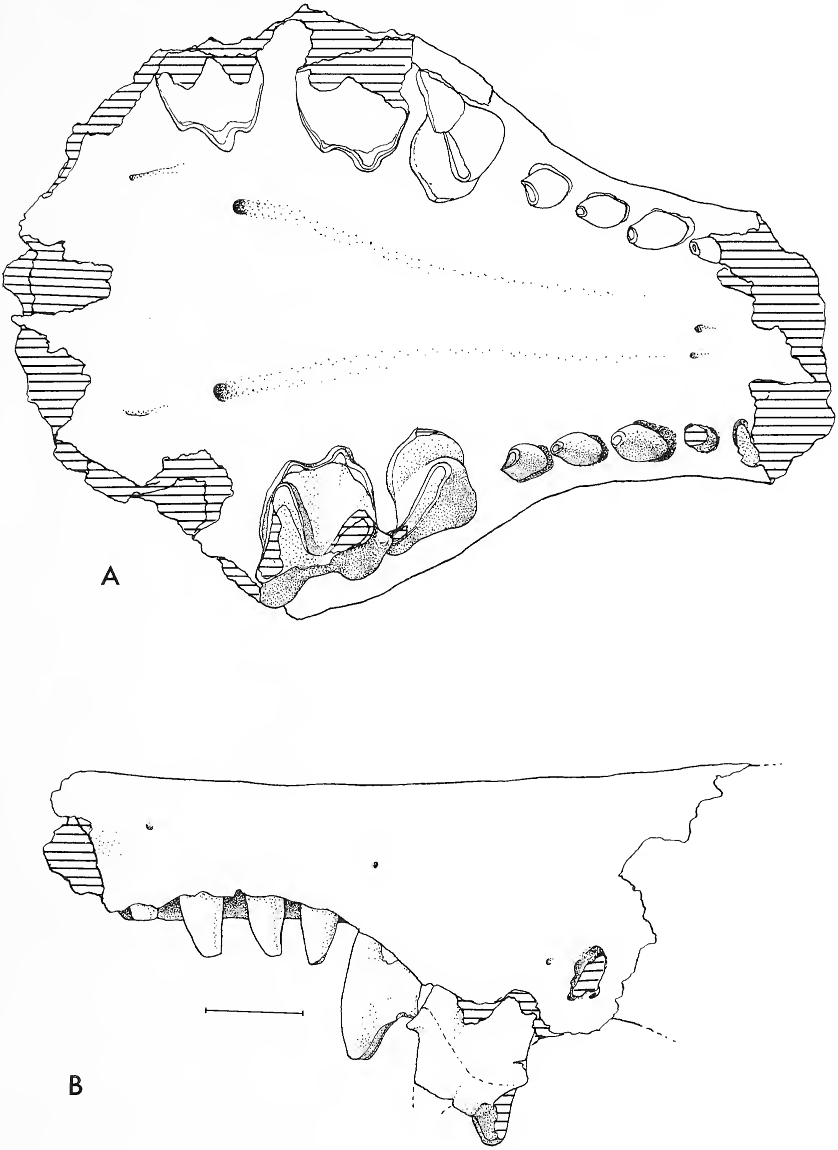


FIGURE 1. *Proscalops evelynae* (Macdonald, 1963), LACM 21416, incomplete rostrum with right I^3 to P^4 and lingual moieties of M^1-M^2 and left C to M^1; A, palatal view; B, lateral view of left side. Scale line equals 1 mm.

specializations. *P. terrenus* is a form species based on the humerus. Specimens referred to this species range in age from Whitneyan (Poleslide Member of Brule Formation) to Hemingfordian (Split Rock Formation, Wyoming). Thus, the concept of *P. terrenus* more than covers the entire chronostratigraphic span of all the species of *Proscalops* named on skulls and jaws. Macdonald (1963: 170) stated in regard to the type humerus of *P. terrenus* that "We can assume that the specimen was found anywhere between Porcupine Creek and the top of the divide east of Wounded Knee creek. The reference to "Upper Rosebud" [by Matthew, 1907] probably precludes the possibility that the type came from beds below the Harrison." Although Macdonald (1970:24) later suggested on less objective criteria that the type came from the Sharps Formation, I accept his original placement. *P. terrenus* is probably a valid species. Proscalopine teeth from the Harrison Formation near Agate, Nebraska, represent either an advanced species of *Proscalops* (more advanced than *P. secundus*) or a primitive species of *Mesoscalops*.

At present there are many reasons to assume that the sequence *Oligoscalops galbreathi* (C. A. Reed, 1956) — *P. tertius* — *P. evelynae* — *P. secundus* — *Mesoscalops* K. M. Reed represents a phyletic lineage with gaps. *O. galbreathi* was first named on the basis of a humerus as *Arctoryctes galbreathi* C. A. Reed, 1956 then later named again as *Oligoscalops whitmanensis* K. M. Reed, 1961 on the basis of a skull from Wyoming and a referred jaw from the same locality as the humerus in northeastern Colorado; there seems to be no reason to assume that the humerus belongs to a different species than the skull. *P. miocaenus* Matthew, 1901 may also belong in the sequence and on size and available dental characters (K. M. Reed, 1961) would fall between *Oligoscalops* and *P. tertius.*

Proscalops evelynae (Macdonald), 1963
  Domninoides evelynae Macdonald, 1963
  Arctoryctes terrenus Matthew, 1907 in part, Macdonald, 1963
  Proscalops evelynae (Macdonald), Hutchison, 1968, including
    Arctoryctes terrenus of Macdonald, 1963
  Proscalops evelynae (Macdonald), Macdonald, 1970
  Arctoryctes terrenus Matthew in part, Macdonald, 1970

A previously unpublished rostrum with C-M^1 and fragments of the M^2 (LACM 21416 from locality 6898 [Fig. 1]), collected by Mr. Robert Machris, aids in comparing *Proscalops evelynae* (previously known only from the type, incomplete mandible, and from humeri) with other proscalopines known from skulls.

The type mandible (SDSM 5338) of *Proscalops evelynae* was originally described under another genus and has not previously been compared in detail to known jaws of other species of *Proscalops*. There is a chronological trend in *Proscalops* towards increasing hypsodonty of the molars. *P. evelynae* appears to be slightly more hyposodont, has greater extension of the enamel down the labial side of the roots, and has narrower anterior cingula than in *P. tertius, P. miocaenus,* and *Oligoscalops*. In size of teeth *P. evelynae* agrees closely with *P. tertius* but is significantly larger than *P. miocaenus* and *Oligoscalops* (see Macdonald, 1963, and K. M. Reed, 1961 for measurements). The low longitudinal crest (entocristid) at the base and lingual opening of the talonid valley is similar in all three species. *P. evelynae* differs markedly from *Mesoscalops scopelotemos* K. M. Reed, 1960, which has greater crown height, enamel extension, very high entocristid, and better developed cingular shelf between the labial bases of the protoconid and hypoconid.

The rostrum (LACM 21416) lacks the tip of the snout and posterolateral margins of the palate, thus only the left M^1 and lingual shelves of the right M^{1-2} are preserved. Preceding the P^4's, three teeth and two alveoli (one with root) are preserved on the left side and four teeth on the right side. Following the dental terminology of K. M. Reed (1961), these are I^3, C, P^{2-3}. The I^3-P^3 are unicuspid and single rooted with ovate to drop-shaped cross-sectional outlines. I^3 is the smallest tooth and canine the largest between the I^3 and P^4 with P^2-P^3 subequal in size (Table 1). The P^4 supports a single labial blade and lingual shelf with cusp. A minute cusp on the anterior side and near the base of the paracone represents the remnant parastyle as in *Proscalops tertius, P. miocaenus,* and *P. secundus* but not *Mesoscalops* in which it is absent. K. M. Reed (1961:286) states that the parastyle is absent in all *Proscalops* and *Mesoscalops* but in the types of all *Proscalops* species my observations indicate

TABLE 1

Measurement (in mm) of the upper teeth of *Proscalops evelynae,* LACM 21416

		Left	Right
P4*	length	2.27	—
	width	2.28	—
P3*	length	0.87	0.87
	width	0.70	0.68
P2	length	0.84	0.87
	width	0.60	0.61
P1	length	0.93	0.94
	width	0.74	0.69
C	length	—	0.55
	width	—	0.48

*P4 maximum length between parallel planes perpendicular to the line connecting the parastyle and posterior tip of ectoloph (this is not the parameter used but undefined by K. M. Reed, 1961). Unicuspid tooth length is the maximum cross-sectional diameter

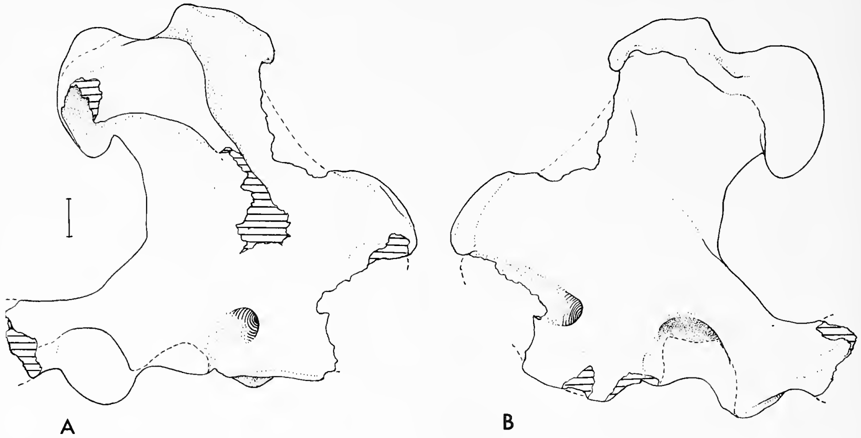
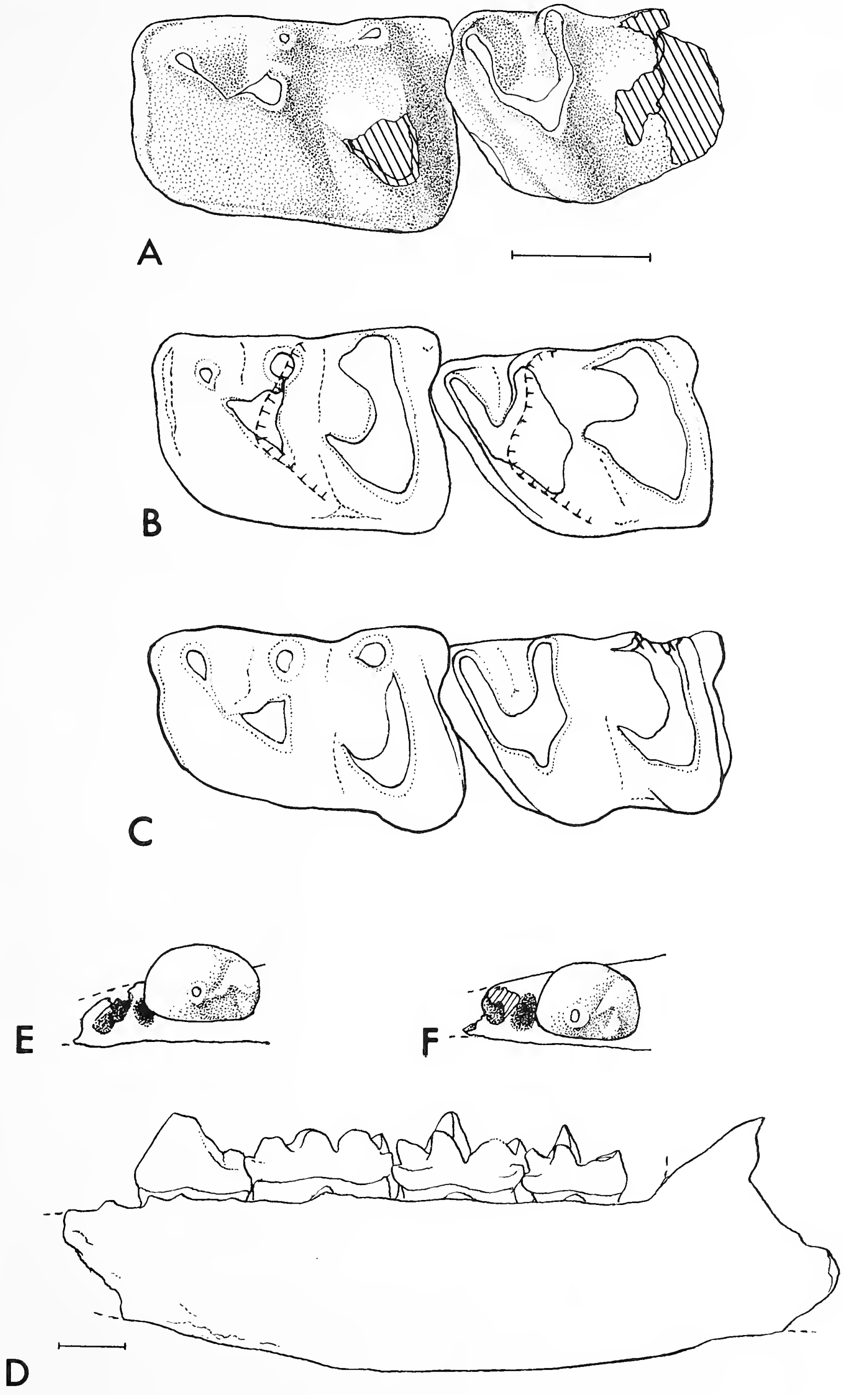


FIGURE 2. *Proscalops evelynae* (Macdonald, 1963), LACM 9362, damaged right humerus; A, anterior view; B, posterior view. Scale line equals 1 mm.

a small vertical ridge or distinct minute cuspation occurred in the ancestral area of the parastyle. The lingual cusp is rather posteriorly situated as in *P. tertius* but more shelflike, although, not to the extreme as in *P. secundus*. There is no indication of a second cusp behind the main lingual cusp as in the unworn P^4 of *Mesoscalops*. The molars as preserved agree closely with *P. tertius* in presence of well-developed metaconules (hypocone of K. M. Reed), protoconules (protostyle of K. M. Reed), and minute "hypostyles." Despite the qualitative differences in degree of angulation and development mentioned by K. M. Reed (1961) between the molars of *P. tertius* and *P. secundus*, I believe that at present it is difficult to distinguish such features on worn teeth; the relative proportions or distinctness of these cusps change significantly due to differential wear and to stage of wear. Unworn teeth and an analysis of wear progression in larger samples of the various species are needed to evaluate these features. The rostrum agrees in detail with those already described by K. M. Reed (1961) for other species of *Proscalops*.

Measurements (following Reed and Turnbull, 1965) on 11 humeri (Fig. 2) from the LACM collections show a wide range in variation, with measurements of the smaller specimens ranging from 74 to 88% of the largest; however, the ratios of these measurements produced ranges essentially identical to those calculated by Reed and Turnbull (1965) for "*Arctoryctes terrenus*" except

FIGURE 3. *Quadrodens wilsoni* Macdonald, 1970; A, LACM 9331 (Type) occlusal view of M_1-M_2; B, SDSM 6244 (referred specimen of *Palaeoscalopus*) reversed occlusal outline of M_1-M_2, hachures indicate edge of apparently anomalous shear wear surface. C-E, SDSM 55135 (Type of *Palaeoscalopus*); C, reversed occlusal outline of M_1-M_2; D, lingual view of dentary fragment with P_4-M_3; E, occlusal view of P_4 and antemolar alveoli; F, SDSM 6244, occlusal view of P_4 and antemolar alveoli. Scale lines equal 1 mm.


A
B
C
E
F
D

those incorporating the measurement of the proximal shaft width. Reed and Turnbull (1965:132) noted that this measurement is difficult to duplicate objectively. The range in gross size is of the magnitude seen within some living species (*Scalopus aquaticus*) but is unusual for a series from a specific local area. However, nearly all the measurable specimens came from different sites of unknown or differing stratigraphic levels. There is no consistent size relationship with stratigraphic level when both are known.

Dentally *Proscalops evelynae* differs only slightly from *P. tertius* and might be considered conspecific, but it is axiomatic that a better understanding of the variability of both proposed species needs to be known. Considering the probably older but uncertain age and locality of *P. tertius* and small samples of the other species of *Proscalops*, it seems prudent to retain *P. evelynae* as a distinct species for the time being.

Talpidae *incertae sedis*
Quadrodens wilsoni Macdonald, 1970:21
Quadrodens wilsoni Harksen, 1967, *nomen nudum*
Palaeoscalopus pineridgensis Harksen, 1967, *nomen nudum*
Palaeoscalopus pineridgensis Macdonald, 1970:23

Macdonald (1970) described *Quadrodens wilsoni* on the basis of a dentary fragment containing the M_1 and trigonid of the M_2. He diagnosed the genus on the basis of the large rectangular M_1 with trigonid cusps confined to approximately one third of the trigonid. He stated (p. 21) "This form seems to be another variation of the "hedgehog" theme." A few pages later he described a new genus and species of talpid, *Palaeoscalopus pineridgensis*, on the basis of two incomplete dentaries including the P_4-M_3. He diagnosed the M_1 of this form as having greatly reduced anterolabial cingulum. In discussion Macdonald stated that *P. pineridgensis* is the earliest record of a shrew-mole in North America.

There is a great similarity between Macdonald's figures (Figs. 6, 8) of *Quadrodens* and *Palaeoscalopus* and subsequent examination of the types revealed that these two forms are congeneric and probably conspecific. The material referred to *Palaeoscalopus* is slightly smaller than the type of *Quadrodens*, but shows the same overall proportions. The three specimens (Fig. 3) show some variation in the M_1 outlines and M_1 anterior cingula, but I regard these as insignificant for generic allocation. A fourth specimen of *Quadrodens* (LACM 9253) consisting of a dentary fragment with M_2 and alveoli of P_4-M_3 was referred to *Domnina greeni* by Macdonald (1970:21). The structure of the M_2 and situation of the mental foramen is nearly identical in all four specimens. Although more than one species may be represented, the sample is too small to meaningfully define even two taxa. The name *Quadrodens wilsoni* has page priority over *Palaeoscalopus pineridgensis* and is more descriptive without implication of relationships; thus I chose *Quadrodens wilsoni* as the senior synonym.

TABLE 2

Measurement of the lower dentition of *Quadrodens wilsoni* Macdonald, 1970

*To posterior margin of posterior root

Macdonald, 1970 reference	Specimen number	LACM loc. numbers	SDSM loc. number	P4		M1		M2		M3	
				length	width	length	width	length	width	length	width
Quadrodens wilsoni (type)	LACM 9331	1821 = 1981	V5359	—	—	2.45	1.60	2.01*	1.42	—	—
"*Palaeoscalopus pineridgensis*" (type)	SDSM 55135	1861 = 1982	V5360	1.75	1.09	2.39	1.54	2.14	1.44	1.56	0.98
"*Palaeoscalopus pineridgensis*" (referred)	SDSM 6244	1861 = 1982	V5360	1.56	1.08	2.16	1.55	2.02	1.43	—	—
"*Domnina greeni*" (referred)	LACM 9253	1955	V541	—	—	—	—	2.08	1.51	—	—

TABLE 3

Measurement of the lower dentition of *Domnina* and *Trimylus*

*Trigonid width

Identification	Specimen number	LACM loc. numbers	SDSM loc. number	M1		M2	
				length	width	length	width
Domnina greeni	SDSM 5895	—	V5413	2.20	1.37	—	1.19*
Domnina dakotensis	LACM 9351	1981 = 1821	V5359	2.33	1.39	1.99	1.31
Trimylus	LACM 9380	1958	V6228	2.35	1.69	1.91	1.51

Macdonald has already fully described the teeth allocated to *Quadrodens* and *Palaeoscalopus;* however, the variation in outline of M_1, variable expression of the M_1 anterior cingulum, and slight range in size should be noted (Table 2). The two preserved P_4's show some variation of the talonid. The hypoconid of SDSM 55135 (Fig. 3E) is a simple distinct cusp flanked by only one ridge which joins the hypoconid to the protoconid. However, SDSM 5244 (Fig. 3F) has a subdued hypoconid which forms the posterolabial rim of a continuous ridge extending posteriorly from the base of the protoconid curving lingually on the hypoconid to the lingual margin and then deflecting anteriorly, thus forming (but not quite enclosing) a small talonid basin.

The dentary is most completely represented in SDSM 55135 and SDSM 6244 but has not previously been described in detail. It shows no transverse curvature and is broadly convex ventrally with the deepest portion below the molars. Its anterior part tapers quite sharply anteriorly, indicating a short antemolar region and reduced dentition, although the tip of the dentary is not preserved. The mandibular symphysis extends posteriorly to below the posterior moiety of the P_4. Alveoli anterior to P_4 are preserved in both specimens but are not identical. SDSM 6244 has one posterior alveolus preceded by two incomplete but apparently subequal and longitudinally aligned smaller ones. Five alveoli (both incomplete and complete) precede the P_4 in SDSM 55135. The posterior wall of the anterior-most alveolus indicates a rather large, long, and anteriorly inclined (about 45°) root. This alveolus is followed by three small and tightly crowded alveoli arranged in a equilateral triangle with two of the alveoli labial. This clustering is followed by a larger centrally placed alveolus and P_4. There are several ways to interpret these alveoli but analogy with talpids and progressive erinaceids suggests that the enlarged anterior alveolus represents an incisor (I_2) followed by two to four crowded antemolars and a P_4.

The family assignment of *Quadrodens wilsoni* is troublesome without more data on the morphology of the mandible, skull, or skeleton. Chiroptera are excluded from consideration on the grounds of their probable rarity in the samples and degree of transverse curvature of their mandibles. Low profile of the teeth, relatively equal height of the talonid and trigonid of the molars, reduced molarity of the P_4, and overall morphology eliminate from consideration most of the more primitive and highly specialized insectivore suborders (fide Van Valen, 1967) except the Erinaceota. Most families of this suborder except the Erinaceidae and Talpidae are either too generalized in molar morphology and P_4 reduction (Nesophonitdae, Adapisoricidae) or too specialized (Soricidae, Dimylidae) for close comparison. Plesiosoricids show a greater and/or more primitive emphasis on development of prominent shearing paralophids on the lower molars (especially the M_1) in contrast to the rather bulbus and crushing-like M_1 of *Quadrodens*. Macdonald's error in describing the same genus under two different families illustrates the difficulties of separating the Talpidae from the Erinaceidae on the basis of molars alone (*Talpa incerta* Matthew, 1924 is a brachyericine hedgehog). Members of both families may be characterized by loss of a distinct hypoconulid and merging of the hypolophid and entoconid of the molars. Most talpids and many erinaceids (Echinosoricinae, Erinaceinae) exhibit quadrate low crowned molars without great disparity between the talonids and trigonids. *Quadrodens wilsoni* resembles some erinaceids and differs from known talpids in: 1) even convexity of the lower margin of the dentary; 2) M_1 larger than M_2; and 3) basined (in one specimen of two) talonid on P_4. *Quadrodens* resembles the Talpidae and differs from the Erinaceidae in: 1) lack of paraconid on P_4; 2) transverse basal posterior cingulum and posterolingual accessory cuspid on M_1-M_2; and 3) mental foramen small and not depressed into dentary. Although the anterior part of the dentary was apparently short, there is no obvious indication in the area of the P_4 suggesting an enlarged incisor as in progressive erinaceids; however, talpids frequently develop a reduced dentition with prominent but not greatly hypertrophied lower incisor (I_2).

Although the above comparisons may not lead to an obligatory conclusion of talpid affinities, I believe that *Quadrodens wilsoni* is a talpid and, on theoretical zoogeographical grounds (Hutchison, 1968:108), this species is probably aligned with the Proscalopinae.

FAMILY Soricidae Fischer von Waldheim, 1817
SUBFAMILY Heterosoricinae Viret and Zapfe, 1951
GENUS *Domnina* Cope, 1873
Domnina greeni Macdonald, 1963

Domnina greeni Macdonald, Hutchison, 1966
Domnina greeni Macdonald, Repenning, 1967
Domnina greeni Macdonald, Macdonald, 1970

This species is still known only from the type specimen; the specimen subsequently referred to it (Macdonald, 1970) belongs to *Quadrodens*. The teeth were described by Macdonald (1963) but the specimen is abraded and much of the lingual side of the M_2 is worn away. Macdonald's (1963, Fig. 5, teeth are incorrectly captioned M_{2-3}) illustration of the type indicates a greater longitudinal compression of the trigonid than exists on the specimen (Fig. 4C). The mental foramen is partly preserved below and just anterior to the M_1 hypoconid.

For discussion of this species see that of *Domnina dakotensis* below.

Domnina dakotensis Macdonald, 1970

Domnina dakotensis Harksen, 1967, *nomen nudum*

This species, known only from the type mandible, was characterized by its widely open M_1 trigonid and closure of the M_1-M_2 talonid valleys by the entoconid crest (entocristid). In addition, there is a postsymphyseal foramen below the level of the M_1 hypoconid and the root of the large incisor extends posteriorly as far as the M_1 hypoconid.

Considering relative temporal and geographic proximity of *Domnina*

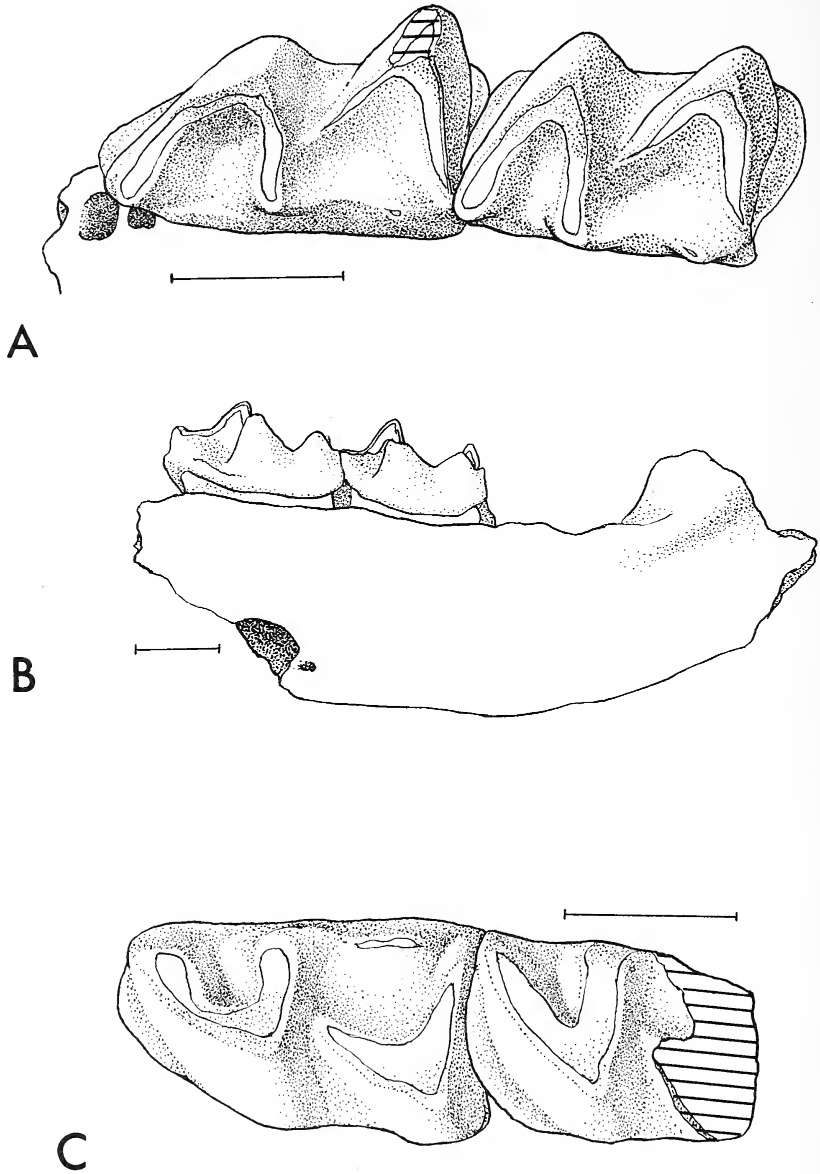


FIGURE 4. A-B *Domnina dakotensis* Macdonald, 1970, LACM 9351 (Type), A, lingual view of dentary fragment with M_1-M_2; B, occlusal view of M_1-M_2; C, *Domnina greeni* Macdonald, 1963, SDSM 5895 (Type), occlusal view of M_1-M_2. Scale lines equal 1 mm.

greeni and *D. dakotensis,* discussion of relationships of these two poorly known species is necessary. The relative openness of the M_1 trigonid of *D. dakotensis* is not particularly diagnostic and may be the same as in *D. greeni* when relative differences in wear, preservation, and individual variation are considered. Macdonald (1970) stressed the uniqueness of the closure of the trigonid valley by the entoconid crest, but I fail to see any difference between the two species in the closure or height of the crest (compare Fig. 4B with Macdonald, 1963, Fig. 5). Indeed, Repenning (1967) characterizes the genus by the entoconid "united to the metaconid by a high ridge (entoconid crest)." Although the "diagnostic" characters are nullified, there are subtle differences between the two specimens which may be of specific significance when better samples are available. The postentoconid valley is comparatively well developed in *D. greeni* (as in *D. gradata* Cope, 1873) but absent in *D. dakotensis* (Fig. 4A). The presence or absence of this valley seems to be relatively constant in other species of shrews; however, if these specimens represent transition to a closed-valley condition, then variability in this character is significant. The molars of *D. dakotensis* appear to be relatively longer (Table 3), more delicate, and have perhaps a better-developed metastylar ridge on the metaconid than in *D. greeni,* although preservation of the *D. greeni* specimen is not ideal for comparison. In the absence of a larger sample of either species, it seems prudent to tentatively retain both species names on the basis of the above characters.

The closure of the postentoconid valley and delicacy of the molars suggests that *Domnina dakotensis* might be on the lineage of *Paradomnina* Hutchison, 1966, but the relatively greater posterior extension of the incisor root, more posterior position of the postsymphyseal foramen, and perhaps fewer antemolars are specialized characters over the later *Paradomnina.* There are no serious obstacles to deriving *D. dakotensis* from *D. gradata.*

GENUS *Trimylus* Roger, 1885

Trimylus sp.

Macdonald (1970:19, Fig. 4) figured a dentary fragment, LACM 9380, and referred it to *Ocajila makpiyake.* The deep robust jaw, position of the mental foramen, and construction of the teeth showed remarkable similarity to those features in the heterosoricine shrews, especially *Trimylus.* Subsequent examination of this specimen confirms its assignment to *Trimylus.*

Macdonald did not describe this specimen in detail and some diagnostic features are misleadingly illustrated or not figured. LACM 9380 consists of a midsection of the horizontal ramus containing M_1-M_2. The dentary (Fig. 5) is deep and robust with a large mental foramen set below the ectoflexus of the M_1 in the posterior end of an elongate depression extending anterodorsad. A prominent postsymphyseal foramen opens anterolabially near the ventral margin of the dentary below the junction of the M_1-M_2. The dentary is broken off just anterior to this foramen with the break extending anterodorsally to just in front of the M_1. No part of the symphysis is preserved. The cavity for

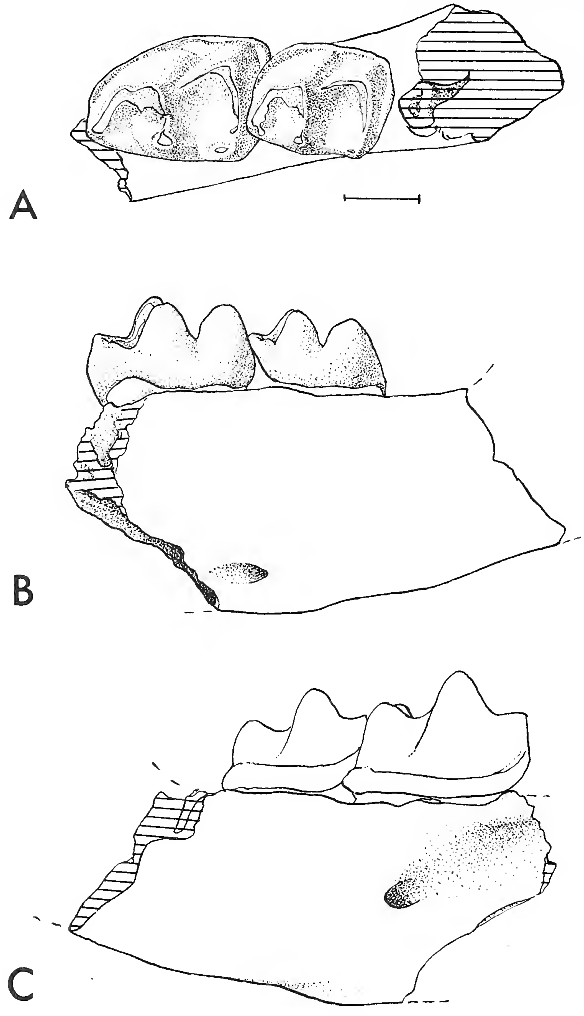


FIGURE 5. A-C, *Trimylus* sp., LACM 9380, dentary fragment with M_1-M_2; A, occlusal view; B, lingual view; C, labial view. Scale line equals 1 mm.

the root of the large incisor extends as far as the symphyseal foramen but none of its external margins are preserved. Remains of one antemolar alveolus (P_4) are preserved just anterior to M_1. There apparently is room for only one or two additional alveoli between the P_4 and I_1.

The molars are graded in size (Table 3) with the M_1 about one-third larger than M_2. M_1 resembles other *Trimylus* in its robust proportions and major features of the trigonid and talonid (see Mawby, 1960, Wilson, 1960, and Repenning, 1967). The anterior cingulum of M_1 is well defined but terminates labially to the lingual extremity of the paraconid. The hypolophid is well fused to the entoconid but a small hypoconulid persists in early wear high up the posterolabial flank of the entoconid. M_2 resembles M_1 but the trigonid is more closed thus shortening and compacting the tooth. A small (adventitous?) cuspid on the posterolabial flank of the paraconid occludes part of the trigonid valley. A slight vertical ridge on the posterolabial wall of the talonid indicates the position of the hypoconulid. Only the anterior root of the M_3 is preserved. No pigmentation is evident on the teeth.

The massive construction of the jaw, large incisor, posteriorly-situated and recessed mental foramen, postsymphyseal foramen, strong size gradation of the robust molars with nearly complete fusion of the entoconid and hypolophid conspire to situate LACM 9380 firmly within the genus *Trimylus* (Mawby, 1960, Repenning, 1967).

The Sharps Formation specimen agrees better with near contemporary forms of *Trimylus* in North America than with later Miocene and Pliocene species of North America and Europe in its more anterior location of the mental foramen and incisor root and retention of vestiges of the hypoconulid on the molars. The Sharps specimen differs from *T. dakotensis* Repenning, 1967 in nearly complete fusion of M_1 and M_2 hypolophids to the entoconids, slightly larger size, persistent anterior cingulum on M_1, and slightly more anterior position of the mental and postsymphyseal foramina. The Sharps specimen closely resembles *T. compressus* (Galbreath, 1953) in tooth morphology but differs in slightly more anterior situation of the mental and postsymphyseal foramina. The Sharps species differs from *T. roperi* in the anterior position of the mental and (?) post-symphyseal foramina, more anterior position of the I_1 root, and possibly the greater prominence of the hypoconulids.

Although nearest in time to *Trimylus dakotensis* (early Hemingfordian), the Sharps specimen seems a little closer to *T. compressus* (Orellan) in those meager features available, such as the greater coalescence of the M_1-M_2 hypolophids and entoconids and persistent M_1 anterior cingulum. I think it prudent, however, to leave specific allocation in abeyance until more diagnostic material (i.e., antemolar region) is found and a better understanding of the variation of the named species is obtained.

SUMMARY

Of the seven insectivores reported from the Sharps Formation by Macdonald (1963, 1970), I recognize five of which two species are only tentatively retained as distinct. The shrew, *Trimylus,* is an addition to the Sharps Formation fauna. The revised insectivore fauna is as follows:

Family: Erinaceidae
Ocajila makpiyahe Macdonald, 1963

Family: Talpidae
Proscalops evelynae (Macdonald, 1963)
Quadrodens wilsoni Macdonald, 1963
(= *Palaeoscalopus pineridgensis* Macdonald, 1970)
Family: Soricidae
Domnina greeni Macdonald, 1963
Domnina dakotensis Macdonald, 1970
Trimylus sp.

Owing to the small sample sizes, I have only tentatively retained *Proscalops evelynae* and *Domnina dakotensis* as distinct species on the basis of a few dental characters of questionable significance.

LITERATURE CITED

GALBREATH, E. C. 1953. A contribution to the Tertiary Geology and Paleontology of northeastern Colorado. Univ. Kans. Publ., Paleontol. Contrib., Vertebrata 4:1-120.

HARKSEN, J. C. 1967. Geology of the Porcupine Butte Quadrangle. S. Dak. Geol. Survey map with text on reverse.

HUTCHISON, J. H. 1966. Notes on some Upper Miocene shrews from Oregon. Univ. Oreg. Mus. Nat. Hist. Bull. 2:1-23.

________. 1968. Fossil Talpidae (Insectivora, Mammalia) from the later Tertiary of Oregon. Univ. Oreg. Mus. Nat. Hist. Bull. 11:1-117.

MACDONALD, J. R. 1963. The Miocene faunas from the Wounded Knee area of western South Dakota. Bull. Am. Mus. Nat. Hist. 125(3):139-238.

________. 1970. Review of the Miocene Wounded Knee faunas of southwestern South Dakota. Bull. Nat. Hist. Mus., Los Angeles Co. Mus. 8:1-82.

MATTHEW, W. D. 1907. A lower Miocene fauna from South Dakota. Bull. Am. Mus. Nat. Hist. 23(9):169-219.

MAWBY, J. E. 1960. A new occurrence of *Heterosorex* Gaillard. J. Paleontol. 34(5):950-956.

REED, C. A. 1956. A new species of the fossorial mammal *Arctoryctes* from the Oligocene of Colorado. Fieldiana, Geol. 10:305-311.

REED, C. A., AND W. D. TURNBULL. 1965. The mammalian genera *Arctoryctes* and *Cryptoryctes* from the Oligocene and Miocene of North America. Fieldiana: Geol. 15(2):99-170.

REED, K. M. 1960. Insectivores of the middle Miocene Split Rock Local Fauna, Wyoming. Breviora, Mus. Comp. Zool. 116:1-11.

REED, K. M. 1961. The Proscalopinae, a new subfamily of talpid insectivores. Bull. Mus. Comp. Zool. 125(14):473-499.

REPENNING, C. A. 1967. Subfamilies and genera of the Soricidae. Geol. Surv. Prof. Pap. 565:1-74.

RICH, T. H. V., AND P. V. RICH. 1971. *Brachyerix,* a Miocene hedgehog from western North America, with a description of the tympanic regions of *Paraechinus* and *Podogymnura.* Amer. Mus. Novitates 2477:1-58.

VAN VALEN, L. 1967. New Paleocene insectivores and insectivore classification. Bull. Am. Mus. Nat. Hist. 135(5):217-284.

WILSON, R. W. 1960. Early Miocene rodents and insectivores from northeastern Colorado. Univ. Kans. Publ., Paleontol. Contrib., Vertebrata 7:1-92.

Accepted for publication April 4, 1972

Printed in Los Angeles, California, by Anderson, Ritchie and Simon