PROCEEDINGS

OF THE

California Academy of Sciences

FOURTH SERIES

Vol. XXXIII

SAN FRANCISCO
PUBLISHED BY THE ACADEMY
1965–1966

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OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 1, pp. 1–46; 26 figs.; 1 table July 28, 1965

THE BRACHYURAN DECAPOD CRUSTACEANS OF CLIPPERTON ISLAND[1]

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INTRODUCTION

Clipperton Island is situated in the eastern tropical Pacific Ocean at Lat. 10° 18′ N. and Long. 109° 13′ W. Because of its isolated position and lack of protected anchorage, it has been seldom visited by scientific expeditions, and even less frequently explored by carcinologists. Among the first to have collected crustaceans there was John T. Arundel, who visited the island in 1897 aboard the *Navarro*. The Hopkins–Stanford Expedition, with R. E. Snodgrass and Edmund Heller, visited Clipperton in 1898 aboard the *Julia E. Whalen*, collecting specimens of *Geograpsus lividus* from Clipperton Lagoon (Rathbun, 1902). A party from the Schooner *Academy* of the California Academy of Sciences in 1905 found the island to be infested with land crabs, *Gecarcinus planatus*, which made bird collecting difficult, since the crabs got to the birds before the collectors, and had them ruined in a few seconds (Slevin, 1931).

Many early accounts of Clipperton Island mention the abundance of land crabs, according to Sachet (1960), whose historical résumé has proved most useful in this connection. One of these, by Captain Detaille (letter to Lockhart of Le Havre), describes "les gros crabes rouges" seen by the crew of the *Amiral* in 1858 while on a phosphate-prospecting mission. Their first mention in the scientific literature was by Lenz (1901), who reported under the name *Gecarcoidea lalandei* specimens brought from Clipperton to Honolulu by vessels engaged in the guano trade. How these crabs found their way into the hands of Professor Schauinsland, on whose Pacific collections Lenz reported, is not known.

The first comprehensive collection of Clipperton Island decapods was made by Waldo L. Schmitt, who in 1938 spent a few hours ashore while en route to the Galápagos Islands aboard the U.S.S. *Houston*. While there he obtained 10 of the 34 species of brachyurans here reported, including the first *Thalamita* from the eastern Pacific. Following his brief visit no further crustacean collecting was done until 1954, when a party from the Acapulco Trench Expedition of the Scripps Institution of Oceanography was landed from the *Spencer F. Baird*. The nine species of brachyurans obtained were identified by the writer for inclusion in a paper by Hertlein and Emerson (1957). A similar landing from the *Spencer*

F. Baird was made in October, 1956, by Conrad Limbaugh. The 15 species of brachyurans obtained were identified by Fenner A. Chace, Jr., and are included in the present report. This was the situation when the International Geophysical Year (I.G.Y.) Clipperton Island Expedition, with Conrad Limbaugh as leader, landed from the *Spencer F. Baird* on August 7, 1958, remaining until September 25 of that year. The extensive collection of Brachyura then made includes all 12 species previously reported from the island, together with an additional 20 here reported for the first time. The Anomura and Macrura from this and the 1956 expedition were the subject of a separate report by Fenner A. Chace, Jr. (1962).

While, according to Sachet (*op. cit.*, p. 11), the collections of Arundel were the first to have been described in the scientific literature of the island, the crabs were not among the groups reported upon. It was therefore with considerable interest that the writer learned of the existence of two specimens of Arundel's collecting among unstudied collections at the U. S. National Museum, to which they had been forwarded from the California Academy of Sciences in 1948, along with Pacific material collected by the *Albatross*. The first of these, *Grapsus grapsus*, had not been reported previously from Clipperton, although it can not have been unobserved there. The second proved to be the ubiquitous *Gecarcinus planatus*. Thus what were probably the first brachyurans collected at Clipperton Island, the Arundel specimens, are being reported simultaneously with the most recent specimens known to have been collected there, those of the I.G.Y. Clipperton Island Expedition. The addition of *Portunus* (*Achelous*) *affinis*, obtained by the Inter-American Tropical Tuna Commission in Clipperton Island waters in February, 1958, brings the total insular brachyuran fauna to 34 species.

The brachyuran material collected by the 1958 Clipperton Island Expedition will be distributed among the following institutions, with due regard to the contribution of representatives of each in collecting, sorting, distributing, and identifying the specimens: the Scripps Institution of Oceanography (SIO), La Jolla; the Natural History Museum, San Diego (SDMNH); the Allan Hancock Foundation (AHF), Los Angeles; the United States National Museum (USNM), Washington; and the Muséum National d'Histoire Naturelle, Paris (MNHNP). The specimens of corals mentioned as hosts for crab commensals have already been deposited in the University of California Museum of Paleontology (UCMP), Berkeley.

ACKNOWLEDGMENT

The writer is indebted to Dr. Carl L. Hubbs of the Scripps Institution of Oceanography, who arranged for him to study the present collection, and to the late Conrad Limbaugh, who personally delivered the major part of it to the Allan Hancock Foundation before departing on his final journey to Monaco and to France. He is also grateful to Dr. Fenner A. Chace, Jr., who relinquished the

brachyuran material sent to the U. S. National Museum upon learning of the writer's prior claim. He wishes to thank the following expedition members who made additional specimens and personal notes available: Dr. Marie-Hélène Sachet for notes on *Gecarcinus planatus*; Mr. C. R. Harbison for a collection of dried crabs from supratidal levels; Dr. Ernst S. Reese for crabs collected from corals and for habitat notes; Dr. Edwin C. Allison for additional specimens of *Troglocarcinus* and information concerning its host. Special thanks are due to Dr. R. Serène for identifying the first specimen of *Troglocarcinus* from the eastern Pacific, to Prof. W. Stephenson for examining and reporting on the *Thalamita* species, and to Mr. Frank G. Alverson of the Inter-American Tropical Tuna Commission and Mr. Eugene L. Nakamura of the Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service, for information concerning the migratory habits and digestive rates of the fish from whose stomachs the specimens of *Portunus* (*Achelous*) *affinis* were extracted.

GEOGRAPHICAL CONSIDERATIONS

With few exceptions, the islands of the eastern tropical Pacific, from the Revilla Gigedos to the Galápagos, have been treated by American workers in a purely American context. That this was too restricted a concept, particularly as regards Clipperton Island, became increasingly apparent during the course of this study as one species after another proved to be of west-Pacific origin or derivation. This should not have been surprising, for perhaps no other island in the eastern Pacific is so favorably situated to receive migrants from the western Pacific, or to provide the accustomed habitat once they have arrived. Accordingly, Clipperton Island may be said to belong neither to the Panamic nor to the Polynesian fauna alone, but to both, since each has contributed substantially to its microcosm.

An evaluation of the trans-Pacific increment called for extralimital experience, supplied by two summers' field work in the Marshall Islands, with observations in Hawaii while en route. Familiarity with the Indo-Pacific coral reef fauna at Eniwetok, an atoll in the western Pacific, facilitated recognition of the west-Pacific element present at Clipperton, the only atoll in the eastern Pacific, and made possible the assignment of each species to its characteristic habitat despite the paucity of accompanying ecological data. It also provided a working acquaintance with the voluminous and scattered literature needed to identify the non-American species, for which no encompassing monograph exists, and to determine their provenance.

The references given in the synonymies, aside from the original description and first use of the name in its present combination, are largely those that report the occurrence of the species at one or more of the islands nearest to Clipperton, either on the Polynesian or American side. Where the occurrence is a west-Pacific one, the islands most frequently mentioned are Hawaii, the Line Islands, the Marquesas, Tahiti, and the Tuamotus. Where the occurrence is an east-Pacific one, the islands are Cape San Lucas, whose insular nature as regards warm-water, current-borne species has been developed in an earlier paper (Garth, 1960), the Revilla Gigedos, where it has been found advisable to anticipate the publication of records of Indo-Pacific species encountered by Hancock Expeditions at Clarion and/or Socorro Island which would otherwise appear restricted to Clipperton in the eastern portion of their range, Cocos, Malpelo, and the Galápagos. Such information, supplemented by an increasing knowledge of current patterns in the eastern Pacific, should lead to an eventual understanding of the routes by which larval stages of littoral species have arrived and have been dispersed. (See also discussion under Distribution following Account of Species.)

THE FAUNA AS KNOWN

The Clipperton Island brachyuran fauna as presently known consists of 34 species, 26 genera, and 9 families, of which 22 species, 17 genera, and 4 families are here reported for the first time. Of the 34 species, 16 (shown with an asterisk) are Indo-Pacific, and of these, 9 have not attained the American mainland. Species earlier reported are shown in the right-hand columns by author and date; those in the left-hand column were obtained by the 1956 and 1958 expeditions and are included in the present report.

LIST OF CLIPPERTON ISLAND BRACHYURA

	Lenz, 1901	Rathbun, 1902	Schmitt, 1939	Hertlein and Emerson, 1957
DYNOMENIDAE				
Dynomene ursula Stimpson				
CALAPPIDAE				
**Calappa hepatica* (Linnaeus)				
HAPALOCARCINIDAE				
**Hapalocarcinus marsupialis* Stimpson				
**Troglocarcinus crescentus* (Edmondson)				
MAJIDAE				
Herbstia pubescens Stimpson				
Teleophrys cristulipes Stimpson			x	
PORTUNIDAE				
**Thalamita picta* Stimpson			x	
Portunus (*Achelous*) *affinis* (Faxon)				
Portunus (*Achelous*) *tuberculatus* (Stimpson)				
Cronius ruber (Lamarck)				
XANTHIDAE				
**Carpilius convexus* (Forskål)				
**Carpilodes cinctimanus* (White)				
Platypodia rotundata (Stimpson)			x	x

	Lenz, 1901	Rathbun, 1902	Schmitt, 1939	Hertlein and Emerson, 1957
Actaea dovii Stimpson			x	x
Actaea sulcata Stimpson			x	x
Actaea species				
Cycloxanthops vittatus (Stimpson)				
Leptodius cooksoni Miers				
Micropanope xantusii (Stimpson)			x	x
Micropanope species				
Pilumnus xantusii Stimpson				
**Domecia hispida* Eydoux and Souleyet				
**Trapezia digitalis* Latreille				x
**Trapezia ferruginea* Latreille				x
GRAPSIDAE				
Grapsus grapsus (Linnaeus)				
**Geograpsus lividus* (Milne Edwards)		x	x	x
**Pachygrapsus minutus* A. Milne Edwards			x	x
**Pachygrapsus planifrons* de Man				
**Plagusia depressa tuberculata* Lamarck				
**Plagusia speciosa* Dana				
**Percnon abbreviatum* (Dana)			x	
Percnon gibbesi (Milne Edwards)				
GECARCINIDAE				
Gecarcinus planatus Stimpson	x		x	x
OCYPODIDAE				
**Ocypode ceratophthalma* (Pallas)				
Total species 34	1	1	10	9

ACCOUNT OF SPECIES[2]

Subsection GYMNOPLEURA
Superfamily DROMIIDEA
Family DYNOMENIDAE

Dynomene ursula Stimpson.

Dynomene ursula STIMPSON, 1860b, p. 239 (Cape San Lucas). RATHBUN, 1937, p. 54, pl. 12, figs. 1–4 (Galápagos). SCHMITT, 1939, p. 25 (Galápagos). GARTH, 1946, p. 349, pl. 61, figs. 5, 6; 1948, p. 16.

RANGE. Gulf of California, Mexico, to La Plata Island, Ecuador. Galápagos Islands. Shore to 70 fathoms.

MATERIAL. Clipperton Island: Northeast side, 45 feet; August 28, 1958; C. Limbaugh, T. Chess, and A. Hambly: 1 male, 2 females (1 ovigerous), 3 young.

MEASUREMENTS. Largest specimen, male: length 13.7 mm., width 17.5 mm.

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[2] All figures are of Clipperton Island specimens of Indo-Pacific species.

Female: length 9.7 mm., width 12.3 mm.; ovigerous female: length 13.5 mm., width 17.9 mm. Young: length 4.2 mm., width 4.9 mm.

Habitat. *Pocillopora* coral.

Remarks. Not previously reported from Clipperton Island.

Subsection OXYSTOMATA

Family Calappidae

Calappa hepatica (Linnaeus).

(Figures 9, 10.)

Cancer hepaticus Linnaeus, 1764, p. 448 (The Indies); 1766, p. 1048.

Calappa tuberculata Fabricius, 1798, p. 345. Owen, 1839, p. 80 (Oahu, Hawaii). Heller, 1865, p. 69 (Tahiti).

Calappa hepatica, De Haan, 1837, p. 70. Nobili, 1907, p. 378 (Tuamotu). Boone, 1934, p. 32, pls. 8–10, synonymy (Marquesas).

Range. Indo-Pacific from the Red Sea and Natal to Hawaii, Tuamotu, and the Marquesas.

Material. Clipperton Island: October, 1956; C. Limbaugh: 1 male, 2 carapaces. August, 1958; E. S. Reese: 1 male; coral reef: 1 male. South shore; August 19, 1958; E. S. Reese, W. Baldwin, and C. Limbaugh: 1 male. Northwest end, high tidepool; August 24, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 male. Northeast side, in sand; depth 1 foot at low tide; August 31, 1958; C. Limbaugh: 3 young females. West shore, on beach; September 16, 1958: 1 carapace.

Measurements. Largest specimen, male: length 37.0 mm., width 59.5 mm. Largest female: length 25.6 mm., width 38.5 mm.

Habitat. Taken in a variety of situations, as indicated above. Its absence from the lagoon, its customary habitat in atolls of the western Pacific, is due no doubt to the increasing freshness of Clipperton Lagoon.

Remarks. This widely ranging Indo-Pacific species may now be reported from Clipperton Island on the strength of eight specimens taken on at least four different occasions. It appears well established on the atoll.

Subsection HAPALOCARCINIDEA

Family Hapalocarcinidae

Hapalocarcinus marsupialis Stimpson.

(Figures 1, 2.)

Hapalocarcinus marsupialis Stimpson, 1859, p. 412 (Hilo, Hawaii); 1907, p. 170, pl. 14, fig. 8. Edmondson, 1923, p. 24 (Palmyra). Schmitt, 1936, p. 34, figs. 36a–f (Port Utria, Colombia). Rathbun, 1937, p. 259, pl. 79, figs. 3–9; text-fig. 46, synonymy (Secas Islands, Panama).

RANGE. Indian and western Pacific oceans east to Hawaii and Palmyra Island. Eastern Pacific at Panama and Colombia.

MATERIAL. Clipperton Island: August, 1958; E. S. Reese: 5 galls in 3 pieces of dry *Pocillopora* coral; 2 ovigerous females. Northeast transect, 36 feet; August 27, 1958; T. Chess and A. Hambly: 2 galls in *Pocillopora* coral; 3 ovigerous females.

MEASUREMENTS. Ovigerous females: length 3.1 mm., width 3.8 mm.; length 4.7 mm., width 4.6 mm.; and length 3.7 mm., width 5.0 mm. Considerable difference in relative lengths and widths was noted.

HABITAT. *Pocillopora* coral, in which it forms galls. The remaining coral genera listed by Edmondson (1923) as hosts to *Hapalocarcinus* in the central and western Pacific, namely, *Seriatopora*, *Stylophora*, *Sideropora*, and *Millepora*, are not among recent stony corals of the eastern Pacific enumerated by Durham and Barnard (1952, p. 13).

REMARKS. In view of the earlier discovery by the *Velero III* of the coral gall crab on the American mainland (Schmitt, 1936), and its apparent absence from the Galápagos Islands, where *Pocillopora* coral was collected with equal diligence by Hancock expeditions, it is of interest to find this obligate commensal established at Clipperton Island. Apparently Clipperton, rather than the Galápagos, has served as the stepping stone enabling *Hapalocarcinus marsupialis* to bridge the central Pacific oceanic barrier.

Troglocarcinus (Troglocarcinus) crescentus (Edmondson).

(Figures 3, 4, 5, 6.)

Cryptochirus crescentus EDMONDSON, 1925, p. 33, text-fig. 6, pls. B, C (Johnston Island).
Troglocarcinus (Troglocarcinus) crescentus, FIZE AND SERÈNE, 1957, p. 62, text-figs. 10, 11c, 11d, 12b, pl. 3, figs. 4–7, pl. 5, fig. 2, pl. 11, fig. B, synonymy and distribution (Nha-Trang, Viet Nam).

RANGE. Western Pacific from Hong Kong, the Palao Islands, and Viet Nam to Johnston Island. Undoubtedly distributed throughout the Indo-Pacific, wherever *Pavona* occurs.

MATERIAL. Clipperton Island: Northeast transect, 78 feet; August 27,

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FIGURE 1. Gall of *Hapalocarcinus marsupialis* Stimpson on *Pocillopora elegans* showing respiratory apertures of female crab imprisoned within.

FIGURE 2. Same as figure 1.

FIGURE 3. *Troglocarcinus crescentus* (Edmondson) in *Pavona varians* Verrill from 15–20 meters, showing method of concealment.

FIGURE 4. Same as figure 3 but enlarged to show characteristic shape of opening.

FIGURE 5. *Troglocarcinus crescentus* (Edmondson) in *Pavona clivosa* Verrill from 15–20 meters, showing entire crab in dorsal view with enlarged inset.

FIGURE 6. Same as figure 5, showing crab at entrance to crescent-shaped burrow, enlarged inset.


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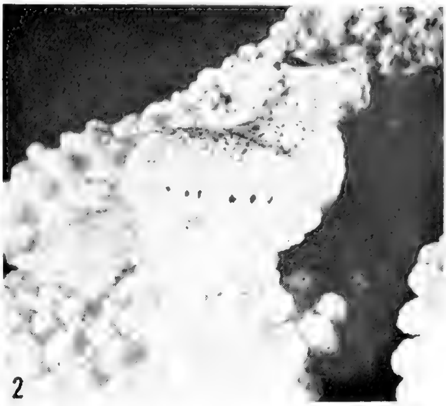
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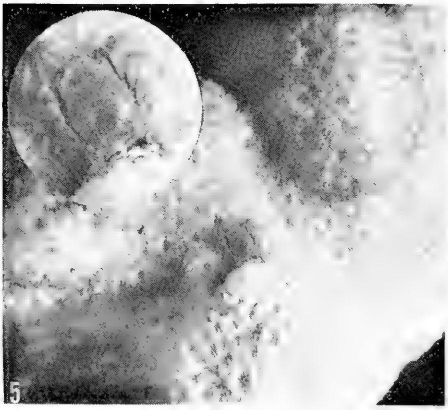
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6

1958; C. Limbaugh: 1 female, without record of host. Fifteen to 20 meters; August 1958; E. C. Allison: 2 dried specimens, on *Pavona* (UCMP no. B-6102).

Measurements. Female, non-ovigerous: length 4.0 mm., width 3.2 mm.

Habitat. Massive corals of the genus *Pavona*, in which they form tunnels of characteristic shape for each species, those of *Troglocarcinus* (*T.*) *crescentus* being crescentic. The opening is closed by the anterior portion of the carapace and the meri of the first pair of walking legs, which together form an operculum.

Remarks. According to Dr. R. Serène, authority on the Hapalocarcinidae, to whom the 4 mm. female was submitted, the specimen belongs to the genus *Troglocarcinus* by the presence of three pairs of pleopods, to the subgenus *Troglocarcinus* by its dorsoventrally flattened carapace and exposed walking legs, and to the group within the subgenus having the walking legs broad and the opening of the lodging crescent-shaped. The first walking leg is characterized by having the superodistal angle of the merus prolonged into a small lobe, and the dactyl strongly curved into a short hook, modifications related to the position taken by the animal to close, as by an operculum, the crescent-shaped gallery that it occupies.

Characters that separate it from *Troglocarcinus* (*T.*) *viridis* Hiro, which has a third maxilliped of similar form, are the subquadrangular carapace, the short, straight anterolateral margins, forming an angle with the true lateral margins, and the inclination of the anterior dorsal ⅕ of the carapace, with which the posterior dorsal ⅘ forms a junction outlining a transverse crest.

Details of structure of the Clipperton Island specimen not agreeing exactly with the species as heretofore defined are a less distinct relief and less spinulation. The crescent-shaped cavity of the inclined anterior part of the carapace is indicated by two feeble depressions only, while the spinules of the carapace and appendages are reduced to tubercles with the tips obliterated. These differences are considered by Dr. Serène as in no way justifying the definition of a new form (species or variety), since they do not surpass the modifications of aging.

Although the specimen was submitted to Dr. Serène without notation as to its host, he was able to predict that it would be found in coral of the genus *Pavona*. Alerted to this possibility, Dr. Edwin C. Allison, then studying the expedition corals, was able to locate two more specimens of the crab, the one inside, the other outside its characteristic crescent-shaped gallery (see figures 4 and 6). He was also able to establish the host of *Troglocarcinus* (*T.*) *crescentus* at Clipperton Island as *Pavona* of at least two species: *P. varians* Verrill 1864 and *P. clivosa* Verrill 1869.

The genus *Troglocarcinus* is now recorded for the first time from the eastern Pacific, joining *Hapalocarcinus* as a second representative of the Indo-Pacific family Hapalocarcinidae.

Subsection BRACHYGNATHA

Superfamily Oxyrhyncha

Family Majidae

Herbstia pubescens Stimpson.

Herbstia pubescens Stimpson, 1871, p. 92 (Manzanillo, Mexico). Garth, 1958, p. 308, pl. S, fig. 7, pl. 34, fig. 3, synonymy.

Range. West coast of Mexico (Stimpson). Otherwise, Costa Rica to Ecuador.

Material. Clipperton Island: Northeast transect, 78 feet; August 27, 1958; C. Limbaugh: 1 young. Northeast side, 45 feet, coral; August 28, 1958; C. Limbaugh, T. Chess, and A. Hambly: 2 post-ovigerous females.

Measurements. Female: length 14.0 mm., width 10.1 mm. Young: length about 2.8 mm.

Habitat. *Pocillopora* coral.

Remarks. When compared with specimens in the collections of the Allan Hancock Foundation, Clipperton Island specimens agreed with *H. pubescens* from Secas Islands, Panama, rather than with *H. pyriformis* (Bell) from Galápagos Islands. It it therefore the mainland species, rather than its insular derivative, that occurs at Clipperton.

Teleophrys cristulipes Stimpson.

Teleophrys cristulipes Stimpson, 1860a, p. 133; 1860b, p. 190, pl. 2, fig. 2 (Cape San Lucas). Rathbun, 1902, p. 284 (Galápagos). Schmitt, 1939, p. 22 (Clipperton). Crane, 1947, p. 73 (Clarion). Garth, 1958, p. 379, pl. W, fig. 1, pl. 42, fig. 3, synonymy (Socorro).

Range. Gulf of California, Mexico, to Ecuador. Clarion, Socorro, Clipperton, and Galápagos Islands.

Material. Clipperton Island: northeast side, 45 feet, coral; August 28, 1958; C. Limbaugh, T. Chess, and A. Hambly: 2 males, 5 females (4 ovigerous). Northeast corner, 45 feet, coral; August 30, 1958; same collectors: 1 ovigerous female. East side, reef flat margin or ridge, 0–2 feet; September 14, 1958; C. Limbaugh and T. Chess: 1 ovigerous female.

Measurements. Largest male: length 6.4 mm., width 6.6 mm.; largest ovigerous female: length 8.3 mm., width 9.0 mm. Largest female from coral: length 8.0 mm., width 8.3 mm.

Habitat. *Pocillopora* coral, but also free-living.

Remarks. One of the most ubiquitous of the smaller spider crabs, *Teleophrys cristulipes* has been recorded from all the major outlying islands of the eastern tropical Pacific. It was first taken at Clipperton by the Presidential Cruise of 1938.

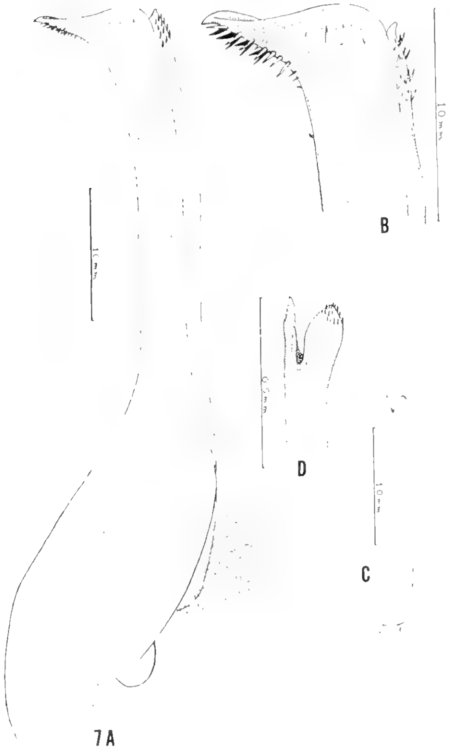

FIGURE 7. *Thalamita picta* Stimpson, male; A and B, first pleopod; C and D, second pleopod. Drawing by Ernest R. Tinkham.

FIGURE 8. *Carpilius convexus* (Forskål), male; A and B, first pleopod; C and D, second pleopod. Drawing by Ernest R. Tinkham.

Superfamily BRACHYRHYNCHA
Family PORTUNIDAE

Thalamita picta Stimpson.

(Figures 7, 11, 12.)

Thalamita picta STIMPSON, 1858a, p. 39 (*Ad insulam "Ousima"*). STEPHENSON AND HUDSON, 1957, p. 344, figs. 2A, 3A; pl. 4, fig. 2; pls. 8K, 10I, synonymy and distribution. FOREST AND GUINOT, 1961, p. 33 (Tahiti).

Thalamita gardineri BORRADAILE, 1902, p. 205, text-fig. 36 (Minikoi).

Thalamita alcocki DE MAN, 1902, p. 646 (Ternate).

Thalamita roosevelti SCHMITT, 1939, p. 16, text-fig. 2 (Clipperton).

RANGE. From Mozambique and the Red Sea to Hawaii, Tahiti, and the Tuamotus. Clipperton Island.

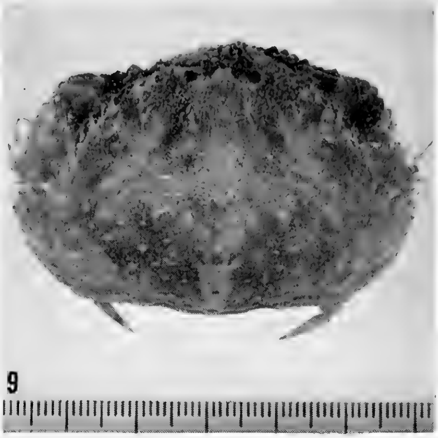

Figure 9. *Calappa hepatica* (Linnaeus), male, dorsal view. Scale in millimeters.
Figure 10. Same, ventral view. Scale in millimeters.

Material. Clipperton Island: October, 1956; C. Limbaugh: 1 young male. Coral reef; August, 1958; E. S. Reese: 3 males. South shore, coral reef, sand; August 11, 1958; E. S. Reese, C. Limbaugh, W. Baldwin, and J. Wintersteen: 5 males. East end, coral reef; August 15, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 13 males, 11 females (6 ovigerous), 8 young. South shore, coral reef; August 19, 1958; E. S. Reese, W. Baldwin, and C. Limbaugh: 3 males, 2 females. Northeast side, low intertidal to 6 inches; September 4, 1958; C. Limbaugh, T. Chess, and A. Hambly: 3 males. Northeast side, low tide, reef flat (collected with "Endrin"); September 13, 1958; C. Limbaugh, T. Chess, and A. Hambly: 44 males, 45 females (34 ovigerous), 2 young. East side, reef flat margin or ridge, 0–2 feet; September 14, 1958; C. Limbaugh and T. Chess: 1 ovigerous female.

Measurements. Largest specimen, male: length 18.2 mm., width including spines 29.0 mm., without spines 26.3 mm. Largest female, ovigerous, length 15.6 mm., width including spines 25.1 mm., without spines 22.8 mm. Young from 2.5 × 3.2 mm.

Habitat. The reef flat, from low intertidal to a depth of 2 feet.

Remarks. The present series of 140 specimens provides a wealth of material with which to supplement the type series of *T. roosevelti*, which consisted of three specimens, of which at least two were immature. It contains the largest specimens recorded, as well as the smallest specimens, and the only ovigerous females, of what was believed to represent a Clipperton Island endemic species, but which now appears to be only an insular population of the widely ranging Indo-west Pacific *T. picta*.

Two male and two female specimens of the *Thalamita* from Clipperton Island described by Schmitt (1939) as *T. roosevelti* were sent for examination to Professor W. Stephenson of the University of Queensland, Australia, an authority on the Indo-west Pacific Portunidae. Of them Dr. Stephenson wrote: "After a careful examination of your specimens of *Thalamita roosevelti*, I can find no points of difference compared with *Thalamita picta*. This applies to all the details of general structure and also to the male pleopod. If the specimen had borne an Indian Ocean or west Pacific Ocean locality label, I should have named it as *T. picta* without hesitation. If *T. roosevelti* is not a synonym of *T. picta*, then the two are sibling species."

Dr. Stephenson also noted that he had included both *T. gardineri* Borradaile and *T. alcocki* de Man, species considered by Schmitt (1939, p. 16) to be most closely related to *T. roosevelti*, and with it constituting a three-species group, as synonyms of *T. picta* (Stephenson and Hudson, 1957, p. 344), having come to the conclusion that the latter was a somewhat variable species. It is therefore apparent that, while *T. roosevelti* might have been considered a good species in an earlier context in which *T. gardineri* and *T. alcocki* were also so considered, it now has no more reason to stand alone than they, and accordingly is synonymized to *T. picta*. The fact that *T. picta* goes further eastward than the majority of the Indo-west Pacific *Thalamita* species, reaching Tahiti (Forest and Guinot, 1961) and the Tuamotus (Holthuis, 1953), establishes it as a likely colonizer of an island outpost like Clipperton.

Portunus (Achelous) affinis (Faxon).

Achelous affinis FAXON, 1893, p. 155 (off Panama and Ecuador); 1895, p. 23.
Portunus (Achelous) affinis, RATHBUN, 1898, p. 595; 1930, p. 80, pls. 38, 39 (Cape San Lucas).

RANGE. Cape San Lucas, Mexico, to Ecuador.

MATERIAL. Vicinity of Clipperton Island: February, 1958; removed from yellowfin tuna 1126 mm.; M.V. *Agressor* sample no. 15; F. G. Alverson, Inter-American Tropical Tuna Commission: 4 males, 5 females. Specimens returned to U. S. National Museum following verification of identification made by F. A. Chace, Jr.

MEASUREMENTS. Largest specimen, male: length 24.4 mm., width 38.5 mm. Largest female: length 21.9 mm., width 35.0 mm.

HABITAT. Pelagic.

REMARKS. The finding of recognizable specimens of *Portunus (Achelous) affinis* in the stomach of a yellowfin tuna caught in the immediate vicinity of Clipperton Island raises the question of how far the fish might have traveled since ingesting the crabs, which are common in offshore Mexican waters. The question is answered in part by Eugene L. Nakamura, fisheries biologist, whose experiments with Hawaiian skipjack indicate a lapse of only 1 hour and 25 minutes between the feeding of shrimp and the appearance of the undigested exoskeletons in the fecal pellets. Frank G. Alverson, senior scientist of the Inter-American Tropical Tuna Commission, thinks that the rate of digestion for the yellowfin, while slower, is probably not more than two or three times as slow as for the skipjack. This relatively rapid digestive rate would rule out the possibility that the crabs were ingested near the mainland and transported by the tuna to Clipperton Island. Rather, the evidence suggests that the portunids were eaten within a very few miles of the place at which the fish was caught. It is for this reason that *Portunus* (*Achelous*) *affinis* is included in this report, which deals otherwise with specimens collected on or from Clipperton Atoll.

Portunus (Achelous) tuberculatus (Stimpson).

Achelous tuberculatus Stimpson, 1860b, p. 223 (Cape San Lucas).

Portunus (*Achelous*) *tuberculatus*, Rathbun, 1898, p. 596 (Panama); 1930, p. 90, pl. 44. Finnegan, 1931, p. 629 (Gorgona Island). Crane, 1937, p. 68 (San Lucas Bay). Garth, 1946, p. 421, pl. 71, fig. 2 (Galápagos); 1948, p. 34 (Ecuador).

Range. Cape San Lucas, Mexico, to Ecuador. Galápagos Islands.

Material. Clipperton Island: Northeast corner, 45 feet; August 30, 1958; C. Limbaugh, A. Hambly, and T. Chess: 1 young female.

Habitat. From *Pocillopora*.

Measurements. Young female: length 10.4 mm., width including spines 21.2 mm., without spines 16.7 mm.

Remarks. Of small size and with distinctive ornamentation, including a spine at the posterolateral angles of the carapace, *Portunus* (*Achelous*) *tuberculatus* is easily recognizable among eastern Pacific portunids. It had not been recorded from Clipperton previously.

Cronius ruber (Lamarck).

Portunus ruber Lamarck, 1818, p. 260 (Brazil).

Cronius ruber, Stimpson, 1860b, p. 225 (Panama). Rathbun, 1924, p. 159 (Galápagos); 1930, p. 139, pls. 62, 63, synonymy (Peru). Finnegan, 1931, p. 630 (Gorgona Island, Colombia). Garth, 1946, p. 422, pl. 72, figs. 3, 4; 1948, p. 36 (La Plata Island, Ecuador). Holthuis, 1954, p. 28, text-fig. 10 (El Salvador).

Range. Lower California, Mexico, to Peru. Galápagos Islands. Occurs also in the Atlantic.

Material. Clipperton Island: Splash zone; September 6, 1958; C. Limbaugh: 1 left cheliped. Northeast side, low tide, reef flat, 0–1 foot; September 13, 1958; C. Limbaugh, T. Chess, and A. Hambly: 1 male.

Measurements. Male specimen: length 20.2 mm., width including spines 32.0 mm., without spines 29.4 mm.

Habitat. Reef flat, intertidal, to 1 foot.

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12

13

Figure 11. *Thalamita picta* Stimpson, male, dorsal view. Scale in millimeters.

Figure 12. Same, ventral view. Scale in millimeters.

Figure 13. *Carpilius convexus* (Forskål), male, dorsal view. Scale in millimeters.

Remarks. The male specimen was collected with "Endrin." The detached cheliped is identifiable by the four spines on the manus. The *Portunus* species with which *Cronius ruber* might be confused have only two spines on the manus. The species is now recorded from Clipperton Island.

Family Xanthidae

Carpilius convexus (Forskål).

(Figures 8, 13.)

Cancer convexus Forskål, 1775, p. 88 (Red Sea).
Carpilius convexus, Rüppell, 1830, p. 13, pl. 3, fig. 2; pl. 6, fig. 6 (Tahiti). Dana, 1852, p.

159; 1855, pl. 7, fig. 5 (Sandwich Islands). Boone, 1934, p. 89, pls. 43–45, synonymy. Edmondson, 1962, p. 223, fig. 1b.

Range. Indo-Pacific from Red Sea to Hawaii and Tahiti.

Material. Clipperton Island: From gut of bass, *Dermatolepis punctata*; August 12, 1958; E. S. Reese: 1 female. In trap, 30–100 feet; August 23–26, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 male. West shore; September 17, 1958; T. Chess: 1 carapace. On beach, W. side; September 21, 1958; C. Limbaugh: 1 male, lacking walking legs and abdomen.

Measurements. Largest specimen, male: length 68.2 mm., width 90.4 mm. Female: length 34.2 mm., width 48.0 mm.

Habitat. The one living specimen was caught in a trap set at a depth of from 30 to 100 feet. The others were either cast up on the beach or were obtained from a fish's stomach, indicating origin below tidal level.

Remarks. The finding of four specimens of *Carpilius convexus*, a widely ranging Indo-Pacific species, at Clipperton Island would seem to indicate that it has not only crossed the Central Pacific oceanic barrier from Hawaii, the Line Islands, or Tahiti, but that it is well established there. Only an ovigerous female is lacking as proof of a breeding population, the single female collected being immature.

Comparison with the Atlantic species, *Carpilius corallinus* (Herbst), from Brazil in the collection of the U. S. National Museum (USNM no. 40576) shows differences best indicated by the following table:

C. convexus	*C. corallinus*
1. Frontal lobes separated from lateral lobes by a shallow, broad sinus; lateral lobes directed outward.	1. Frontal lobes separated from lateral lobes by a deep, U-shaped sinus; lateral lobes directed forward.
2. Supraorbital margins thick, rimmed.	2. Supraorbital margins thick, not rimmed.
3. Anterolateral portion of carapace rugose.	3. Anterolateral portion of carapace punctate only.
4. Anterolateral margins moderately thickened, rimmed.	4. Anterolateral margins very thick, not rimmed.
5. Male abdomen narrow, tip with length and breadth equal, sides convex.	5. Male abdomen wider, especially at bases of somites 3 and 7; tip broader than long, sides concave.
6. Walking legs somewhat more slender; meri not noticeably thickened proximally.	6. Walking legs robust; meri thickened proximally.

On the other hand, specimens from Clipperton Island agree well with specimens of *Carpilius convexus* in Hancock collections from the Marshall Islands and Hawaii. The absence of *Carpilius* from the west coast of tropical America is therefore the more remarkable in view of the fact that the greater distance from the mid-Pacific islands to Clipperton has been negotiated, whereas the lesser distance from Clipperton to the American mainland has not been bridged.

Carpilodes cinctimanus (White).

Carpilius cinctimanus White, 1847a, p. 336, pl. 2, fig. 3 (Indian Ocean and Eastern Seas); 1847b, p. 14.

Carpilodes cinctimanus, Miers, 1880, p. 234; 1886, p. 133. Rathbun, 1930, p. 242, pl. 100. Crane, 1937, p. 69 (Arena Bay, Gulf of California); 1947, p. 74. Garth, 1946, p. 426, pl. 74, figs. 1–4; 1948, p. 38 (Gorgona Island, Colombia). Buitendijk, 1960, p. 256, text-fig. 2a.

Liomera cocosana Boone, 1927, p. 184, text-fig. 63 (Cocos and Galápagos).

Range. Indo-Pacific from Gulf of Aden eastward. Eastern Pacific from Gulf of California, Mexico, to Colombia. Cocos Island and Galápagos Islands.

Material. Clipperton Island: October, 1956; C. Limbaugh: 1 female. Northeast transect, 36 feet; August 27, 1958; T. Chess and A. Hambly: 1 female. Northeast side, 45 feet, *Pocillopora* coral; August 28, 1958; C. Limbaugh, T. Chess, and A. Hambly: 1 female. East side, reef flat margin or ridge, 0–2 feet; September 14, 1958; C. Limbaugh and T. Chess: 1 female.

Measurements. Largest specimen, female: length 18.0 mm., width 32.3 mm.

Habitat. The *Pocillopora* coral colony.

Remarks. Of undoubted Indo-Pacific origin, but well established on the tropical American west coast, as well as at outlying islands of Cocos and Galápagos, this unmistakable concomitant of the coral colony may now be reported from Clipperton.

Platypodia rotundata (Stimpson).

Atergatis rotundatus Stimpson, 1860b, p. 202 (Cape San Lucas).

Platypodia rotundata, Rathbun, 1910, p. 584; 1930, p. 248, pl. 102, figs. 1–3 (Ecuador). Finnegan, 1931, p. 633 (Galápagos). Schmitt, 1939, p. 21 (Clipperton). Garth, 1946, p. 430; 1948, p. 38 (Humboldt Bay, Colombia). Hertlein and Emerson, 1957, p. 5 (Clipperton).

Range. Gulf of California, Mexico, to Ecuador. Galápagos Islands; Clipperton Island.

Material. Clipperton Island: December 12, 1954; R. L. Fisher, J. B. Jordan, and S. O'Neil: 2 young. East end, coral reef; August 15, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 young female. Northeast side, reef flat, low tide, 0–1 foot; September 13, 1958; C. Limbaugh, T. Chess, and A. Hambly: 1 female, collected with "Endrin."

Measurements. Female specimen: length 5.3 mm., width 7.8 mm. Young: length 2.2 mm., width 3.1 mm.

Habitat. Low intertidal, to 1 foot. Often encountered in sponges.

Remarks. The present record is the third for Clipperton, the species having been obtained by both the Scripps Expedition of 1954 aboard the *Spencer F. Baird* and the Presidential Cruise of 1938 aboard the *Houston*. The young specimens are sharply granulate.

Actaea sulcata Stimpson.

Actaea sulcata Stimpson, 1860b, p. 203 (Cape San Lucas). Rathbun, 1930, p. 259, pl. 105, figs. 3, 4. Crane, 1937, p. 69 (Arena Bank, Gulf of California); 1947, p. 74. Schmitt, 1939, p. 21 (Clipperton). Garth, 1946, p. 434, pl. 77, fig. 1 (Galápagos); 1948, p. 39 (La Plata Island, Ecuador). Buitendijk, 1950, p. 276. Hertlein and Emerson, 1957, p. 5 (Clipperton).

Range. Gulf of California, Mexico, to Ecuador. Galápagos Islands and Clipperton Island.

Material. Clipperton Island: December 12, 1954; R. L. Fisher, J. B. Jordan, and S. O'Neil: 1 male, 1 female. October, 1956; C. Limbaugh: 1 male. Northwest end, reef; August 14, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 female. South shore, coral reef; August 19, 1958; E. S. Reese, W. Baldwin, and C. Limbaugh: 1 female. Northeast transect, 36 feet, *Pocillopora* coral; August 27, 1958; T. Chess and A. Hambly: 1 female. Northeast side, 45 feet, *Pocillopora* coral; August 28, 1958; C. Limbaugh, T. Chess, and A. Hambly: 1 male, 1 female. Northeast corner, 45 feet, *Pocillopora* coral; August 30, 1958; C. Limbaugh, T. Chess, and A. Hambly: 1 male, 1 young female.

Measurements. Largest specimen, female: length 11.7 mm., width 17.7 mm. Largest male: length 11.4 mm., width 17.1 mm. Young female: length 4.9 mm., width 7.2 mm. Young male: length 4.7 mm., width 7.0 mm.

Habitat. The *Pocillopora* coral colony.

Remarks. Previously collected by both the 1938 Presidential Cruise (Schmitt) and the 1954 Scripps Acapulco Trench Expedition (Hertlein and Emerson), *Actaea sulcata* was found whenever *Pocillopora* coral was obtained by the several skilled divers who accompanied the 1958 Scripps I.G.Y. Expedition. The largest female had the areoles more widely separated than is usual for the species; the other specimens were noted as having shallow sulci. This is evidence of weak endemism at the populational level.

Actaea dovii Stimpson.

Actaea dovii Stimpson, 1871, p. 104 (San Salvador and Panama). Rathbun, 1902, p. 281 (Galápagos); 1930, p. 254, pl. 104, figs. 1, 2. Schmitt, 1939, pp. 21, 25 (Clipperton). Garth, 1946, p. 431, pl. 79, figs. 2, 6; 1948, p. 38 (Colombia). Crane, 1947, p. 74. Hertlein and Emerson, 1957, p. 5 (Clipperton).

Range. El Salvador to Ecuador. Galápagos Islands; Clipperton Island.

Material. Clipperton Island: December 12, 1954; R. L. Fisher, J. B. Jordan, and S. O'Neil: 1 young. Northeast transect, 36 feet, *Pocillopora* coral;

August 27, 1958; T. Chess and A. Hambly: 1 male. Northeast side, 45 feet, *Pocillopora* coral; August 28, 1958; C. Limbaugh, T. Chess, and A. Hambly: 1 male, 1 young. Without accompanying data: 1 female.

Measurements. Male specimen: length 10.9 mm., width 15.6 mm. Female specimen: length 9.2 mm., width 13.3 mm. Young specimen: length 3.7 mm., width 5.3 mm.

Habitat. The *Pocillopora* coral colony.

Remarks. The species was obtained previously at Clipperton by both the U.S.S. *Houston* (Schmitt) and the *Spencer F. Baird* (Hertlein and Emerson).

Actaea species.

Material. Clipperton Island: Northeast transect, 78 feet; August 27, 1958; C. Limbaugh: 1 young.

Measurements. Young specimen: length 1.8 mm., width 2.3 mm.

Habitat. Probably from *Pocillopora* coral.

Remarks. This tiny specimen, too young to permit positive identification, may represent a new species. It is close to, but not identical with, *Actaea angusta* Rathbun (1898, p. 582) of the Galápagos Islands.

Cycloxanthops vittatus (Stimpson).

Xantho vittata Stimpson, 1860b, p. 206 (Panama and Cape San Lucas).

Cycloxanthops vittatus, Rathbun, 1907, p. 70; 1930, p. 291, pl. 133, figs. 3, 4; pl. 134, fig. 3. Boone, 1927, p. 197, text-fig. 68 (Galápagos). Sivertsen, 1933, p. 15. Garth, 1946, p. 445, pl. 79, fig. 5. Crane, 1947, p. 75.

Range. Gulf of California, Mexico, to Panama. Galápagos Islands.

Material. Clipperton Island: October, 1956; C. Limbaugh: 1 male. Coral reef; August, 1958; E. S. Reese: 1 male. South shore, coral reef, sand; August 11, 1958; C. Limbaugh, W. Baldwin, and J. Wintersteen: 1 male. East end, coral reef; August 15, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 male, 1 female, 1 young. Northeast side, reef flat, low tide, 0–1 foot; September 13, 1958; C. Limbaugh, T. Chess, and A. Hambly: 5 males, 8 females (1 ovigerous); collected with "Endrin."

Measurements. Largest specimen, male: length 16.4 mm., width 24.4 mm. Largest female: length 12.7 mm., width 17.3 mm. Ovigerous female: length 11.8 mm., width 16.2 mm. Young: length 2.8 mm., width 3.2 mm.

Habitat. Coral reef or reef flat at low tide, to a depth of 1 foot.

Remarks. Known previously from the Galápagos Islands, as well as from a number of mainland localities, *Cycloxanthops vittatus* is now recorded from Clipperton Island, where a breeding population exists, as shown by the recovery of an ovigerous female and young. Success in obtaining this species in numbers may be attributed to poisoning with "Endrin." The vertical stripes of color characteristic of this species are faintly visible on a male measuring 11.1 × 15.8 mm.

Leptodius cooksoni Miers.

Leptodius cooksoni Miers, 1877, p. 73, pl. 12, figs. 1, 1a–d (Charles Island, Galápagos). Rathbun, 1930, p. 310, pl. 142, synonymy (Socorro, Clarion). Sivertsen, 1933, p. 14. Schmitt, 1939, pp. 11, 25, 26. Steinbeck and Ricketts, 1941, p. 469 (Gulf of California). Garth, 1946, p. 448, pl. 77, fig. 3; pl. 79, fig. 3.

Xanthodius lobatus, A. Milne Edwards, 1880, p. 271, pl. 49, figs. 4, 4a, b (Chile).

Xantho cooksoni, Buitendijk, 1950, p. 277 (San José del Cabo).

Range. Gulf of California, Mexico. Socorro and Clarion islands; Galápagos Islands. Chile? (Apart from this all records are either insular or peninsular.)

Material. Clipperton Island: October, 1956; C. Limbaugh: 1 male. Northwest end, reef; August 14, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 2 males, 2 females. South shore, coral reef; August 19, 1958; E. S. Reese, W. Baldwin, and C. Limbaugh: 1 male, 1 female. Northwest end, high tidepool; August 24, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 7 males, 1 female. September 10–15, 1958; C. R. Harbison: 30 males, 18 females (3 ovigerous), 1 young.

Measurements. Largest specimen, male: length 18.1 mm., width 30 mm. Largest female: length 15.3 mm., width 24.8 mm. Largest ovigerous female: length 9.8 mm., width 15.6 mm.; smallest ovigerous female: length 7.8 mm., width 12.1 mm. Young: length 6.0 mm., width 8.7 mm.

Habitat. Reef and high tidepool.

Remarks. Already reported from Socorro and Clarion islands to the northwest and from the Galápagos Islands to the southeast, it is not unexpected that *Leptodius cooksoni* should occur at Clipperton Island. What is remarkable is that it has not been found there before, in view of its apparent abundance. The series of nearly 50 specimens collected by C. R. Harbison of the San Diego Museum is noteworthy for the small size of the ovigerous females.

Micropanope xantusii (Stimpson).

Xanthodes xantusii Stimpson, 1871, p. 105 (Cape San Lucas).

Micropanope xantusii, Rathbun, 1930, p. 438, pl. 179, figs. 1–4, synonymy (Clarion). Crane, 1937, p. 72 (Arena Bank, Gulf of California); 1947, p. 80. Schmitt, 1939, p. 21 (Clipperton). Garth, 1946, p. 457, pl. 77, fig. 6; 1948, p. 42 (La Plata Island, Ecuador). Hertlein and Emerson, 1957, p. 5 (Clipperton Island).

Range. Gulf of California, Mexico, to Ecuador. Galápagos Islands (see Garth, 1946, p. 459). Clarion Island. Clipperton Island.

Material. Clipperton Island: December 12, 1954; R. L. Fisher, J. B. Jordan, and S. O'Neil: 3 males, 1 female, 1 young (look different). October, 1956; C. Limbaugh: 1 male. Coral reef; August, 1958; E. S. Reese: 1 ovigerous female. Northeast side, west wall of "canyon," 45 feet; August 18, 1958; C. Limbaugh: 1 male. Northeast side, 45 feet, *Pocillopora* coral; August 28, 1958; C. Limbaugh, T. Chess, and A. Hambly: 3 males, 5 females (3 ovigerous), 2 young. Northeast corner, 45 feet, *Pocillopora* coral; August 30, 1958; C. Limbaugh, T. Chess, and A. Hambly: 4 males, 1 female. Northeast end, shore to 6 inches; September 4, 1958; C. Limbaugh, T. Chess, and A. Hambly: 1 male. Northeast side, reef flat, low tide, 0–1 foot; September 13, 1958; C. Limbaugh, T. Chess, and A. Hambly: 1 female. East side, reef flat margin or ridge, 0–2 feet; September 14, 1958; C. Limbaugh and T. Chess: 1 male. Northeast side, 50–60 feet; September 20, 1958; C. Limbaugh: 1 male.

MEASUREMENTS. Largest specimen, male: length 9.7 mm., width 14.1 mm. Largest female, ovigerous: length 8.9 mm., width 12.9 mm.; smallest ovigerous female: length 6.5 mm., width 9.0 mm. Young: length 3.0 mm., width 4.1 mm.

HABITAT. A common but not exclusive inhabitant of the *Pocillopora* coral colony.

REMARKS. This species was taken previously at Clipperton Island by both Schmitt (1939) and the *Spencer F. Baird* party (Hertlein and Emerson, 1957). Specimens are of large size, the chelipeds thick, almost without furrows. This is the "different look" remarked upon in connection with the 1954 specimens, again evidence of weak endemism.

Micropanope species.

MATERIAL. Clipperton Island: Northeast transect, 78 feet; August 27, 1958; C. Limbaugh: 1 young.

MEASUREMENTS. Young specimen: length 1.5 mm., width 1.9 mm.

HABITAT. Believed to be from *Pocillopora* coral.

REMARKS. The specimen is too immature to permit ready identification with any of the known *Micropanope* species.

Pilumnus xantusii Stimpson.

Pilumnus xantusii STIMPSON, 1860b, p. 213 (Cape San Lucas). RATHBUN, 1930, p. 486, pl. 201, figs. 1–3. GARTH, 1946, p. 471, pl. 59, figs. 1–5; pl. 79, fig. 4; 1948, p. 45 (La Plata Island, Ecuador). CRANE, 1947, p. 81.

Eriphides hispida, BOONE, 1927, fig. 87B (Galápagos). Not *Eriphides hispida* (Stimpson).

Pilumnus crosslandi FINNEGAN, 1931, p. 643 (Galápagos).

RANGE. Lower California, Mexico, to Ecuador. Galápagos Islands.

MATERIAL. Clipperton Island: Twenty to 40 feet, coral; August, 1958; E. Allison and C. Limbaugh: 1 male, 1 female, 2 young. Northeast transect, 36 feet; August 27, 1958; T. Chess and A. Hambly: 1 male, 1 female. Northeast transect, 78 feet; August 27, 1958; C. Limbaugh: 3 males. Northeast side, 45 feet, *Pocillopora* coral; August 28, 1958; C. Limbaugh, T. Chess, and A. Hambly: 2 females, 3 young.

Measurements. Largest specimen, female: length 8.5 mm., half-width 5.8 mm. Largest male: length 7.7 mm., width 9.6 mm. Young: length 2.0 mm., width 2.3 mm.

Habitat. The *Pocillopora* coral colony, in the sublittoral.

Remarks. Although previously reported from the Galápagos Islands (Boone, 1927, as *Eriphides hispida*, young; Finnegan, 1931, as *Pilumnus crosslandi*), *Pilumnus xantusii* had not been collected at Clipperton Island, probably because of the 20- to 78-foot depths at which it is found there.

Domecia hispida Eydoux and Souleyet.

Domécie hérissée Eydoux and Souleyet, 1842 (or 1843), Atlas, p. 2, figs. 5–10.
Domecia hispida Eydoux and Souleyet, 1844 (or 1845), p. 235 (Sandwich Islands). Rathbun, 1930, p. 554, pl. 227. Finnegan, 1931, p. 647 (Gorgona Island). Crane, 1937, p. 73 (Arena Bank, Gulf of California); 1947, p. 82 (Clarion). Garth, 1946, p. 489, pl. 81, fig. 5 (Galápagos); 1948, p. 50 (La Plata Island, Ecuador).

Range. Indo-west Pacific from Red Sea to Hawaii. Eastern Pacific from Gulf of California to Ecuador. Clarion Island. Galápagos Islands.

Material. Clipperton Island: Northeast side, west wall of "canyon," 45 feet; August 18, 1958; C. Limbaugh: 2 females (1 ovigerous). Northeast transect, 36 feet; August 27, 1958; T. Chess and A. Hambly: 1 ovigerous female, 1 young. Northeast transect, 78 feet; August 27, 1958; C. Limbaugh: 1 female, 1 young. Northeast side, 45 feet, *Pocillopora* coral; August 28, 1958; C. Limbaugh, T. Chess, and A. Hambly: 5 females, 6 young. Northeast side, 50–60 feet; September 20, 1958; C. Limbaugh: 2 males.

Measurements. Largest specimen, ovigerous female: length 10.3 mm., width 13.6 mm. Largest male: length 4.0 mm., width 5.3 mm. Smallest ovigerous female: length 5.4 mm., width 6.9 mm. Smallest young: length 2.9 mm., width 3.6 mm.

Habitat. The *Pocillopora* coral colony.

Remarks. Of western Pacific origin but known from islands to the northwest and southeast and from the American mainland, *Domecia hispida* is now recorded from Clipperton Island.

Trapezia digitalis Latreille.

Trapezia digitalis Latreille, 1825, p. 696 (Red Sea). Rathbun, 1930, p. 559, pl. 228, figs. 5, 6, synonymy (Socorro, Clarion). Schmitt, 1933, p. 22 (Galápagos). Crane, 1937, p. 73 (Arena Bank, Gulf of California); 1947, p. 83. Garth, 1946, p. 493, pl. 81, fig. 6; 1948, p. 51 (La Plata Island, Ecuador). Hertlein and Emerson, 1957, p. 5 (Clipperton).
Trapezia nigro-fusca Stimpson, 1860b, p. 219 (Cape San Lucas).

Range. Indo-west Pacific from Red Sea to Hawaii. Eastern Pacific from Gulf of California, Mexico, to Ecuador. Socorro and Clarion islands; Galápagos Islands; Clipperton Island.

Material. Clipperton Island: December 12, 1954; R. L. Fisher, J. B. Jordan, and S. O'Neil: 1 male, 1 female; 1 young (not measured). Northeast transect, 36 feet; August 27, 1958; T. Chess and A. Hambly: 2 males, 3 females (1 ovigerous). Northeast side, 45 feet, *Pocillopora* coral; August 28, 1958; C. Limbaugh, T. Chess, and A. Hambly: 6 males, 6 females (3 ovigerous). Northeast corner, 45 feet, *Pocillopora* coral; August 30, 1958; C. Limbaugh, T. Chess, and A. Hambly: 1 ovigerous female. Northeast side, 50–60 feet; September 20, 1958; C. Limbaugh: 1 young female.

Measurements. Largest specimen, male: length 9.3 mm., width 11.5 mm. Largest female (ovigerous): length 8.3 mm., width 10.4 mm.; smallest ovigerous female: length 5.9 mm., width 7.6 mm. Young female: length 3.1 mm., width 4.4 mm.

Habitat. Inhabits exclusively the *Pocillopora* coral colony.

Remarks. Collected at Clipperton Island on the 1954 expedition of the *Spencer F. Baird*, *Trapezia digitalis* was found by the 1958 expedition whenever *Pocillopora* coral was obtained by diving.

Trapezia ferruginea Latreille.

Trapezia ferruginea Latreille, 1825, p. 695 (Red Sea). Buitendijk, 1950, p. 278.

Trapezia cymodoce ferruginea, Rathbun, 1907, p. 58; 1930, p. 557, pl. 228, figs. 1, 2 (Clarion). Boone, 1927, p. 240, text-fig. 88 (Cocos and Galápagos). Crane, 1937, p. 73 (Arena Bank, Gulf of California); 1947, p. 83. Garth, 1946, p. 491, pl. 81, fig. 4; 1948, p. 51 (La Plata Island, Ecuador). Hertlein and Emerson, 1957, p. 5 (Clipperton).

Range. Indo-west Pacific from Red Sea to Hawaii. Eastern Pacific from Gulf of California to Ecuador. Clarion Island. Galápagos Islands. Clipperton Island.

Material. Clipperton Island: December 12, 1954; R. L. Fisher, J. B. Jordan, and S. O'Neil: 3 males (not measured). October, 1956; C. Limbaugh: 1 ovigerous female. Twenty to 40 feet, in coral, sublittoral; August, 1958; E. Allison and C. Limbaugh: 17 males, 15 females (7 ovigerous). Shore; August 7–26, 1958; E. S. Reese: 1 male. Reef, NW. end; August 14, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 male. Northeast side, west wall of "canyon," 45 feet; August 18, 1958; C. Limbaugh: 9 males, 7 females. Northeast transect, 36 feet; August 27, 1958; T. Chess and A. Hambly: 4 males, 6 ovigerous females, 3 young. Northeast side, 45 feet, *Pocillopora* coral; August 28, 1958; C. Limbaugh, T. Chess, and A. Hambly: 15 males, 20 females (10 ovigerous), 4 young. Northeast corner, 45 feet, *Pocillopora* coral; August 30, 1958; C. Limbaugh, T. Chess, and A. Hambly: 6 males, 13 females (8 ovigerous). East side, reef flat margin or ridge, 0–2 feet, *Pocillopora* coral; September 14, 1958; C. Limbaugh and T. Chess: 5 males, 3 females (2 ovigerous); 1 ovigerous female with reticulate chelae. Northeast corner, 45 feet, *Pocillopora* coral; August 30, 1958; C. Limbaugh, T. Chess, and A. Hambly: 2 males, 1 ovigerous female, also with reticulate chelae.

MEASUREMENTS. Largest specimen, male: length 15.6 mm., width 18.3 mm. Largest female, ovigerous: length 15.9 mm., width 19.4 mm. Smallest ovigerous female: length 3.0 mm., width 4.0 mm. Young: length 1.7 mm., width 2.4 mm.

HABITAT. The *Pocillopora* coral colony. Sublittoral.

REMARKS. In the absence of a notation to the effect that specimens were collected from coral, or of the inclusion of a piece of coral with the specimens collected, the presence of *Trapezia ferruginea* among an assortment of small Xanthidae was taken as *prima facie* evidence that the sample came from *Pocillopora*. Because it predominates over the related *Trapezia digitalis* by a ratio of 3 to 1 or more, *T. ferruginea* is the better indicator of the two species. Although the number of coral heads is not mentioned, the large number of specimens obtained from several of the diving stations tends to support the writer's observation (Garth, 1946, p. 492) that many more than a single pair of crabs occupy the same coral head. The high proportion of ovigerous females indicates either a seasonal peak in August–September, or continuous breeding.

The writer follows Ortmann (1897a) and Alcock (1898), rather than Rathbun (1907, 1930), in considering *Trapezia ferruginea* specifically distinct from *T. cymodoce* (Herbst).

Family GRAPSIDAE

Grapsus grapsus (Linnaeus).

Cancer grapsus LINNAEUS, 1758, p. 630 (America and Ascension Island).

Grapsus grapsus, IVES, 1891, p. 190. RATHBUN, 1918, p. 227, pls. 53, 54 (Socorro, Clarion, Galápagos). BOONE, 1927, p. 244, fig. 90. SIVERTSEN, 1933, p. 18. CRANE, 1937, p. 77; 1947, p. 83. GARTH, 1946, p. 504, pl. 86, figs. 1, 2; 1948, p. 55 (Malpelo). HOLTHUIS, 1954, p. 36.

RANGE. Lower California and Gulf of California, Mexico, to Chile. Socorro and Clarion islands. Galápagos Islands. Malpelo Island. Occurs also in the Atlantic.

MATERIAL. Clipperton Island: October, 1956; C. Limbaugh: 2 males, 5 females (4 ovigerous). August, 1958; Marie-Hélène Sachet: 2 males, 1 female. Coral reef; August, 1958; E. S. Reese: 3 males, 4 females (2 ovigerous). Camp to U. S. Base counterclockwise; August 8, 1958; C. R. Harbison: 1 male. Northwest end, reef; August 14, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 3 males, 2 females, 1 young. South shore, coral reef; August 19, 1958; E. S. Reese, W. Baldwin, and C. Limbaugh: 1 female. Northwest end, high tidepool; August 24, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 male, 3 females, 1 carapace. Lagoon shore, NE., above water; September 4, 1958; C. Limbaugh: 1 female, 1 cast. Northeast side, high intertidal; September 4, 1958; C. Limbaugh and T. Chess: 4 males, 1 female, 4 young. Northeast side, splash zone; September 6, 1958; C. Limbaugh: 1 young. Northeast side, high intertidal; September 10, 1958; C. Limbaugh and T. Chess: 20 males, 14 females (3 ovigerous). September 10–15, 1958; C. R. Harbison: 2 males, 2 ovigerous females.

Measurements. Largest specimen, male: length 60 mm., width 69 mm. Largest female, ovigerous: length 63 mm., width 79.2 mm.; smallest ovigerous female: length 42.8 mm., width 46.4 mm. Young: length 8.8 mm., width 10.0 mm.

Habitat. Throughout all rocky intertidal areas. (E. S. Reese) High intertidal. Splash zone. (C. Limbaugh)

Remarks. Lack of an earlier record of *Grapsus grapsus* from Clipperton Island has at last been rectified. In a letter dated June 7, 1963, Dr. F. A. Chace, Jr., Curator of Marine Invertebrates, U. S. National Museum, informed the writer of a fine female specimen in perfect condition collected by John T. Arundel, presumably while visiting the island in 1897 aboard the *Navarro*. According to Dr. Chace, the specimen even retains traces of the original color pattern. While collectors with limited time may have neglected this common and conspicuous crab in favor of less abundant and therefore more desirable species, it is gratifying now to have some 80 specimens, in good size range, including ovigerous females as well as young, and to be able to report that it is the eastern Pacific–tropical Atlantic species, rather than the Indo-Pacific *G. tenuicrustatus* (Herbst), that occurs on Clipperton Island. With this report, *G. grapsus* is now known to have reached all the tropical outliers of the western American coast.

Geograpsus lividus (Milne Edwards).

Grapsus lividus Milne Edwards, 1837, p. 85 (Antilles).

Geograpsus lividus, Stimpson, 1860b, p. 230 (Cape San Lucas). Rathbun, 1902, p. 278 (Clipperton); 1918, p. 232, pl. 55 (Galápagos). Boone, 1927, p. 251, fig. 91. Sivertsen, 1933, p. 19. Garth, 1946, p. 506, pl. 86, figs. 3, 4; 1957, p. 94, synonymy. Hertlein and Emerson, 1957, p. 5 (Clipperton).

Range. Central Pacific at Hawaii. Eastern Pacific from Lower California to Chile. Galápagos Islands. Clipperton Island. Occurs also in the Atlantic.

Material. Clipperton Island: December 12, 1954; R. L. Fisher, J. B. Jordan, and S. O'Neil: 1 female (not measured). October, 1956; C. Limbaugh: 7 males, 4 females. August, 1958; Marie-Hélène Sachet: 1 male, 2 females. Coral reef, intertidal; August, 1958; E. S. Reese: 1 male, 1 female. Camp to U. S. Base counterclockwise; August 8, 1958; C. R. Harbison: 1 male. Northwest end, reef; August 14, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 male, 2 females (1 ovigerous). Northeast corner; August 29, 1958; C. Limbaugh: 1 ovigerous female. Lagoon, E. shore; August 29, 1958; C. Limbaugh:

1 male. Same locality, above water; September 4, 1958; C. Limbaugh: 1 male, 2 females, 1 young. Northeast side, splash zone; September 6, 1958; C. Limbaugh: 1 male, 2 young. Northeast side, high intertidal; September 10, 1958; C. Limbaugh and T. Chess: 2 males. September 10–15, 1958; C. R. Harbison: 3 males, 2 ovigerous females. Northeast side, crest of atoll, near burrows under rocks; September 12, 1958; C. Limbaugh: 1 young.

Measurements. Largest specimen, male: length 34.4 mm., width 40.8 mm. Largest female, ovigerous: length 29.0 mm., width 36.4 mm. Smallest ovigerous female, length 14.4 mm., width 18.8 mm. Young: length 5.3 mm., width 6.2 mm.

Habitat. Intertidal; high intertidal; splash zone. Crest of atoll [an unusual situation; needs confirmation].

Remarks. The species has been taken at Clipperton Island on two previous occasions: by the Hopkins–Stanford Expedition (Rathbun, 1902) and by the Scripps Expedition of 1954 (Hertlein and Emerson). It is a more secretive species by day than *Grapsus grapsus*, dwelling in crevices above the water line and revealing its presence by the glint of sunlight on the long yellow hairs with which the legs are liberally provided.

Pachygrapsus minutus A. Milne Edwards.

(Figure 14.)

Pachygrapsus minutus A. Milne Edwards, 1873, p. 292, pl. 14, fig. 2 (New Caledonia). Cano, 1889, p. 240 (Hawaii). Boone, 1934, p. 180, pl. 91 (Samoa). Schmitt, 1939, p. 22 (Clipperton). Holthuis, 1953, p. 31 (Onotoa). Hertlein and Emerson, 1957, p. 5 (Clipperton). Edmondson, 1959, p. 171, figs. 8c, 9d, 9e (Line Islands). Forest and Guinot, 1961, p. 155, synonymy (Tahiti).

Sesarma murrayi Calman, 1909, p. 708, pl. 72, figs. 4, 5 (Christmas Island, Indian Ocean).

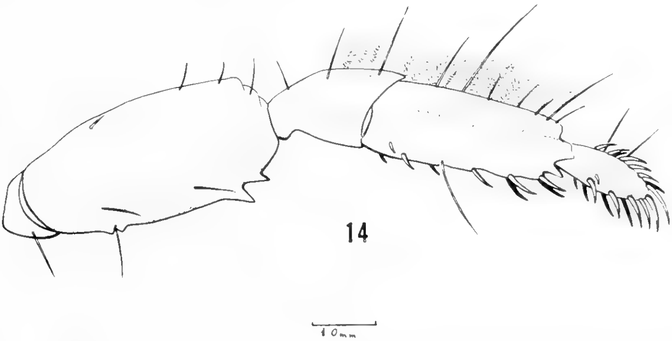

Figure 14. *Pachygrapsus minutus* A. Milne Edwards, right fourth walking leg. Drawing by Isolda Wisshaupt.

Range. Indo-Pacific from Red Sea and Zanzibar to Hawaii, Line Islands, and Tahiti. Eastern Pacific at Clipperton Island.

Material. Clipperton Island: December 12, 1954; R. L. Fisher, J. B. Jordan, and S. O'Neil: 1 female, 2 young. October, 1956; C. Limbaugh: 1 male, 2 females, 3 young. August 7–26, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 4 males, 3 females. East side, coral reef; August 9, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 4 young. Northwest end; August 14, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 female. East end, coral reef; August 15, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 2 females, 22 young. South shore, coral reef; August 19, 1958; E. S. Reese, W. Baldwin, and C. Limbaugh: 1 male. Northwest end, high tidepool; August 24, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 5 males, 1 ovigerous female. Northeast end, low intertidal to 6 inches; September 4, 1958; C. Limbaugh and T. Chess: 7 males, 5 females (2 ovigerous), 15 young.

Measurements. Largest specimen, male: length 8.6 mm., width 10.8 mm. Largest ovigerous female: length 6.4 mm., width 8.4 mm.; smallest ovigerous female: length 4.2 mm., width 5.6 mm. Young: length 2.0 mm., width 2.6 mm.

Habitat. High tidepool; low intertidal to 6 inches. Owing to the mingling of this and the following species in collecting, their habitats cannot be differentiated at present.

Remarks. A preliminary examination of the small grapsids from Clipperton Island disclosed the presence of two species of *Pachygrapsus* among them. Because of formalin preservation and consequent loss of legs, separation using the obvious character of presence or absence of the bituberculate tooth at the proximal end of the merus of the fourth walking leg proved impossible in many cases. Fortunately, the third maxilliped provided a reliable character for separating *P. minutus* from the following *P. planifrons*. Other differences between the two species are listed under *P. planifrons*.

The finding of two small *Pachygrapsus* species at Clipperton where only one, *P. minutus*, had been reported before (Schmitt, 1939; Hertlein and Emerson, 1954) led to a reexamination of specimens from Clarion, Socorro, and Galápagos in Hancock collections previously attributed to *P. transversus* (Gibbes), the amphi-American species. As a result it can be reported that *P. minutus* occurs

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Figure 15. *Pachygrapsus planifrons* de Man, male, dorsal view. Scale in millimeters.

Figure 16. Same, ventral view.

Figure 17. *Plagusia depressa tuberculata* Lamarck, female, dorsal view. Scale in millimeters.

Figure 18. Same, ventral view.

Figure 19. *Percnon abbreviatum* (Dana), male, dorsal view. Scale in millimeters.

Figure 20. Same, ventral view.


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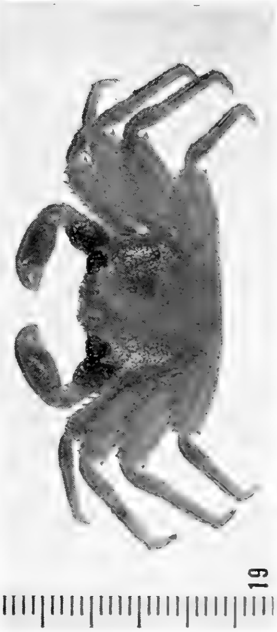
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also at Clarion and Socorro islands, although not, apparently, in the Galápagos Islands. It is felt that this information should be made available at this time, rather than waiting for the Hancock Grapsidae to be monographed.

Pachygrapsus planifrons de Man.

(Figures 15, 16.)

Pachygrapsus planifrons DE MAN, 1888, p. 368, pl. 16, fig. 2 (Noordwachter Island); 1908, p. 218. TESCH, 1918, p. 77 (Lombok). WARD, 1934, p. 25 (Christmas Island). EDMONDSON, 1959, p. 173, figs. 10b, 11a–e (Oahu, Midway, Guam, Line Islands, Canton, Penrhyn, Johnston).

Pachygrapsus longipes RATHBUN, 1893, p. 247; 1906, p. 840, pl. 8, fig. 7 (Hawaii).

RANGE. Indian Ocean, Indonesian seas, and Pacific Ocean east to Hawaii and the Line Islands. Rather common about the equatorial islands of the central Pacific Ocean (Edmondson).

MATERIAL. Clipperton Island: October, 1956; C. Limbaugh: 1 ovigerous female. August 7–26, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 male, 3 young. East shore, coral reef; August 9, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 young female, 1 young. Northwest end, reef; August 14, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 male, 1 ovigerous female. East end; August 15, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 young. Northwest end; August 24, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 6 males, 2 females (1 ovigerous). Northeast side, September 4, 1958; C. Limbaugh, T. Chess, and A. Hambly: 8 males, 3 females (1 ovigerous).

MEASUREMENTS. Largest specimen, male: length 9.0 mm., width 11.4 mm. Largest female (post-ovigerous): length 8.2 mm., width 10.4 mm. Ovigerous females from 4.4 × 5.8 mm. to 7.9 × 9.8 mm. Young not measured.

HABITAT. Low intertidal to 6 inches; high tidepool. Because of the fact that specimens of this and the foregoing species were combined in collecting, no differentiation is possible between their habitats.

REMARKS. Were it not for the work of Edmondson (1959), who reported it from a number of central Pacific islands, *Pachygrapsus planifrons* might have remained an obscure Indo-west Pacific species and a most unlikely colonizer of

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FIGURE 21. *Plagusia speciosa* Dana, female, dorsal view. Scale in millimeters.

FIGURE 22. Same, ventral view. Scale in millimeters.

FIGURE 23. *Ocypode ceratophthalma* (Pallas), male, dorsal view. Scale in millimeters.

FIGURE 24. Same, ventral view.

FIGURE 25. *Ocypode ceratophthalma* (Pallas), female, dorsal view. Scale in millimeters.

FIGURE 26. Same, ventral view.


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Clipperton Island. True, it had been reported from Oahu by Rathbun (1893) under the name of *P. longipes*, but it more likely arrived from Johnston Island, or one of the Line Islands, in the same latitude. According to Ward (1934) the distinctive characters are the flat carapace, the sinuous front, the concave lateral margins, and the hairs at the fingertips. *Pachygrapsus planifrons* is now recorded from the eastern Pacific.

Plagusia depressa tuberculata Lamarck.

(Figures 17, 18.)

Plagusia tuberculata Lamarck, 1818, p. 247 (Ile de France).

Plagusia depressa tuberculata, Laurie, 1906, p. 430. Rathbun, 1906, p. 841 (Hawaii); 1918, p. 334, pl. 102. Edmondson, 1959, p. 190, fig. 22a.

Plagusia orientalis Stimpson, 1858b, p. 103 (Hong Kong and Hawaii); 1860b, p. 231 (Cape San Lucas).

Range. Indo-Pacific from Arabian Sea to Hawaii. Eastern Pacific at Cape San Lucas.

Material. Clipperton Island: Coral reef; August, 1958; E. S. Reese: 2 young females. East end; August 15, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 1 young female, 2 young. Northeast side; September 4, 1958; C. Limbaugh, T. Chess, and A. Hambly: 10 males, 8 females.

Measurements. Largest specimen, male: length 16.8 mm., width 18.0 mm. Young: length 5.2 mm., width 5.3 mm.

Habitat. Low intertidal to 6 inches. The species is pelagic and is transported on floating logs.

Remarks. The commonly encountered species for this part of the world is *Plagusia immaculata* Lamarck (cf. Garth, 1957, p. 102), of which the Hancock collections contain specimens from Cocos Island, Costa Rica. *Plagusia depressa tuberculata* has been recorded only once before from the eastern Pacific, at Cape San Lucas, Lower California, where it was obtained by John Xantus (Stimpson, 1860b). It may now be said to have been reported from two insular localities in the eastern tropical Pacific, Cape San Lucas being no less an island for warm-water species than Clipperton, since it is cut off from the mainland by cold water to the north (cf. Garth, 1960, p. 118 ff.). Most of the specimens examined are young or adolescent. The species grows to at least 52 × 55 mm.

Plagusia speciosa Dana.

(Figures 21, 22.)

Plagusia speciosa Dana, 1851, p. 252; 1852, p. 369; 1855, Atlas, pl. 23, fig. 9 (Waterland Island, Tuamotu). Kingsley, 1880, p. 223 (Tahiti). Borradaile, 1900, p. 591 (Funafuti, Ellice Islands; Rotuma, Fiji Islands). Boone, 1934, p. 185, pls. 95, 96 (Tahiti). Holthuis, 1953, p. 34 (Ailuk, Marshall Islands). Edmondson, 1959, p. 193, fig. 22c (Guam and Washington Island). Forest and Guinot, 1961, p. 162, figs. 177a–c, 178 (male pleopods figured).

Range. Western Pacific from Guam and Fiji to Washington and Tuamotu islands.

Material. Clipperton Island: West side, on beach; September 21, 1958; C. Limbaugh: 1 female.

Measurements. Female: length 25.1 mm., width 27.2 mm.

Habitat. Pelagic; on floating logs.

Remarks. Although preserved in alcohol for nearly six years, the single female specimen shows well the color pattern described by Boone (1934, p. 185): "a creamy ground color with a large crimson shield on the gastric-cardiac region, two large crimson spots on each side, one on the hepatic region and the other on the outer lateral margin." The ambulatory legs, while bicolored, are not conspicuously banded as in the *Alva* specimen.

The occurrence of this rare and handsomely sculptured species at Clipperton is remarkable in view of its apparent restriction to a mid-Pacific parallelogram having Guam, Fiji, Washington, and Tuamotu islands at its four corners. According to Edmondson (1959, p. 193) it has not yet been recorded from Hawaii. Its specific distinctiveness from other *Plagusia* species is supported by figures of the first and second pleopods of a male from Tuamotu (Forest and Guinot, 1961, figs. 177, 178). A dried carapace from Waterland Island, Paumotu Islands (an older name for Tuamotu), in the collections of the U. S. National Museum is one of the very few Dana types still extant, according to Dr. F. A. Chace, Jr.

Percnon abbreviatum (Dana).

(Figures 19, 20.)

Acanthopus abbreviatus Dana, 1851, p. 252; 1852, p. 373; 1855, Atlas, pl. 23, fig. 11 (Tahiti).

Percnon abbreviatum, Rathbun, 1906, p. 842 (Hawaii). Schmitt, 1939, p. 22 (Clipperton). Edmondson, 1959, p. 195, figs. 25b, 26a–c (Line Islands, Wake Island, American Samoa).

Range. Indian Ocean [?], Tahiti, Hawaii, Fanning, Ocean, and Wake islands (*fide* Schmitt). Clipperton Island.

Material. Clipperton Island: 1958: 1 male. Northwest end, reef; August 14, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 3 young. East side, coral reef; August 15, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 5 females (1 ovigerous). Northeast side, 45 feet, *Pocillopora* coral; August 28, 1958; C. Limbaugh, T. Chess, and A. Hambly: 2 males. Northeast corner, 45 feet, *Pocillopora* coral; August 30, 1958; C. Limbaugh, T. Chess, and A. Hambly: 1 ovigerous female, 1 young. Northeast side, reef flat, 0–1 foot; September 13, 1958; C. Limbaugh, T. Chess, and A. Hambly: 12 males, 8 females (6 ovigerous), 1 young; collected with "Endrin." East side, reef flat margin or ridge, 0–2 feet; September 14, 1958; C. Limbaugh and T. Chess: 1 female, 1 young.

Measurements. Largest specimen, ovigerous female: length 14.9 mm., width 15.1 mm. Largest male: length 14.4 mm., width 14.8 mm. Smallest ovigerous female: length 12.7 mm., width 12.5 mm. Young: length 5.9 mm., width 5.4 mm.

Habitat. Reef flat margin or ridge, 0–2 feet. Specimens obtained from coral at a depth of 45 feet included an ovigerous female, as well as young.

Remarks. First reported from the eastern Pacific by Schmitt (1939), *Percnon abbreviatum* is known from a number of central Pacific localities. According to Edmondson (1959, p. 199), earlier records of its occurrence in the western Pacific and Indian oceans are unreliable because of possible confusion with *P. demani* Ward (1934, p. 24). Clipperton Island specimens have been compared with specimens of *P. abbreviatum* from Bikini, Marshall Islands, and from the Ryukyu Islands, and with specimens of *P. demani* from Ulithi, Caroline Islands, in the collections of the Hancock Foundation. A key to the species of *Percnon* is given by Schmitt (1939, p. 23).

Percnon gibbesi (Milne Edwards).

Acanthopus gibbesi Milne Edwards, 1853, pp. 146, 180 (Antilles).

Percnon gibbesi, Rathbun, 1918, p. 337, pl. 105; 1919, p. 25. Hult, 1938, p. 14 (Galápagos). Schmitt, 1939, p. 25. Garth, 1946, p. 512, pl. 86, figs. 5, 6; 1948, p. 57; 1957, p. 104.

Range. Cape San Lucas, Mexico, to Chile (?). Galápagos Islands. Occurs also in the Atlantic Ocean.

Material. Clipperton Island: October, 1956; C. Limbaugh: 1 young. Coral reef; August, 1958; E. S. Reese: 2 males. South shore, coral reef; August 11, 1958; E. S. Reese, C. Limbaugh, and J. Wintersteen: 3 males, 1 young. East end, coral reef; August 15, 1958; E. S. Reese, W. Baldwin, and J. Wintersteen: 3 males, 3 females, 18 young. South shore; August 19, 1958; E. S. Reese, W. Baldwin, and C. Limbaugh: 1 male, 1 female, 1 young. Northeast corner, August 29, 1958; C. Limbaugh: 1 young male. Northeast side, low intertidal to 6 inches; September 4, 1958; C. Limbaugh, T. Chess, and A. Hambly: 11 young. Northeast side, reef flat, 0–1 foot; September 13, 1958; C. Limbaugh, T. Chess, and A. Hambly: 37 males, 27 females (20 ovigerous), 2 young; collected with "Endrin."

Measurements. Largest specimen, ovigerous female: length 24.2 mm., width 22.5 mm. Largest male: length 22.2 mm., width 20.4 mm. Smallest ovigerous female: length 16.8 mm., width 15.3 mm. Young: length 6.0 mm., width 5.2 mm.

Habitat. Reef flat; low intertidal to 1 foot. Unlike the preceding species, *Percnon gibbesi* was not collected in *Pocillopora* coral, nor from a depth of 45 feet.

Remarks. Although not previously reported from Clipperton Island, *Percnon gibbesi* is the common species there, predominating over the earlier reported

P. abbreviatum by three or four to one. Since in the Hawaiian Islands (Edmondson, 1959, p. 197) and elsewhere in the central Pacific a similar position of dominance over *P. abbreviatum* is occupied by *P. planissimum* (Herbst), it was at first thought that the second species of the genus at Clipperton Island would prove to be of Indo-Pacific origin also. However, comparison of Clipperton Island specimens with specimens of *P. planissimum* from the Marshall Islands leaves no doubt that it is the amphi-American form that is found at Clipperton, as also in the Galápagos Islands. Whether these should be considered as full species, as advocated by Rathbun (1918, p. 338), or as subspecies of a single circumtropical species, as advocated by Balss (1922, p. 6), should not be settled on the basis of Clipperton Island specimens alone, but rather on a reappraisal of the relationships between the several regional populations, including the West African (Monod, 1956, p. 454). Sufficient for present purposes is the fact that Clipperton Island specimens are clearly separable from Marshall Islands specimens, and by those very characters given by Schmitt (1939, p. 25), but earlier enunciated by Rathbun (1919, p. 25), for separating *P. gibbesi* from *P. planissimum*.

Family Gecarcinidae

Gecarcinus planatus Stimpson.

Gecarcinus planatus Stimpson, 1860b, p. 234 (Cape San Lucas). Rathbun, 1918, p. 359, pls. 123, 124, text-fig. 163 (Revilla Gigedo, Clipperton). Schmitt, 1939, p. 24. Hertlein and Emerson, 1957, p. 5. Garth, 1948, p. 59.

Gecarcinus malpilensis Faxon, 1893, p. 157; 1895, p. 28, pl. 4, figs. 2–2b (Malpelo).

Gecarcoidea lalandei, Lenz, 1901, p. 473 (Clipperton). (Not *G. lalandii* Milne Edwards, 1837).

Range. Lower California to Acapulco, Mexico. Revilla Gigedo Islands; Clipperton Island; Malpelo Island, Colombia.

Material. Clipperton Island: December 12, 1954; R. L. Fisher, J. B. Jordan, and S. O'Neil: 2 males, 2 females (1 young). October, 1956; C. Limbaugh: 2 males, 3 young females. August, 1958; Marie-Hélène Sachet: 4 males, 8 females. Camp to U. S. Base counterclockwise; August 8, 1958; C. R. Harbison: 2 males, 1 female. Same locality and collector; August 9, 1958: 1 male. Northeast top of atoll, 7–10 feet above sea level; September 4, 1958; C. Limbaugh: 2 males, 4 females (1 ovigerous), 2 young. Northeast side, lagoon shore, above water; September 4, 1958; C. Limbaugh: 1 male, 2 females. September 10–15, 1958; C. R. Harbison: 1 male, 1 female. Crest of atoll, northeast side; September 12, 1958; C. Limbaugh: 17 males, 3 females.

Measurements. Largest specimen, male: length 60.2 mm., width 78.3 mm. Largest female: length 47 mm., width 60.2 mm. Ovigerous female: length 34.6 mm., width 42.7 mm. Young: length 4.2 mm., width 4.6 mm.

Habitat. Primarily nocturnal; live in burrows under rocks; feed on rotten animals and coconut. (Limbaugh)

Remarks. Apparently the first mention of the land crab of Clipperton Island in carcinological literature was by Lenz (1901), who wrote concerning the collections gathered by Prof. Schauinsland: "Von dieser ansehnlichen Landkrabbe sind 5 Examplare (4♂♂, 1♀) vorhanden. Dieselben fanden sich in lebendem Zustande im Guano, der von Clipperton Island (109° w. L. 10° n. Br.) nach Honolulu gebracht worden war." Lenz attributed them to *Gecarcoidea lalandii* Milne Edwards, a species reported from Brazil but which probably inhabits only Indo-Pacific islands, according to Rathbun (1918).

Writing of them in 1939, Schmitt reports: "In former years this species was exceedingly abundant on Clipperton. It is possible that the drove of wild pigs loose on the island has so reduced their numbers that they now seem scarce." In view of the situation at that time, the following observations of Marie-Hélène Sachet, expedition botanist (personal communication), are pertinent:

"Many papers on Clipperton Island mention the extraordinary abundance of land crabs on the atoll (cf. Sachet, 1960, for a brief discussion and bibliography). The first person to report their remarkable decrease was Dr. Waldo Schmitt (1939). It is not easy for me to evaluate from Dr. Schmitt's paper whether they were more abundant in 1938 than 1958, or less, as time of day, insolation, etc., would have influenced his observations, which were, of necessity, very brief. I would say that in 1958 the crabs were common, but not abundant. Anyone wanting to make a large sampling of the population could have done so with little trouble, but they were not crawling all over the island as they did 50 years ago, and they were absolutely no problem in camp. . . The crabs appeared to live in natural holes under overhanging ledges of phosphatic rock, or in holes they dug in the soft phosphatic silt under the protection of stones, boulders, or even pebbles lying below the vegetation cover. I never saw what they ate. Many pigs were killed and were swiftly disposed of with the help of flies and other organisms, but I did not see crabs near the carcasses. I suspect, but did not observe, that they may kill nestling birds if they are weakened, and that they probably eat much plant material.

"On a hot sunny day, they were not in evidence, although if the edge of their shelter cast a little shade, they could be seen peering out from under it. On a cool, overcast day, they would be scrambling about and in the late afternoon, they came out. I definitely saw them go to the lagoon about 5 or 6 p.m. and let themselves fall from small cliffs and rocks into the water. I also saw them scrambling back from the ocean across the beaches and beach ridges. I had no chance to check whether only the egg-bearing females, or all females, or males and females, did this.

"The pigs ate great quantities of them, as evidenced by some of their droppings, which seemed to be entirely made up of crab carapaces. How they caught the crabs I did not observe, as the pigs were very shy and could not be easily approached."

In a letter dated May 15, 1962, Dr. F. A. Chace, Jr., Curator of Marine Invertebrates, U. S. National Museum, wrote: "A female of what I assume to be *Gecarcinus planatus*, labeled 'Clipperton Isl.—John T. Arundel' has just come to my attention. This specimen was apparently inadvertently extracted from the California Academy when the *Albatross* material was retrieved from that institution in 1948. It was probably part of the collection made by Arundel when he visited Clipperton on the *Navarro* in 1897. According to Miss Sachet (1960), 'Ces collections sont importantes car elles sont les premières à avoir été décrites dans la littérature scientifique de l'île (Wharton, Teall, Garman).'" Thus, after more than half a century, what was possibly the first crab to have been collected at Clipperton now becomes a matter of record, along with the most recent crabs known to have been collected there.

Family Ocypodidae

Ocypode ceratophthalma (Pallas).

(Figures 23–26.)

Cancer ceratophthalmus Pallas, 1772, p. 83, pl. 5, fig. 17.

Ocypode ceratophthalma Fabricius, 1798, p. 347. Ortmann, 1897b, p. 364 (synonymy). Rathbun, 1906, p. 833 (Hawaii). Stimpson, 1907, p. 108, pl. 12, fig. 2 (Hawaii, Tahiti). Holthuis, 1953, p. 29 (Tuamotu).

Range. Distributed throughout the entire Indo-Pacific region. From Red Sea, Port Elizabeth, and Madagascar to Tokyo, New South Wales, Tahiti, Fanning and Hawaiian islands. (Ortmann)

Material. Clipperton Island: October, 1956; C. Limbaugh: 1 male, 1 female.

Measurements. Largest specimen, male, length 40.2 mm., width 43.7 mm. Female, length 38.2 mm., width 43.8 mm.

Habitat. On sandy beaches in deep burrows, near or above high tide.

Remarks. In view of the circumtropical distribution of *Ocypode*, the presence of a member of the genus at Clipperton might have been anticipated. However, it was not until specimens of Conrad Limbaugh's 1956 collecting became available that it could be determined whether it would be the eastern Pacific *O. gaudichaudii* Milne Edwards and Lucas, found at Cocos and Galápagos and along the Central and South American mainland from El Salvador to Chile, or the western Pacific *O. ceratophthalma*. Comparison of the above specimens with a pair of the latter from Eniwetok Atoll in the Marshall Islands left no doubt of their identity with the Indo-west Pacific species, for while both species have the eyestalks prolonged beyond the cornea, the fingers of *O. ceratophthalma* are pointed, those of *O. gaudichaudii* truncate. The random nature of insular dispersal is again illustrated, with chance in this instance favoring the establishment of the western rather than the eastern Pacific species.

Distribution

Clipperton Island shares with Clarion Island to the northwest and the Galápagos Islands to the southeast the role of outlier to the American continent, and with them forms a line roughly parallel to the Mexican–Central American axis at a distance of about 600 nautical miles. Clipperton is more isolated than the others, however, for between Clarion and the mainland lie Socorro and San Benedicto, between Galápagos and the mainland lie Cocos and Malpelo, while between Clipperton and the mainland there is only the unbroken ocean. To the west of Clarion the nearest land is the Hawaiian Islands; to the west of the Galápagos are the Marquesas; while west of Clipperton itself are the Line Islands (Palmyra, Washington, Fanning, and Christmas), which trend in the same NW.–SE. direction as their American counterparts. Between these outliers of Polynesia and the American outliers stretches nearly 2,000 miles of unbroken ocean, the Central Pacific Oceanic Barrier, constituting a most formidable obstacle to the migration of terrestrial and shore-bound marine animals.

It is of considerable interest, therefore, to find that nearly one-half (16 of 34) of the brachyuran crab species inhabiting Clipperton Island are of Indo-Pacific origin, and that of these over half (9 of 16) have not yet reached the American mainland. Remarkable also is the fact that of the same nine species, eight have not been recorded from one or more of the other outliers of the American continent, the sole exception being *Pachygrapsus minutus*, recorded herein as occurring at Clarion and Socorro islands as well. Since these other islands appear equally well situated to receive such immigrants and present more extensive coastlines suitable for their establishment, it must be concluded that Clipperton is more favorably located with respect to routes of dispersal eastward from the central Pacific, or that its uniqueness as a coral atoll gives it an advantage over them in assuring the survival of current-borne species.

Endemism

While, with the synonymizing of *Thalamita roosevelti* Schmitt with *T. picta* Stimpson, there remains no Clipperton Island brachyuran endemic species, evidence of incipient speciation persists in the Xanthidae, where both *Actaea sulcata* Stimpson and *Micropanope xantusii* (Stimpson) exhibit minor but consistent differences from their mainland counterparts. Moreover, two minute specimens recovered by diving in 78 feet, the one belonging to *Actaea*, the other to *Micropanope*, cannot with certainty be identified with known eastern Pacific representatives of these genera. Pending recovery of adult specimens of these, or discovery of additional species, it may be concluded that endemism among brachyurans at Clipperton is weakly expressed, and does not manifest itself above the populational level.

Faunal Boundaries

Should the proportion of western Pacific to eastern Pacific species found at Clipperton Island reach or surpass the 50 per cent mark that it now approaches, consideration might be given to relocating the boundary between the faunas so that it passes between Clipperton Island and the American mainland.

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 2, pp. 47–58; 11 figs.; 1 table July 28, 1965

ON THE IDENTIFICATION OF *SCHIZOPYGA CALIFORNIANA* CONRAD, A CALIFORNIA PLIOCENE GASTROPOD[1]

By

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Abstract

Widely differing identifications of the Pliocene gastropod originally described as *Schizopyga californiana* Conrad (1856), but now placed in the genus *Nassarius*, have resulted from a vague original description, poor figure, and missing type specimen. Isolated exposures of marine upper Pliocene strata in northwestern Santa Clara County, California, considered to be laterally equivalent to the generalized type locality of this species, contain two species of *Nassarius*. One, a rather small slender species particularly characteristic of these strata, closely resembles the type figure and is believed to be Conrad's species. Several other late Cenozoic nassariids from California have at one time been figured or identified as *N. californianus*. They are: *N. coalingensis* (Arnold), *N. delosi* (Woodring), *N. grammatus* (Dall), *N. iniquus* (Stewart), *N. moranianus* (Martin), and *N. rhinetes* Berry. *Nassarius californianus* is characteristic of marine Pliocene formations from the San Francisco Bay area southward to Santa Maria Basin.

Introduction

The identity of *Schizopyga californiana* Conrad (1856), the first nassariid gastropod described from Tertiary strata of the Pacific Coast of North America, has been obscured by a cryptic original description and incomplete figure, indefinite locality data, and missing type specimen. Curiously, the name *Nassarius*

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[1] Publication authorized by the Director, U. S. Geological Survey.

californianus (Conrad) has become widely known by virtue of its continuing, if not consistent, usage in published faunal lists from the later Cenozoic of California. No less than six different species, ranging in age from Pliocene to Recent, have been figured as representing *N. californianus*. These taxa have one principal trait in common, reticulate or papillose ornamentation of the body whorl. Yet they represent three supraspecific groups that are sometimes afforded full generic standing.

It is here concluded that the name *Nassarius californianus* can be fairly confidently fixed on a small Pliocene nassariid whose geologic and geographic occurrence seem to satisfy the vague requirements of the original locality description. As is characteristic of the Cenozoic species of *Nassarius* from the Pacific Coast of North America, *N. californianus* is very useful in stratigraphic correlation.

Acknowledgments

Parts of the manuscript have been reviewed by F. S. MacNeil, J. G. Vedder, A. M. Keen, and L. G. Hertlein. Their comments and informal discussions of taxonomic problems are greatly appreciated. T. W. Dibblee, E. H. Pampeyan, and E. E. Brabb have pointed out Pliocene fossil localities in the northeastern Santa Cruz Mountains and have freely discussed details of Pliocene and Pleistocene stratigraphy of this area. I am indebted to J. H. Peck, Jr., of the Museum of Paleontology, University of California, Berkeley, for granting access to the Cenozoic collections, and to L. G. Hertlein and A. M. Keen for providing access to the collections of the California Academy of Sciences and Stanford University, respectively. The photographs were made by Kenji Sakamoto of the U. S. Geological Survey.

Typology of *Schizopyga californiana*

Conrad described *Schizopyga californiana* in 1856 (p. 315) as the only species of *Schizopyga*, a new genus. Subsequently the description was reprinted with a drawing (Conrad, 1857, p. 69, pl. 2, fig. 1) of an incomplete specimen consisting of the penultimate and body whorls but with the outline of the spire restored. The type material, which has been lost, consisted of small samples of sandstone containing abundant specimens of only this species which were collected by a Lieutenant Trowbridge of the U. S. Army from a bed overlying a 3-foot stratum of coal or lignite "12 miles back from Santa Clara" (Newberry, 1857, p. 67). Newberry described the "coal" as lignite and consolidated carbonaceous mud containing a large amount of earthy material. Lignitic material occurs at many places in the lower part of the Santa Clara Formation, a Pliocene and Pleistocene unit composed chiefly of nonmarine gravel and sand. It is not known to be characteristic of other formations in this area. Northeast of the San Andreas fault the Santa Clara Formation crops out in a linear pattern

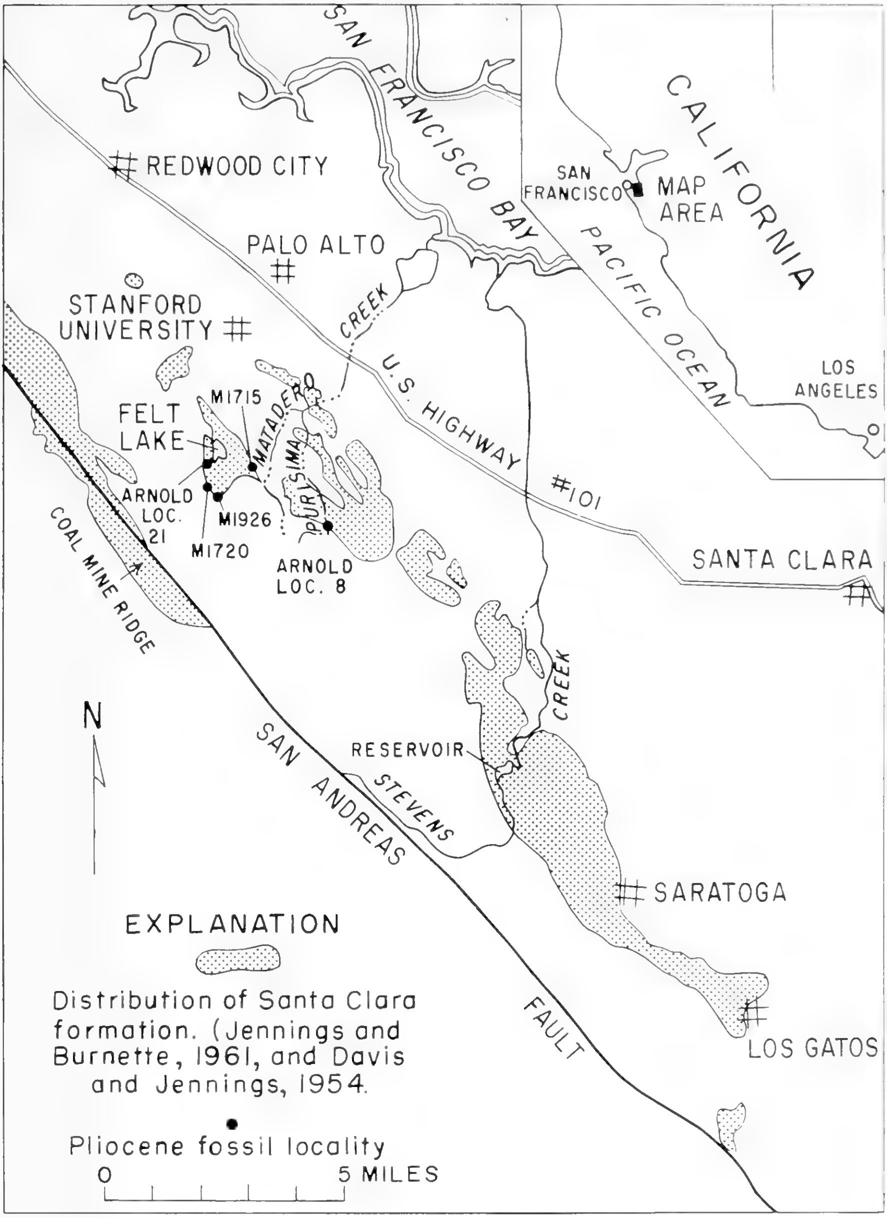

Figure 1. Index map of part of San Francisco Peninsula showing distribution of the Santa Clara Formation and localities at which *Nassarius californianus* has been collected from marine strata which interfinger with the basal part of the formation.

from a point near Los Gatos northwestward to the vicinity of Redwood City (fig. 1), a distance of about 25 miles (Branner and others, 1909; Davis and Jennings, 1954). In the southern part of the belt, lignitic material is locally abundant in road cuts and rock quarries in the basal part of the formation, particularly in the vicinity of Stevens Creek Reservoir (T. W. Dibblee, oral communication, July 1963). It is also characteristic of the basal part of the formation in the vicinity of Coal Mine Ridge, located immediately southwest of the San Andreas fault and about 5 miles south–southwest of Stanford. The presence of lignitic material at the type locality of *N. californianus* suggests that the type material was collected from marine strata which interfinger with the Santa Clara Formation, presumably near the base.

An arc of 12 miles' radius scribed from the present location of the Mission at Santa Clara, California, intersects outcrops of the Santa Clara Formation in two areas: about 2 miles south of Los Gatos and about 3 miles south of Stanford University near Matadero Creek (fig. 1). Marine fossils are not recorded from the first area, although indexes to geologic mapping in California (Strand and others, 1958; Koenig, 1962; and Jennings and Strand, 1963) indicate that it has not been mapped in detail. A rich molluscan fauna of late Pliocene age, including two species of *Nassarius*, is known from several localities in the second area, which is about 12 miles west–northwest of Santa Clara (fig. 1).

The meaning of Newberry's phrase "back from Santa Clara" (1857, p. 67) is not clear. It could imply "back" in the sense of retracing the route from San Francisco, the staging point for the railroad surveys. The fossiliferous exposures south of Stanford seem to fit the description, although no carbonaceous material other than scattered fragments have been found in the Santa Clara Formation in this area (E. Pampeyan, oral communication, August, 1963). Or it could mean directly back from Santa Clara in the Santa Cruz Mountains; if it does, the area of outcrop south of Los Gatos would be a probable location. The abundance of a species of *Nassarius* in marine strata which appear to intertongue with the basal part of the Santa Clara Formation, together with the characteristic occurrence of lignitic material in the basal part of the formation within a 12-mile radius of Santa Clara, suggests that Conrad's material was from this general stratigraphic position. Because of the ambiguity of the original description, it is doubtful that the precise locality will be found.

Nassariids from Pliocene Strata Near Stanford, California

Stratigraphic occurrence. Pliocene marine mollusks are known from several localities south of Stanford (fig. 1). Arnold (*in* Branner and others, 1909, p. 6) cited three localities of "characteristic lower Merced fossils" from the southwest side of Felt Lake southeast to Purisima Creek, a distance of about 4 miles. Over the years students from Stanford University have collected additional material from the area south of Felt Lake. New collections have been made from recent pipeline and building excavations along Arastradero Road west of Matadero Creek and south of Felt Lake. At one of these, U. S. Geological Survey Cenozoic locality M1715 (fig. 1), abundantly fossiliferous poorly consolidated, somewhat gravelly sandstone overlies massive diatomaceous siltstone. The siltstone contains Foraminifera indicative of a late Miocene, Delmontian age (Cummings and others, 1962). A well developed zone of "pholad" pelecypod burrows in the underlying siltstone with the valves preserved, in place, suggests that the contact is unconformable, although there does not appear to be an appreciable difference in attitude between the two stratigraphic units. Conformably overlying the fossiliferous beds along Arastradero Road are unfossiliferous sands and sandy gravels of similar composition referable to the Santa Clara Formation. The gravels are composed of pebbles and cobbles derived from the Franciscan Formation and what appears to be Monterey Shale. The fossiliferous beds are about 10 feet thick in this area. They contain locally abundant concentrations of gravel but seem to have a higher proportion of sand than do the overlying unfossiliferous strata. If two stratigraphic units are to be differentiated, their recognition must depend upon the presence or absence of marine fossils. The fossiliferous sand apparently represents a brief southerly extension of the late Pliocene embayment in which the Merced Formation and correlative marine strata to the north of San Francisco were deposited. It is therefore tentatively referred to the Merced Formation. Following withdrawal of the sea from this area, fluvial sands and gravels of the Santa Clara Formation were deposited. As first noted by Arnold (*in* Branner and others, 1909, p. 6) invertebrates from the localities south of Stanford are comparable to the fauna of the lower part of the type Merced Formation near San Francisco, nearly 30 miles to the northwest. Branner and others (1909), however, included these localities with their underlying Purisima Formation as a convenience in mapping, although the Merced Formation was considered to be the lateral equivalent of the Santa Clara Formation.

Comparison with Conrad's description and figure. The Pliocene molluscan fauna consists of nearly 40 species of gastropods and pelecypods. Two species of *Nassarius* occur in this assemblage. The most common (figs. 2–4, 6, 7) is a relatively small slender species with ornamentation and whorl proportions comparable to Conrad's drawing (1857, pl. 2, fig. 1) of *Schizopyga californiana*. The other is a larger species with an inflated body whorl (figs. 8–11), *N. grammatus* (Dall, 1917), which can be readily discriminated from the slender species through all stages of growth. The species of *Nassarius* that was originally described by Conrad can best be determined by comparison with the original figure (Conrad, 1857, pl. 2, fig. 1). The type material is lost (Woodring and others, 1946, p. 74) and the original description, "Volutions rounded, having revolving ribs and longitudinal furrows, giving the ribs a nodulous character;

Table 1. *Ratio of body-whorl height to combined height of penultimate and body whorls of the two species of* Nassarius *from USGS Cenozoic locality M1715.*

Slender Nassarius [N. californianus *(Conrad)*]				*Large* Nassarius [N. grammatus *(Dall)*]			
Penultimate whorl	*Body whorl*	*Total*	*BW/Total*	*Penultimate whorl*	*Body whorl*	*Total*	*BW/Total*
2.8 mm.	10.2 mm.	13.0 mm.	0.785	4.8 mm.	25.0 mm.	29.8 mm.	0.845
2.5	9.0	11.5	0.783	4.0	21.0	25.0	0.840
2.6	11.0	13.6	0.809	4.7	22.5	27.2	0.827
2.8	10.9	13.7	0.796	3.7	20.5	24.2	0.848
2.4	9.7	12.1	0.802	5.0	28.1	33.1	0.849
2.9	9.8	12.7	0.771	4.3	27.0	31.3	0.865
2.8	9.8	12.6	0.778	3.4	20.8	24.2	0.864
2.3	9.6	11.9	0.807	3.2	20.1	23.3	0.867
2.6	10.0	12.6	0.794	3.7	23.1	26.8	0.862
2.8	10.8	13.6	0.794	4.0	22.8	26.8	0.852

basal excavation profound" (Conrad, 1856, p. 315), is of little value, as it could apply to either species.

Identification of the slender species (figs. 2–4, 6, 7) as *Nassarius californianus* is suggested by the evenly nodose sculpture, rounded profile and relatively large size of the penultimate whorl, and the rather slender spire, all indicated by Conrad's figure (1857, pl. 2, fig. 1), which is reproduced herein (fig. 5). The ratio of height of the body whorl to combined height of the penultimate and body whorls of the type figure is compared with the ratio of measurements for randomly selected specimens of the two species of *Nassarius* from U. S. Geolog-

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Figure 2. *Nassarius californianus* (Conrad). Height 13.3 mm., width 7.6 mm. Hypotype, USNM no. 648590. Merced(?) Formation, Pliocene, Santa Clara County, California, USGS Cenozoic loc. M1720.

Figures 3, 4. *Nassarius californianus* (Conrad). Height 13.8 mm., width 7.7 mm. Hypotype, USNM no. 648551. Same locality as fig. 2.

Figure 5. Reproduction of original figure of *Schizopyga californiana* Conrad (Conrad, 1857, pl. 2, fig. 1). Santa Clara, California, holotype lost.

Figure 6. *Nassarius californianus* (Conrad). Height 16 mm., width 8.6 mm. Hypotype, USNM no. 648591. Merced(?) Formation, Pliocene, Santa Clara County, California, USGS Cenozoic loc. M1715.

Figure 7. *Nassarius californianus* (Conrad). Height 15.8 mm., width 8.6 mm. Hypotype, USNM no. 648548. Same locality as fig. 6.

Figure 8. *Nassarius grammatus* (Dall). Height 27.9 mm., width 17.9 mm. Hypotype, USNM no. 648569. Same locality as fig. 6.

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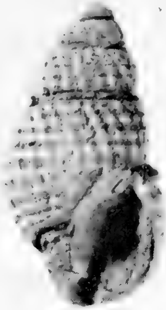

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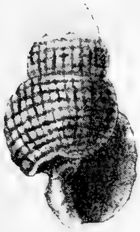

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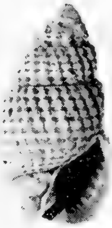

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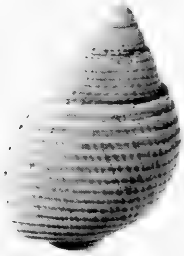

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Figure 9. *Nassarius grammatus* (Dall). Height 33.4 mm., width 21.5 mm. Hypotype, USNM no. 648568. Same locality as fig. 6.

Figures 10, 11. *Nassarius grammatus* (Dall). Height 27.6 mm., width 18.2 mm. Hypotype, USNM no. 648592. Same locality as fig. 6.

ical Survey Cenozoic locality M1715 in table 1. The ratio of 0.794 for the type figure falls near the midpoint of the range of values for the slender species, 0.783 to 0.809. The values for the larger species, *N. grammatus*, are appreciably larger, 0.827 to 0.867, and do not overlap with those for the slender species. There are 9 or 10 spiral ribs on the body whorl of the original figure of *N. californianus*. This number compares very closely with the rib count of 9 for the slender species, whereas it is significantly less than the 14 spiral ribs on intermediate and adult specimens of the larger species from locality M1715.

The dimensions of the original figure of *Nassarius californianus* (Conrad, 1857, pl. 2, fig. 1) are about one and one-half times as large as the largest of more than 200 individuals of the slender species from U. S. Geological Survey Cenozoic localities M1715 and M1720 (fig. 1). They are smaller than the average size of about 20 specimens of *N. grammatus* from these localities. If the slender species is identical to Conrad's *N. californianus*, then the type figure must be somewhat enlarged.

Because of the close similarity of many morphological characteristics of the slender species of *Nassarius* with the original figure of *N. californianus*, it is concluded that it is the taxon which Conrad described in 1856 (p. 315) from "Santa Clara, California." That a relatively small specimen of *Nassarius* was the type is suggested by Newberry's description (1857, p. 67) of the original material: "in the small specimens of this rock [sandstone] . . . but a single species of fossil shell is distinguishable, though this is represented by considerable numbers."

Nassarius californianus is common in collections from Pliocene formations in the San Francisco Bay area, Santa Cruz Mountains, Kettleman Hills, and Santa Maria Basin. There are no known occurrences of this taxon in beds younger than Pliocene. In the Kettleman Hills area (Woodring and others, 1940) and the Santa Maria Basin (Woodring and Bramlette, 1950) this species has been known as *N. waldorfensis* (Arnold).

SPECIES CONFUSED WITH *NASSARIUS CALIFORNIANUS*

In 1903, Arnold (p. 231, pl. 4, fig. 3) figured a large coarsely sculptured species with widely spaced axial ribs from upper Pleistocene strata of the San Pedro area, southern California, as *Nassa californiana* (Conrad). Many years later this species was renamed "*Nassa*" *delosi* by Woodring (*in* Woodring and others, 1946, p. 74, pl. 35, figs. 12–15). This is a very rare species once thought to be restricted to beds of late Pleistocene age. Recently, living specimens have been found in southern California near Balboa [Newport Beach] and San Diego (Chace, 1957, 1962).

Other early records of *Nassarius californianus* by Arnold (1908; *in* Branner and others, 1909) from upper Pliocene strata in central California, which include the Felt Lake locality, are of the species later named *N. grammatus* (Dall, 1917, p. 575) (*N. moranianus* of authors). ,A second species of *Nassarius* in Arnold's collections from the Felt Lake locality is Conrad's *N. californianus.* This species appears to have been identified as either *N. mendicus* or *N. perpinguis* by Arnold (1908, p. 355), the only other species of *Nassarius* on his "Merced" faunal list.

A third species from Pliocene strata in the southern San Joaquin Valley figured as *Nassa californiana* by Arnold (1909, pl. 27, fig. 8) was renamed "*Nassa*" *miser iniqua* by Stewart (*in* Woodring and others, 1940, p. 87, pl. 34, fig. 8). The presence of a varix on the body whorl of this species is a subgeneric characteristic that distinguishes it from *Nassarius californianus*, which has a simple outer lip.

Until recently, Pacific Coast malacologists (Demond, 1952; Abbott, 1954; and others) used the name *Nassarius californianus* for a moderately large species usually occurring at moderate depth in the sublittoral zone (low tide to 100 fathoms) from southern Oregon to the outer coast of Baja California. This usage can be traced to Rivers (1891), who first figured and described a Recent specimen. Dall's figure of *N. californianus* (1921, pl. 11, fig. 4) has been informally recognized as the standard of reference for the living species. Woodring (*in* Burch, 1945, no. 51, p. 7; and *in* Woodring and Bramlette, 1950, p. 74) seems to have been the first to recognize that this species was distinct from *N. californianus* (Conrad) and merited a new name. Later, Berry (1953, p. 415–416, pl. 28, fig. 7) proposed the name *N. rhinetes* for the taxon which "has long been known to California students as one of the strange congeries of forms which has passed under the name *Nassa californiana* (Conrad)." Although Dall's (1921, pl. 11, fig. 4) and Demond's (1952, pl. 2, fig. 6) earlier figures were not mentioned by Berry, they very closely resemble his figured specimen.

Nassariid gastropods from the upper part of the type Merced Formation south of San Francisco which have been identified as *Nassarius* cf. *N. californianus* (Glen, 1959, p. 157) probably are immature specimens of *N. moranianus* (Martin).

LOCALITY DESCRIPTIONS

U. S. GEOLOGICAL SURVEY CENOZOIC LOCALITY.

M1715. Cut and pipeline trench on north side of Arastradero Road, 1,200 feet west of intersection with Page Mill Road, Palo Alto 7½′ quadrangle, California. Merced(?) Formation, late Pliocene. Collectors: E. H. Pampeyan, J. G. Vedder, and W. O. Addicott, 1963.

M1720. Cut on south side of highest building site for American Institute for Research buildings on southwest side of Arastradero Road, 2,200 feet due east of intersection with Alpine Road, Palo Alto 7½′ quadrangle, California. Collectors: M. D. Crittenden and W. O. Addicott, 1962.

M1926. About 2,700 feet southeast of intersection of Arastradero and Alpine roads, 400 feet north of lat. 37° 22′ 30″ N., 6,000 feet west of long. 122° 10′ W., altitude 650 feet, Palo Alto 7½′ quadrangle, California. Collector: E. H. Pampeyan, 1963.

Stanford University locality.

Arnold No. 8. About 1½ miles southeast of the forks of Page Mill Road (southern intersection of Page Mill and Arastradero roads). Also listed as 2 miles up the east fork of Madera [Matadero] Creek between the "e" and "p" of "Concepcion," Santa Cruz 30′ quadrangle, California.

Arnold No. 21. Immediately southwest of Felt Lake, Santa Cruz 30′ quadrangle, California. Merced(?) Formation, late Pliocene.

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 3, pp. 59–64 October 8, 1965

TYPE SPECIMENS OF ORTHOPTERA IN THE COLLECTION OF THE CALIFORNIA ACADEMY OF SCIENCES TO 1965

By

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The following is an annotated list of the Orthoptera holotypes, allotypes, and lectotypes only, on hand in the collection of the California Academy of Sciences as of January 1, 1965. All were individually checked against original designations in the literature. Types in the entomology collection of the Academy are housed in specially assigned cases. All the drawers in these cases were carefully examined for specimens. The alcoholic collection, which is kept separate from the pinned collection, was also checked for type specimens; types in alcohol are segregated. There is only a slight possibility that a type specimen in the Academy collection may have been overlooked.

The type names and localities were taken directly from the labels on the specimens. Abbreviations of localities are frequently given in full and additional data, such as county names, are sometimes included for clarity. Obvious exclusions are inserted within brackets [ ].

Following the author's name, the exact date of publication, original citation, and title of the paper appear in respective sequence. The three orthopteran lectotypes in the Academy collection have lectotypic citations included as well as a reference to the original description of the species or the subspecies involved.

TYPE SPECIMENS IN THE ACADEMY'S COLLECTION

TETRIGIDAE

Rehnidium mendosum Grant. October 3, 1956, Trans. Amer. Ent. Soc., vol.

82, pp. 104–105. The taxonomy of *Batrachia puigaria*, *Lophoscirtus*, *Eutettigidea*, and *Rehnidium*.

HOLOTYPE, ♂. Peru, Monson Valley, Tingo Maria, 2–XI–1954. E. I. Schlinger and E. S. Ross, collectors.

Tetrix ornata insolens REHN AND GRANT. October 3, 1956, Proc. Acad. Nat. Sci. Phila., vol. 108, pp. 150–152. The components of *Tetrix ornata*.

HOLOTYPE, ♀. California, Kern County, Kernville, 25–V–1940. "Grasses." C. G. Lewis, collector.

EUMASTACIDAE

Eumorsea pinaleno REHN AND GRANT. January 16, 1959, Trans. Amer. Ent. Soc., vol. 84, pp. 300–302. Review of the genera *Psychomastax* and *Eumorsea*.

ALLOTYPE, ♀. Arizona, Graham County, Mt. Graham, Shake Trail, 9,000 feet altitude, 20–VIII–1952. H. B. Leech and J. W. Green, collectors.

PYRGOMORPHIDAE

Icthiacris elongata KEVAN, SINGH, AND AKBAR. November 30, 1964, Proc. Acad. Nat. Sci. Phila., vol. 116, pp. 247–250. A revision of the Mexican Pyrgomorphidae. 1. Genera other than *Sphenarium*.

HOLOTYPE, ♂, no. 8905. Mexico, Sinaloa, 26 miles north of Pericos, 13–VIII–1960. P. H. Arnaud, E. S. Ross, and D. C. Rentz, collectors.

ALLOTYPE, ♀. Mexico, Sonora, Alamos, 12–VIII–1960. P. H. Arnaud, E. S. Ross, and D. C. Rentz, collectors.

Parasphenula obscura KEVAN. March 7, 1962, Proc. Calif. Acad. Sci., fourth Ser., vol. 31, pp. 235–240. Pyrgomorphidae (Orthoptera: Acridoidea) collected in Africa by E. S. Ross and R. E. Leech, 1957–1958, with descriptions of new species.

HOLOTYPE, ♀. Northern Rhodesia, Abercorn, 1,600 meters altitude, 16–II–1958. E. S. Ross and R. E. Leech, collectors.

ALLOTYPE, ♂. Same data as for holotype.

Rutioderes concolor KEVAN. March 7, 1962, Proc. Calif. Acad. Sci., fourth ser., vol. 31, pp. 231–233. Pyrgomorphidae (Orthoptera: Acridoidea) collected in Africa by E. S. Ross and R. E. Leech, 1957–1958, with descriptions of new species.

HOLOTYPE, ♂. Belgian Congo, Tshibati, Lwiro River, 47 kilometers north of Bukavu, 1,950 meters altitude, 17–XII–1957. E. S. Ross and R. E. Leech, collectors.

ACRIDIDAE

CYRTACANTHACRIDINAE

Agnostokasia sublima GURNEY AND RENTZ. June 19, 1964, Proc. Calif. Acad. Sci., fourth ser., vol. 31, pp. 503–513. A new spine-throated grasshopper from the White Mountains of California. (Orthoptera: Acrididae: Cyrtacanthacridinae).

Holotype, ♂, no. 8784. California, Mono County, White Mountains, Mt. Barcroft, 12,500 feet altitude, 21–VII–1961. D. C. Rentz, collector.

Allotype, ♀. Same data as for holotype.

Clematodes vanduzeei Hebard. July 21, 1923, Proc. Calif. Acad. Sci., fourth ser., vol. 12, pp. 327–328. Expedition of the California Academy of Sciences to the Gulf of California in 1921.

Holotype, ♀, no. 1240. [Mexico], San Pedro Bay, Gulf of California, 7–VII–1921. E. P. Van Duzee, collector.

Halmenus eschatus Hebard. December 30, 1920, Proc. Calif. Acad. Sci., fourth ser., vol. 2, pp. 329–332. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906.

Holotype, ♀, no. 717. Wenman Island, Galápagos Islands. F. X. Williams, collector.

Allotype, ♂, no. 718. Same data as for holotype.

Hebardacris mono Rehn. July 31, 1964. Notulae Naturae, no. 368, pp. 1–16. Contributions to our knowledge of the North American Melanoplini (Orthoptera: Acrididae: Cyrtacanthacridinae).

Holotype, ♂, no. 8915. California, Northwest Inyo County, near Mono Pass, 12,000 feet altitude, 9–VIII–1959. D. C. Rentz, collector.

Allotype, ♀. Same data as for holotype.

Hypsalonia petasata Gurney and Eades. December 29, 1961, Trans. Amer. Ent. Soc., vol. 87, pp. 303–306. A new genus of wingless grasshoppers from California related to *Bradynotes*.

Holotype, ♂. California, Northwestern Inyo County, near Mono Pass, 12,000 feet elevation, 9–VIII–1959. D. C. Rentz, collector.

Allotype, ♀. Same as for holotype.

Melanoplus lithophilus Gurney and Buxton. January 8, 1965, Occas. Papers, Bur. Ent. Calif. Dept. Agr., no. 7, pp. 1–3. New California grasshoppers of the genus *Melanoplus* (Orthoptera, Acrididae).

Holotype, ♂, no. 8913. California, Trinity County, Weaver Bally, *ex* slate on summit, 26–IX–1963. G. M. Buxton, F. L. Blanc, collectors.

Allotype, ♀. Same data as for holotype.

ACRIDINAE

Esselenia vanduzeei Hebard. December 29, 1920, Proc. Calif. Acad. Sci., fourth ser., vol. 10, pp. 71–75. A new genus and species of grasshopper from California.

Holotype, ♀, no. 736. Bryson, California, Monterey County, 27–IV–17. E. P. Van Duzee, collector.

TETTIGONIIDAE

Phaneropterinae

Insara psaronota Hebard. July 21, 1923, Proc. Calif. Acad. Sci., fourth ser., vol. 12, pp. 332–335. Expedition of the California Academy of Sciences to the Gulf of California in 1921.

Holotype, ♂, no. 1241. [Mexico], Coyote Bay [= cove?], Concepcion Bay, Gulf of California, 18–VI–1921. J. C. Chamberlain, collector.

Allotype, ♀, no. 1242. [Mexico], San Marcus Island, Gulf of California, 19–VI–1921. Virgil Owen, collector.

Conocephalinae

Xiphidium exitiosum McNeill. November 7, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 501. Papers from the Hopkins Stanford Galápagos Expedition, 1898–1899. IV. Entomological results.

Lectotype, ♂, Galápagos Islands, James Island, 22–IV–1899. L. Stanford, Jr. U. lot 310, sub. 30. (Hebard, December 30, 1920, lectotype designation. Proc. Calif. Acad. Sci., fourth ser., vol. 2, pp. 335–337. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906.)

Decticinae

Eremopedes spinosa Hebard. July 21, 1923, Proc. Calif. Acad. Sci., fourth ser., vol. 12, pp. 337–339. Expedition of the California Academy of Sciences to the Gulf of California in 1921.

Holotype, ♂, no. 1243. Mejia Islands, Gulf of California, Angel de la Guardia Island, 28–VI–1921. E. P. Van Duzee, collector.

Allotype, ♀. Same data as for holotype.

Plagiostira gillettei utahensis Tinkham. December 31, 1962, Great Basin Naturalist, vol. 22, no. 4, pp. 105–109. Studies in Nearctic sand dune Orthoptera. Part VII. A new dwarf race of *Plagiostira gillettei* from a Utah dune, with generic key.

Holotype, ♂, no. 8785. Coral Pink Dunes, Utah, 22–VIII–1961. J. R. Helfer, collector.

Mecopodinae

Exogryllacris ornata Willemse. January 1, 1963, Entomologische Berichten, Deel 23, no. 1, pp. 1–4. A new genus and species of Orthoptera from Australia.

Holotype, ♀, Phillipine Islands, Los Banos, 1914. Ledyard, collector.

The locality given in the original description disagrees with that found on the label at the present time. The locality given in the paper was "Australia, N.

Queensland, collector H. Peters." The type and other material studied by Dr. Willemse were returned subsequent to his death. A specimen determined as *Eumecopoda cyrtoscelis* Karsch by him bears the same locality data as given for the type of *Exogryllacris ornata*. None of the other returned specimens studied by Dr. Willemse bear either locality. Comparison of the type specimen in question with the original description reveals that the specimen with the Philippine Island label is the one described. Since Dr. Willemse photographed most of the specimens we sent him for study, it is believed by this author that the labels were mixed at the time the photos were made and the present labeling of the type specimen of *Exogryllacris ornata* Willemse is in error.

GRYLLACRIDIDAE

Rhaphidophorinae

Daihiniodes valgum Strohecker. March 18, 1960, Pan-Pac. Ent., vol. 36, no. 1, pp. 31–32. Several new species of North American Orthoptera.

Holotype, ♂, California, Riverside County, Palm Springs, 1–VI–1949. L. M. Smith, collector.

Stenopelmatinae

Stenopelmatus intermedius Davis and Smith. July 14, 1926, Pan-Pac. Ent., vol. 2, no. 4, pp. 178–179. Notes on the genus *Stenopelmatus* with description of a new species.

Holotype, ♀, California, Oakland, XII–1925. L. M. Smith, collector.

Allotype, ♂. Same data as for holotype.

Gryllidae

Nemobiinae

Nemobius speculi McNeill. November 7, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 503. Papers from the Hopkins Stanford Galápagos Expedition, IV. Entomological results, 1898–1899.

Lectotype, ♂, Galápagos Islands, Albemarle Island, 23–I–1899. L. Stanford, Jr. U. lot 310, sub. 37. (Hebard, December 30, 1920, lectotype designation. Proc. Calif. Acad. Sci., fourth ser., vol. 3, pp. 341–342. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906.)

Mogoplistinae

Cycloptilum lepismoide McNeill. November 7, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 501. Papers from the Hopkins Stanford Galápagos Expedition, 1898–1899, IV. Entomological results.

Lectotype, ♂, Galápagos Islands, Albemarle Island, Tagus Cove, 23–III–

1899. L. Stanford, Jr. U. lot 310, sub. 33. (Hebard, December 30, 1920, lectotype designation. Proc. Calif. Acad. Sci., fourth ser., vol. 2, pp. 340–341. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906.)

PHASMATODEA

TIMEMIDAE

Timema boharti TINKHAM. September 30, 1942, Bull. So. Calif. Acad. Sci., vol. 41, no. 2, pp. 77–78. A new Californian species of *Timema* with zoogeographical notes.

HOLOTYPE, ♂. [California, San Diego County], Borrego Desert, 23–III–1941. "Ex grass."

ALLOTYPE, ♀. Same data as for holotype. Both specimens are preserved in alcohol.

DICTYOPTERA

Temnopteryx snodgrassi MCNEILL. November 7, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 493. Papers from the Hopkins Stanford Galápagos Expedition, 1898–1899, IV. Entomological results.

LECTOTYPE, ♀. Galápagos Islands, Albemarle Island, 6–IX–1899. L. Stanford, Jr. U. lot 310, sub. 5. (Hebard, December 30, 1920, lectotype designation. Proc. Calif. Acad. Sci., fourth ser., vol. 2, p. 315. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906.)

The type specimen was originally designated as placed in the collection of the U. S. National Museum but this was a case of mistaken ownership. The specimen has been returned to the California Academy of Sciences through the courtesy of Drs. Harold J. Grant and Ashley B. Gurney.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No 4, pp. 65–68; 6 figs. January 31, 1966

ZONORCHIS MEYERI, NEW SPECIES, A PARASITE OF THE GALL BLADDER OF A RAIL IN THE GALÁPAGOS ISLANDS (TREMATODA: DICROCOELIIDAE)[1]

By

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During the expedition of the Galápagos International Scientific Project of January, 1964, which was sponsored by the Charles Darwin Foundation, organized by the University of California, and supported by the National Science Foundation, the California Academy of Sciences, the Belvedere Scientific Fund, and the Shell Oil Company, the gallbladder of a rail (*Laterallus jamaicensis* Gmelin), was found to be infested by a worm belonging to the genus *Zonorchis*.

The single specimen collected is unfortunately a juvenile, but characters are sufficiently differentiated to allow a proper identification of a new species, here named *Zonorchis meyeri*. This species is respectfully dedicated to Professor Karl F. Meyer, Director Emeritus of the G. W. Hooper Foundation (University of California Medical Center, San Francisco).

Zonorchis meyeri Vercammen-Grandjean, new species.

A. Diagnosis. Lanceolate body, diameter of acetabulum twice that of oral suckers; coeca slender and torose, three-quarters as long as the body; elongate cylindriform cirrus pouch with oval seminal vesicle; multilobate testes; pyriform ovary; vitellagenous follicles distributed laterally through one-third of the body length.

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[1] This study was supported by P.H.S. Research Grant AI-03793-03 from the National Institute of Allergy and Infectious Disease, U. S. Public Health Service.

B. HOST AND PARASITOPE. *Laterallus jamaicensis;* gallbladder.

C. LOCALITY AND DATE. Galápagos Islands, Ecuador; January 24, 1964.

D. DESCRIPTION.

1) *Measurements*: in micra, of the holotype, a unique specimen.

Body		*Oral sucker*	*Acetabulum*	*Pharynx*	*Ovary*		*Testes*	*Cirrus*		*Vit.*	*Bladder*
length	*width*	Ø	Ø	Ø	*l*	*w*	Ø	*l*	Ø	*l*	*l*
1830	530	190	425	100	55	50	65	145	44	760	475

2) *Morphology*: Body lanceolate; the cuticle is glabrous and shows a considerable number of very small pseudopapillae (Ø 8 μ) (fig. 1). The more or less sharply pointed posterior end of the body is terminated by a small cuticular thickening in the form of a cap. Diameter of oral sucker less than half that of the acetabulum; oral region provided with conspicuous papillae distributed in a regular pattern (fig. 2: anterointernal group of two papillae—one larger, at 9 o'clock; fig. 3: anteroexternal papillae at 10 o'clock; fig. 4: posteroexternal papillae at 6 o'clock). Pharynx spherical, no esophagus; coeca divided, immediately after the pharynx, into two long, slender, torose tubes reaching the posterior third of the excretory bladder.

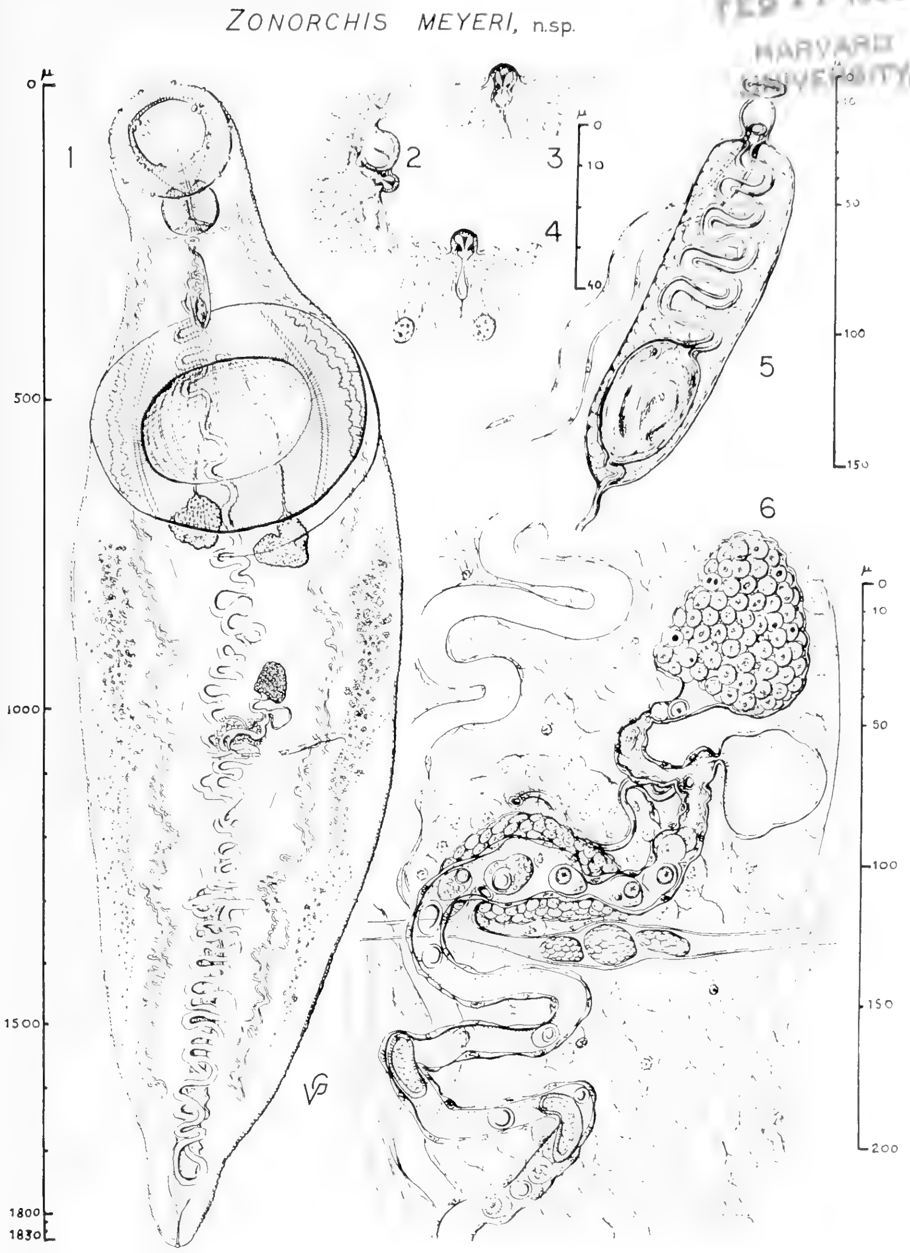
Genital system:

a) *Male*: (fig. 5) Two more or less multilobate testes, the left placed slightly more forward. Each is somewhat larger in diameter than the ovary. The *vasa deferentia* are united near the cirrus pouch into a single, short vessel. The cirrus pouch is elongate and regularly cylindriform, three times as long as broad. Oval seminal vesicle (44 μ long by 26 μ in diameter) opening to a serpentiform prostatic and penial vessel. Following this, is an oval atrium opening to the genital pore (sphincter).

b) *Female*: (fig. 6) Ovary pyriform, delivering its oocytes to the conic oviduct and thence to a somewhat inflated insemination chamber into which opens, on one side, the *receptaculum seminalis,* and from which proceeds, on the other side, Laurer's canal. The oviduct then continues and arrives in the ootype, surrounded by the Mehlis' glands. The short, united vitellagenous duct opens into the ootype. The immature eggs are then propelled through the long uterus, in which they undergo slow maturation. The uterus proceeds backwards in numerous convolutions, the last of which is near the end of the excretory bladder; it then returns forward in other numerous convolutions and opens into the genital atrium.

In the present immature specimen, only two eggs are to be seen. They are probably unfertilized, the *receptaculum seminalis* being empty.

Of the two vitellagenous ducts, only the right one contains some vitelline follicles.



Zonorchis meyeri, new species. Fig. 1, entire female.

Figures 2, 3, 4, anteromedian, anteroexternal, and posteroexternal papillae on oral sucker. Fig. 5, testis. Fig. 6, ovary.

The entire female genital tract is displayed under ideal conditions because of the absence of eggs, which generally impair vision in mature worms, so that Laurer's canal is apparent to its dorsal aperture.

Excretory system:

Two long, slender and straight vessels converging into a long, large and somewhat torose bladder and forming a typical "Y." The bladder connects to the terminal excretory pore through a narrow tubule 60 μ long.

E. TYPE MATERIAL. The holotype, a unique specimen, is deposited in the George Williams Hooper Foundation, University of California Medical Center, San Francisco 22, California.

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 5, pp. 69–90; 9 figs.; 1 table January 31, 1966

REDESCRIPTION OF *AMPHISBAENA VERMICULARIS* WAGLER, WITH COMMENTS ON ITS RANGE AND SYNONYMY (AMPHISBAENIA: REPTILIA)[1]

By

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INTRODUCTION

Few names in the proverbially confused genus *Amphisbaena* have been the subject of as many misconceptions as *A. vermicularis* Wagler, 1824, the third species therein described, and the type species of *Glyptoderma* Fitzinger (1843). Contributing to this confusion have been the antiquity of the name, the obscure status of the holotype, the extensive range across areas poorly represented in most museum collections, lack of understanding regarding the nature of character variation in amphisbaenids, and the arbitrary identification by authorities.

Thus Boulenger (1885, p. 442) based his description of *A. vermicularis* upon one specimen of *A. dubia* Müller and on a second and disintegrating individual that remains to be identified. Burt and Burt (1931, p. 240) included a specimen of *A. mitchelli* Procter, a mistake later repeated by da Cunha (1961, p. 168; *cf.* Gans, 1964). Amaral (1935b, p. 255 and in later papers) erected a new race for specimens from northeast and central Brazil, and included the perfectly valid form "*Amphisbaena*" [= *Bronia*] *brasiliana* and *A. steindachneri* in synonymy. He also considered *A. vermicularis* to be conspecific with *A. darwini* Duméril and Bibron, a valid form of southern Brazil and Uruguay (*cf.* Vanzolini, 1949, p. 105, for comments on these decisions). Even Schmidt (1936, p. 30) described specimens of *A. vermicularis* from Rio Grande do Norte, Brazil, as *A. spixi* with-

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[1] Notes on amphisbaenids 20.

out considering the one valid amphisbaenid described from specimens brought back by the Spix expedition.

The present standardized (Gans and Alexander, 1962) redescription and synonymy is based upon a reexamination of the several types and on some 150 specimens from European, United States, and South American collections. While we are aware of more than sixty papers mentioning the species, we have cited only those involving certain identifications, as most are obviously meaningless without the specimens at hand or are known to have been based on other species.

This discussion gives but the minimal presentation of the major patterns of variation in the meristic characters of this species. Details have been omitted, and no attempt has been made to correlate the observed trends with climatic or other factors, since such correlation represents a project being undertaken by Dr. P. E. Vanzolini and his students.

Vanzolini (1951, manuscript, p. 31) has suggested that *A. mertensi* Strauch, 1881, may well be a race of *A. vermicularis*. Our material does not confirm him, though the sample has not been sufficient to rule out this possibility, and it will be discussed in a later paper.

We are grateful to the following curators of institutions (identified by abbreviation symbols in parentheses) for loan of specimens in their care: Charles M. Bogert, and Richard G. Zweifel, American Museum of Natural History, New York (AMNH); Miss Alice G. C. Grandison, British Museum (Natural History), London (BM); Alan Leviton, California Academy of Sciences, San Francisco (CAS); Neil D. Richmond, Carnegie Museum, Pittsburgh, Pa. (CM); Hymen Marx and Robert F. Inger, Chicago Natural History Museum, Chicago, Illinois (CNHM); A. S. Rand and P. E. Vanzolini, Departamento de Zoologia, São Paulo, S. P., Brazil (DZ); F. W. Braestrup, Universitetets Zoologiske Museum, Copenhagen, Denmark (KM); Ernest E. Williams, Museum of Comparative Zoology, Cambridge, Mass. (MCZ); Dalcy Albuquerque, Museo E. Goeldi, Belem, Pará, Brazil (MEG); Villy Aellen, Muséum de Genève, Switzerland (MG); Antenor L. de Carvalho and Bertha Lutz, Museo Nacional, Rio de Janeiro, G. A., Brazil (MN); Konrad Klemmer, Senckenbergische Naturforschende Gesellschaft, Frankfurt a. M., Germany (SMF); Heinz Wermuth, Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS); Charles F. Walker, University of Michigan Museum of Zoology, Ann Arbor, Michigan (UMMZ); Doris M. Cochran, United States National Museum, Washington, D. C. (USNM); Joseph Eiselt, Naturhistorisches Museum zu Wien, Vienna, Austria (VM); Heinz Wermuth and G. Peters, Zoologisches Museum der Universität, Berlin, Germany (ZMU); and Walter Hellmich, Zoologische Sammlung des Bayerischen Staates, Munich, Germany (ZSM). Dr. Virginia Cummings drew the specimens and Misses Geraldine Franklin and Charlyn Rhodes furnished technical assistance. The

overall project is supported by grants NSF G-9054, G-21819, and GB-2460 from the National Science Foundation.

Amphisbaena vermicularis Wagler.

Amphisbaena vermicularis Wagler, 1824, p. 73. Terra typica: "in provincia Bahiae," "aux environs de la ville de Bahia," Brazil. HOLOTYPE: ZSM 660/0.

Amphisbaena vermicularis centralis Amaral, 1935, p. 255 (also 1937, p. 1705). Terra typica: "Canna Brava, Goias," Brazil. HOLOTYPE: DZ 6618. PARATYPES: DZ 1925, 6588, 6619-6621, 6673 (Cana Brava); 6575, 6622 (Rio Pandeiro, Minas Gerais).

Amphisbaena spixi Schmidt, 1936, p. 30. Terra typica: "Ceara Mirim, Rio Grande do Norte," Brazil. HOLOTYPE: CAS 49423. PARATYPES: CNHM 64421–64422 (Marx, 1958, p. 453); CAS 49896 (Brazil).

Diagnosis. A medium- to large-sized, elongate form of *Amphisbaena* having a fairly blunt snout; without fusion of head shields; with the prefrontals the largest segments by far; with minimal enlargement of parietals; with generally four supra- and three infralabials; and with a relatively long, cylindrical, bluntly terminating tail. The form has 211 to 254 body annuli; five to seven (generally six) caudal annuli up to the autotomy constriction (at which the tail is autotomized in 23.6 per cent of the specimens); 23 to 30 caudal annuli from the cloaca to the tip of the tail, which may be slightly compressed in a very few specimens; 18 to 26 dorsal and 18 to 25 ventral segments to a mid-body annulus; and four round precloacal pores in all specimens. The tail is characteristically elongate and cylindrical; the species has only lateral sulci. The color of preserved specimens is a uniform brownish dorsally, becoming lighter ventrally. The coloration occasionally gives the impression of being denser along the anterior edge of each annulus, with the fading-out along the side occurring diagonally from posterior to anterior edge of an annulus. The dorsal surface of the tail and of the head are darker, but the intersegmental sutures are lightened, thereby giving the neck a characteristic reticulated pattern.

Geographic variation. The available samples are insufficient for more than a preliminary estimation of trends. Adequate representation is most clearly available for some localities in the states Pernambuco, Bahia, Minas Gerais, and Goiás, though even these states hardly show a complete sampling. The records for Pará come from enough sources to suggest that *A. vermicularis* occurs in that state, though the specimens may not actually stem from the (rain forest?) sites from which they are recorded. The São Paulo and Rio de Janeiro records are probably spurious, but there is no reason to doubt the Bolivian one, so that the species may well extend close to the foothills of the Andes. Unfortunately there is a large, but disappointing (since probably composite) series labeled with such central Brazilian place names as Borba, Cuyaba, and Rio Branco. These Vienna Museum specimens stem from the Natterer collection, known to have become confused (Gans, 1955), and internal evidence suggests that this is indeed the case.

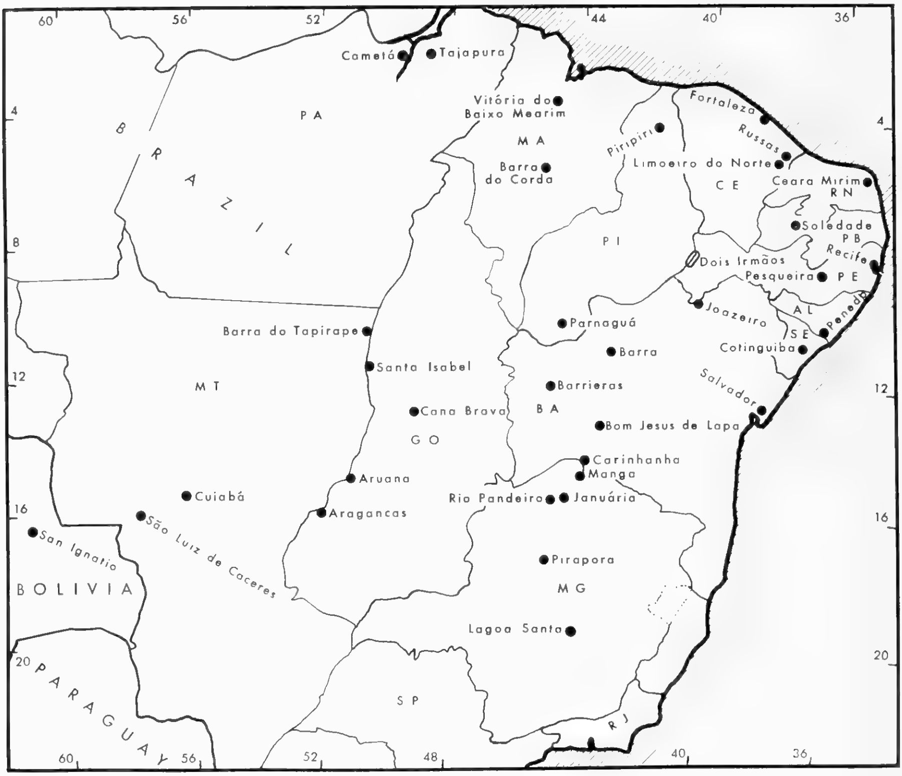


FIGURE 1. *Amphisbaena vermicularis.* Sketch map to show localities mentioned in text.

The general pattern of geographical variation is highly complex, and shows only a few sharp boundaries and almost no concordance. While there are several instances of marked local differences for individual characters, as yet there is no reason for recognizing subspecies within this assemblage. Publication of the available data may permit future workers to test and refine the roughly sketched pattern.

(1) *Number of body annuli.* Figure 2A presents a summary of the variation of number of body annuli. The highest values are found in the northeast where *A. vermicularis* overlaps *A. pretrei* (Gans, 1965) which also has high values. Somewhat lower values are found in Goiás and possibly in a narrow corridor extending into Bolivia. The two latter groupings are separated by an area of very low counts in inland Bahia. Equivalent low counts are found in southern Minas Gerais (Lagoa Santa), while southern Bahia, northern Minas Gerais specimens, as well as those from the northernmost parts of the species range, have intermediate values.

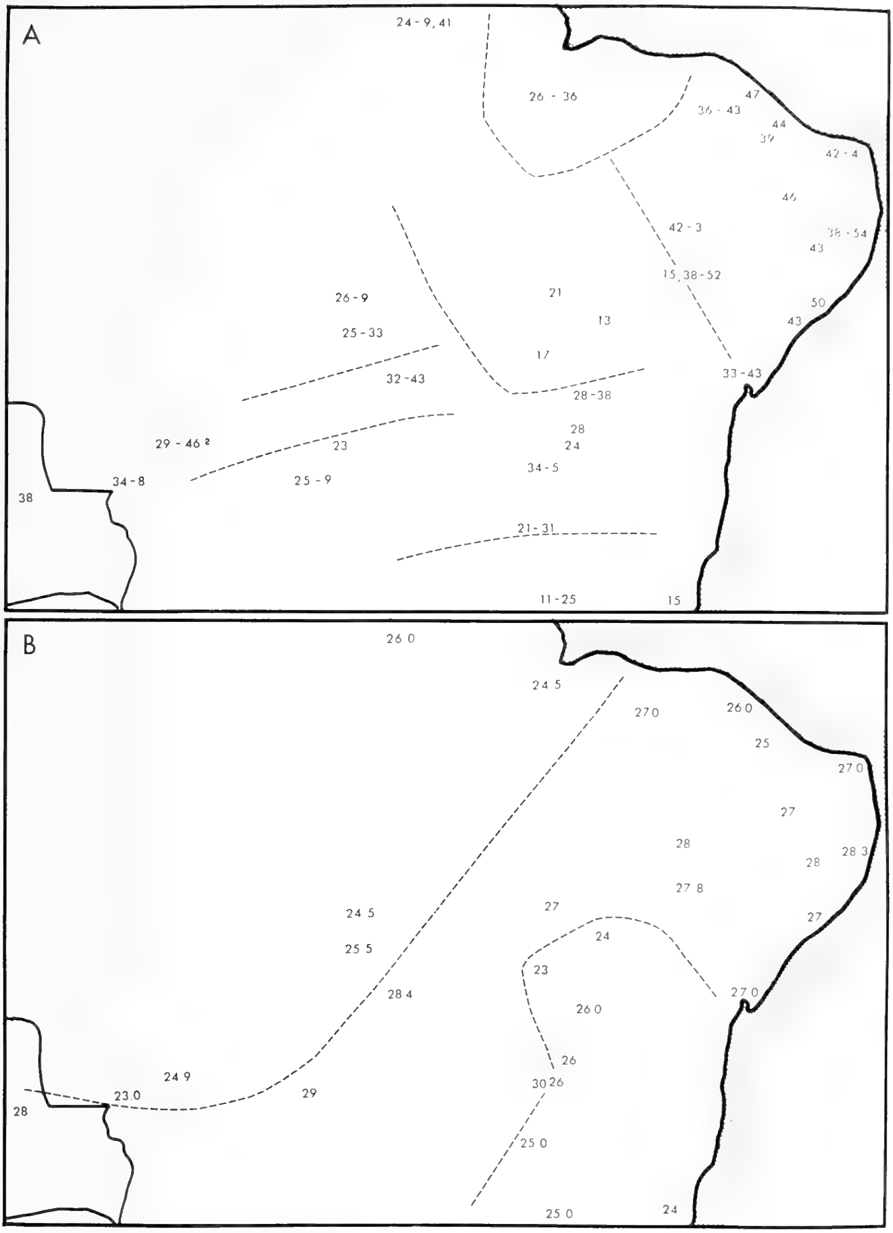


FIGURE 2. *Amphisbaena vermicularis.* Sketch maps (traced from the central portion of fig. 1), to show the pattern of character variation. The lines are added to facilitate visualization; they are obviously not calculated. A. Counts of body annuli with the first numeral (= 2) omitted. B. Counts of caudal annuli. Means are shown to one additional significant figure.

(2) *Number of caudal annuli.* Figure 2B presents a summary of the variation of this character. Again there is a tendency for high values in the northeast and in a belt inland to Bolivia. Yet the borders of the region are shifted significantly from those for high numbers of body annuli. There is no significant difference between the counts of the southern and the northern populations. The high values in the zone of sympatry with *A. pretrei* are of interest as these increase the difference between the two forms.

(3) *Number of segments to a mid-body annulus.* This character shows great intraspecimen and intrasample variation, which masks any geographic variation. The reality of the trends in the present material will have to be checked on the basis of larger series.

(4) *Body size. Amphisbaena vermicularis* is a much smaller species than *A. pretrei.* Histograms for several geographically defined populations (fig. 3) do not furnish grounds for assuming differences between them. The northern samples are obviously too small to permit comment.

(5) *Relative tail length.* The tail of *A. vermicularis* is relatively longer than that of *A. pretrei* or *A. leucocephala.* Tendency to intermediacy occurs in specimens of *A. vermicularis* from outside of the region of sympatry. Specimens from Bahia and Minas Gerais have the longest, and those from Ceara to Sergipe and Goiás to Bolivia relatively the shortest tails, though there is extensive scatter and broad overlap between samples (fig. 3). It is interesting to note that the sample from Bom Jesus de Lapa differs from the rest of the Bahia sample by having a significantly shorter tail, as do some of the Vienna Museum specimens from "Mato Grosso." These samples show no other correlated differences.

(6) *Color pattern.* A number of specimens from localities in Pará, Goiás, Minas Gerais, and Bolivia show an accentuation of the pigment along the anterior edge of each segment (*cf.* fig. 6). Only in Santa Isabel is this pattern found in all specimens of a sample; its frequency is low in other cases. Such accentuation (as opposed to an evenly distributed dorsal pigmentation) is always restricted to the anterior segmental edge, rather than covering half the segment as in *A. mertensi* Strauch (Gans, manuscript).

(7) *Head segmentation.* The parietals are generally small segments but slightly larger than the oculars, though they very occasionally exceed the frontals in size. Considerable variation exists within the species, indeed between the left and right sides of some specimens (fig. 5), but this does not seem geographically correlated or constant within single populations. The specimens with enlarged parietals are thus scattered over the entire range. Furthermore, the enlargement is extensive relative only to the condition found in most specimens of *A. vermicularis*; it almost never attains the proportions shown by specimens of *A. mertensi.*

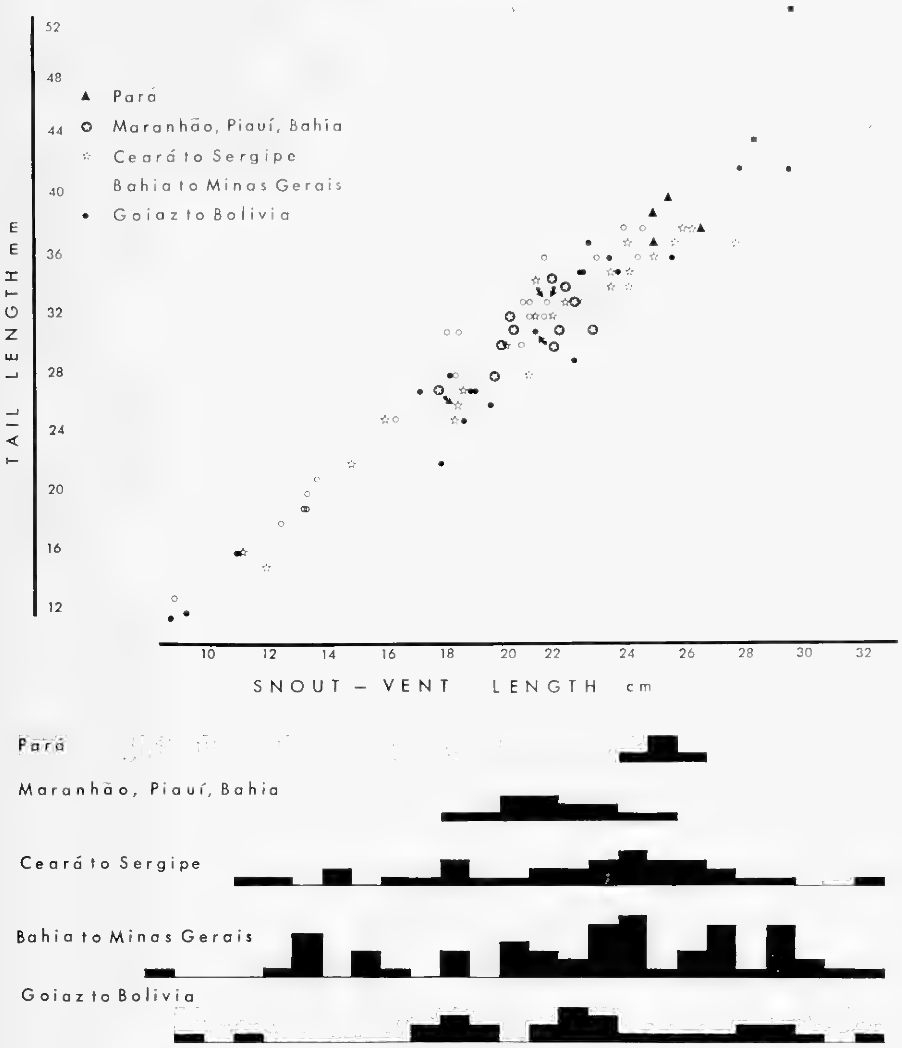
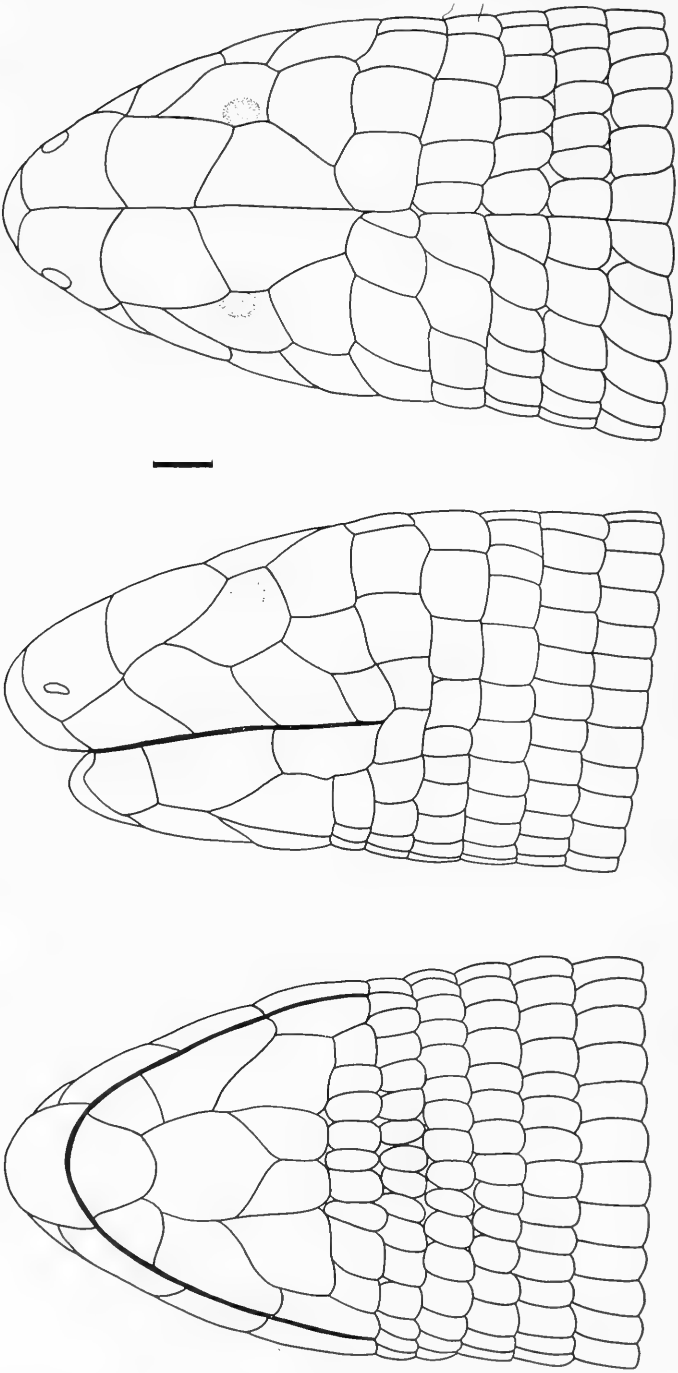


Figure 3. *Amphisbaena vermicularis.* Scatter diagram of tail-length versus snout-vent length and histograms for snout-vent length for the several geographical samples. The smallest vertical unit stands for a single specimen.

(8) *Precloacal pores.* All specimens except three out of a series of seven from Cana Brava, Goiás have four precloacal pores. The latter series has four specimens with four, two with five, and one with six pores. This suggests some similarity to the northern samples of *A. mertensi* (which have six or more pores).

Notes on the types. The holotype of *A. vermicularis* was collected by Spix and with other materials from his collection deposited in Munich where it



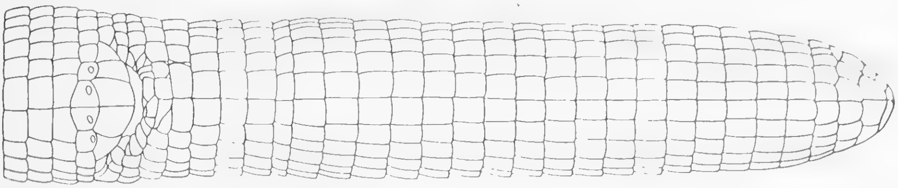


Figure 5. *Amphisbaena vermicularis.* Ventral view of cloaca and tail of ZSM 660/0, holotype from Bahia, Brazil. The line equals 1 mm. to scale. Drawn by Dr. V. Cummings.

remains (ZSM 660/0). The specimen is clearly the type and has been reported on at least twice (Strauch, 1881, col. 73; Hellmich, 1960, p. 97). Burt and Burt's claim (1931, p. 240) that the holotype was part of the (Wied) collection in the American Museum, is hence wrong. The specimen was available for analysis.

The typical material of *A. v. centralis* was in 1953 transferred from the Instituto Butantan (IB) to the Departamento de Zoologia (DZ), both of São Paulo, Brazil, and recatalogued there. Its data were used in the analysis. They show no differences justifying the retention of this race and thus confirm Vanzolini's remarks (1949).

All specimens referred to in Schmidt's 1936 study have been available for analysis. They show that the types of *A. spixi* are clearly assignable to *A. vermicularis* and the name thus belongs in the synonymy of that species.

Description. Figure 4 of the present paper shows views of the head of the holotype; fig. 5 shows the ventral surface of the cloaca and tail; and figs. 6 through 9, inclusive, show details of segmentation and coloration. Figure 3 shows body proportions of specimens from different regions. Meristic data are listed in table 1.

This is a medium- to large-sized species of *Amphisbaena* of a uniform brownish color dorsally, lighter ventrally, with the color dropping out gradually along the sides of the trunk. The lighter ventral coloration extends anteriorly onto the supralabials and posteriorly onto the anterior portion of the tail. In general the dorsal segments are evenly pigmented, without central pigment emphasis, but the intersegmental sutures are lightened. The dorsal surfaces of the head (nasals through parietals) and of the tail are more densely pigmented. The ventral surfaces, including the infralabials, are light colored. The pigment line first dips ventrad in the nuchal region and then rises again. The sides of the trunk dorsolateral to the cloaca exhibit half-moon-shaped zones of denser pigmentation that vary in extent and that may even meet at the dorsal

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Figure 4. *Amphisbaena vermicularis.* Dorsal, lateral, and ventral views of the head of the holotype ZSM 660/0, from Bahia, Brazil. The line equals 1 mm. to scale. Drawn by Dr. V. Cummings.

TABLE 1. *Data for specimens of* Amphisbaena vermicularis.

Collection No.	*Body, Lateral, and Caudal Annuli*	*Dorsal and Ventral Segments*	*Chin Segments*	*Labials*	*Cloaca*	*Total Length*
AMNH 1096	248+5+(7)26	20+20–1	3+8	4+3	4+7+15	225+30
CAS 49 896	252+3+(6)28	22+22	2+(5)+9	4+3	4+6+12	213+30
MSNUP 109	240+4+(7)28	20+22	4+7	3+3	4+8+14	261+39
SMF 11820	243+3+(5)28	20+21–2	2+9	4+3	4+8+13	270+38
ZMU 1381	218+4+(5)26	20+19–20	2+9	4+3	4+7+14	283+46
MHNP 1077	242+4+(6)27	20+22	2+9	4+3	4+8+15	248+39
USNM 6035A	224+4+(6)26	22+22	2+9	4+3	4+8+15	252+37
USNM 6035B	229+5/4+(5)26	22–3+22	2+9	4+3	4+6+13	257+40
VM 19A	226+4+(6)25	20–2+20	2+8	4+3	4+7+14	268+38
VM 19B	229+3/4+(6)27	21–2+22	2+9	4+3	4+8+14	252+39
MCZ 4658	241+4/3+(5)x	20+24	2+11	4+3	4+8+—	250+x
DZ 7053	234+4+(5)x	21+24–7	2+8	4+3	4+8+15	259+x
DZ 6377	234+4+(5)25	21–2+22–4	2+9	4+3	4+8+15	201+30
DZ 6378	226+3+(5)25	20–2+23–4	2+6	4+3	4+8+12	222+34
DZ 6379	233+4+(6)25	20–2+22–3	2+8	4+3	4+8+14	220+31
DZ 6380	231+3/4+(5)24	21–4+24	2+(1)+8	4+3	4+9+14	231+31
DZ 6381	227+4+(6)24	22–3+23–4	2+7	4+3	4+6+13	198+28
DZ 6382	230+4+(5)x	21–2+24–5	2+9	4+3	4+7+14	243+x
DZ 6383	232+4+(5–6)24	18–9+21–2	2+8	4+3	4+7+15	205+31
DZ 6458	228+4+(5)27	20–1+20–2	2+(1)+8	4+3	4+8+14	216+33
DZ 6459	236+3+(6)27	21–2+22–3	2+4+8	4+3	4+8+13	212+31
DZ 6460	235+3+(5–6)27	21+22–3	3+8	4+3	4+8+12	205+31
VM 12335-1	221+4+(5)27	23–4+22–4	2+9	4+3	4+8+14	203+32
DZ 6447	239+4+(5)27	21+21–2	2+8	4+3	4+7+12	227+29
DZ 3571	243+4+(5)27	20–1+22	5+(2)+9	4+3	4+8+14	238+33
MN 2101	241+4+(5)x	20–1+22	3+8	4+3	4+6+13	316+x
MN 2102	242+4+(6)25	21–2+22–3	2+8	4+3	4+7+12	287+37
MN 2103	236+4+(6)27	20–1+21–2	2+10	4+3	4+8+14	252+36
MN 2104	243+4+(6)25	20–1+22–3	2+9	4+3	4+7+14	210+28
MN 2090	244+4+(6)x	21–2+23–4	2+8	4+3	4+6+15	254+x
SMF 57919	239+3+(6)25	19–20+22	3+10	4+3	4+7+12	259+37
CAS 49423	244+4+(5)27	19–21+20–2	2+(3)+9	4+3	4+18+13	188+27
CNHM 64421	242+4/3+(7)x	20+20	——	——	4+8+16	144+x
CNHM 64422	244+3/4+(6)27	20+20–2	2+8	4+3	4+6+12	202+30
DZ 6474	246+4/3+(6)27	23–4+23	2+(1)+9	4+3	4+6+14	265+38
BM 87.9.5.4	247+3+(6)28	20+20	2+9	4+3	4+6+12	243+34
BM 87.9.5.5	240+4+(6)27	24+22	3+10	4+3	4+8+12	191+27
GM 983-59	249+4+(6)28	19–20+20	5+9	3+2½	4+6+14	121+15
MCZ 1464	240+4+(6)29	20+22–3	2+(3)+9	4+3	4+6+12	243+37
USNM 59067	246+4+(6)28	20+22	3+10	3+2½	4+6+12	238+35

TABLE 1. *Continued.*

Collection No.	*Body, Lateral, and Caudal Annuli*	*Dorsal and Ventral Segments*	*Chin Segments*	*Labials*	*Cloaca*	*Total Length*
USNM 59068	254+4+(6)x	———	5+9	3+2½	4+6+12	233+x
SMNS 3662A	242+¾+(6)x	20–1+22–3	3+(2)+11	4+3	4+6+—	227+x
SMNS 3662B	238+4+(6)x	22+21–2	3+9	4+3	4+7+13	176+x
DZ 2670	239+4+(6)27	22+22	2+(1)+9	4+3	4+7+15	113+16
DZ 2671	250+3+(6)29	20+21	2+8	4+3	4+8+14	185+25
MN 1765	247+3+(6)28	20–1+22–3	3+9	4+3	4+7+14	262+38
MN 2087	246+4+(6)28	21–2+23–4	3+9	4+3	4+7+13	244+35
MN 2088	254+4+(6)30	19–20+23–4	5+9	4+3	4+8+14	161+25
MN 2083	246+3+(6)x	20–1+21–2	4+8	4+3	4+———	229+x
MN 2084	—————	19+21–2	4+9	4+3		
MN 2085	244+4+(6)28	18–20+21–2	3+10	4+3	4+7+13	218+32
MN 2086	242+¾+(7)29	22–3+22	2+8	4+3	4+7+—	222+33
MN 2089	253+3+(7)28	20–1+23–4	3+8	3½+2½	4+8+—	212+32
MN 2091	242+4+(5)x	20–1+20	3+9	4+3	4+7+15	233+x
MN 2092	243+¾+(6)28	20–1+22	5+10	4+3	4+8+—	186+26
CM 1046	250+3+(6)27	20+20	——	3½+3	4+———	150+22
KM R-4462	243+4+(7)x	20–2+22	2+(3)+9	3+3	4+8+13	284+x
ZMU 9387A	237+4/5+(6)28	20+20–1	2+10	4+3	4+6+11	210+33
DZ 6446	243+3+(6)29	19–20+22	2+9	4+3	4+7+12	215+36
ZSM 660/0	223+3/2+(6)25	22–4+21–2	2+9	4+3	4+6+—	216+33
MN 2110	213+3+(6)x	24–6+24	3+8	4+3	4+8+13	327+x
MN 2111	242+3+(4)28	20–2+21–2	2+8	4+3	4+8+14	233+36
MN 2112	239+4+(7)30	19+20	2+5+8	4+3	4+8+14	182+31
MN 2113	245+4/3+(6)x	18–20+23	3+9	4+3	4+8+14	243+x
MN 2114	237+5/4+(6)30	20–1+22	2+3+9	4+3	4+8+14	186+31
UMMZ 103073A	237+4+(6)27	21–2+20–2	2+9	3+2½	4+8+13	305+46
UMMZ 103073B	236+4+(6)x	22+23–4	2+8	3+2½	4+6+12	274+x
UMMZ 103073C	241+4+(5)28	20+22	2+2+(10)	3+2½	4+8+13	250+38
UMMZ 103073D	242+4/3+(6)x	20+22	3+8	3+2½	4+7+14	248+x
UMMZ 103073E	237+4+(6)28	18–21+22	3+2+9	3+2½	4+7+10	165+25
VM 12330	252+3+(5)x	20+22	5+9	4+3	4+6+14	320+x
VM 20A	233+4+(6)27	22+24	2+8	4+3	4+8+13	294+45
VM 20B	237+4+(6)x	19–20+22	4+9	——	4+6+14	260+x
VM 20C	239+4+(6)x	22+24	4+10	4+3	4+8+14	242+x
VM 12	229+3+(5)24	22+24	2+10	4+3	4+6+14	225+33
MN 2109	220+4/3+(5)x	23–5+21–2	2+3+10	4+3	4+8+16	235+x
UMMZ 103072	217+4+(5)23	22+24–5	2+9	4+3	4+6+16	300+45
MN 2108	230+2+(7)26	20+20–2	2+8	4+3	4+8+13	240+33
MN 2115	228+3+(6)26	22–4+22–3	2+9	4+3	4+8+14	268+36
UMMZ 103071A	228+3+(6)26	24+22	2+7	4+3	4+8+13	325+45

Table 1. *Continued.*

Collection No.	*Body, Lateral, and Caudal Annuli*	*Dorsal and Ventral Segments*	*Chin Segments*	*Labials*	*Cloaca*	*Total Length*
UMMZ 103071B	234+4⁄3+(6)26	20+21–2	2+(3)+8	4+3	4+6+12	233+32
UMMZ 103071C	238+4+(5)x	23–4+24	2+(5)+11	4+3	4+7+12	237+x
MN 2107	228+4+(6)x	23–4+22	3+(1)+10	4+3	4+8+14	288+x
UMMZ 103070	224+3+(6)26	24+24	2+10	4+3	4+6+13	292+44
MCZ 3724	235+4+(7)x	22+24	2+9	4+3	4+8+10	270+x
UMMZ 103068A	235+4+(7)26	22+22–3	2+8	4+3	4+5+14	157+20
UMMZ 103068B	234+4+(6)x	22+22	2+10	4+3	4+6+12	137+x
DZ 6575	235+3+(7)30	20+24	3+8	4+3?	4+8+15	274+46
DZ 6622	x+(6)x	24+24	2+11	4+3	4+8+12	———
MN 2105	231+3+(6)25	21–2+19–20	4+10	4+3	4+8+13	215+32
MN 2106	221+3+(6)26	20+19–20	4+9	4+3	4+6+14	210+32
UMMZ 103069A	224+3+(5)24	23+23	2+8	4+3	4+7+12	308+44
UMMZ 103069B	226+4+(6)25	22+22	2+(1)+8	3½+2½	4+6+13	207+30
KM R-4444	218+4+(5)25	22+24	2+10	4+3	4+8+14	247+36
KM R-4445	213+4+(5)23	24+22	2+9	4+3	4+6+16	248+38
KM R-4446	215+4+(5)25	22+20	2+10	4+3	4+6+13	271+42
KM R-4447	219+4+(6)x	22+20	2+10	4+3	4+6+—	272+x
KM R-4449	217+4+(6)25	22+22	———	———	4+6+14	126+18
KM R-4450	217+4+(6)26	20–1+20	2+10	4+3	4+7+12	242+38
KM R-4451	219+3+(5)24	22–3+20–2	2+10	4+3	4+7+15	228+33
KM R-4452	224+4+(6)x	22–3+23	2+9	4+3	4+8+14	298+x
KM R-4453	224+3+(6)27	19–22+20	2+8	4+3	4+7+14	138+21
KM R-4454	217+3+(5)26	22+21–2	2+8	4+3	4+6+13	134+19
KM R-4455	212+3+(6)24	22+22	2+9	4+3	4+6+13	158+23
KM R-4456	224+4+(5)25	20+20	2+10	4+3	4+6+14	218+35
KM R-4457	221+4+(5)25	22+22	2+10	4+3	4———	208+33
KM R-4458	214+¾+(5)25	20–2+20	2+10	3½+2½	4+7+14	185+28
KM R-4459	221+4+(6)25	21–2+22	2+10	4+3	4+6+14	135+20
KM R-4460	225+4+(5)26	21+21–2	2+9	4+3	4+6+12	135+19
KM R-4461	225+4+(5)26	20+20	2+9	4+3	4+8+14	90+13
KM R-4463	220+4+(6)24	20+22	2+10	4+3	4+8+15	273+40
MN 1425	220+4+(6)26	21–3+21–3	2+9	4+3	4+8+12	277+42
MN 1426	211+3+(6)24	22–3+20–2	2+9	4+3	4+6+14	157+22
MCZ 20651	235+4+(4)x	20+20	3+9	3½+2½	4+6+11	307+x
VM 12335-2	215+4+(5)24	20+18–9	3+8	3½+2½	4+7+12	237+30
DZ 1925	232+3+(6)29	21–3+20–1	3+9	4+3	4+6+15	245?+x
DZ 6588	238+4+(6)29	23+22–4	3+8	4+3	6+7+12	111+16
DZ 6618	240+¾+(7)29	22–3+24	3+10	4+3	4+8+14	298+42
DZ 6619	238+5+(5)27	21–2+24–6	3+11	4+3	4+8+13	237+36
DZ 6620	236+4+(5)26	20–1+22	2+(4)+10	4+3	5+8+13	183+28

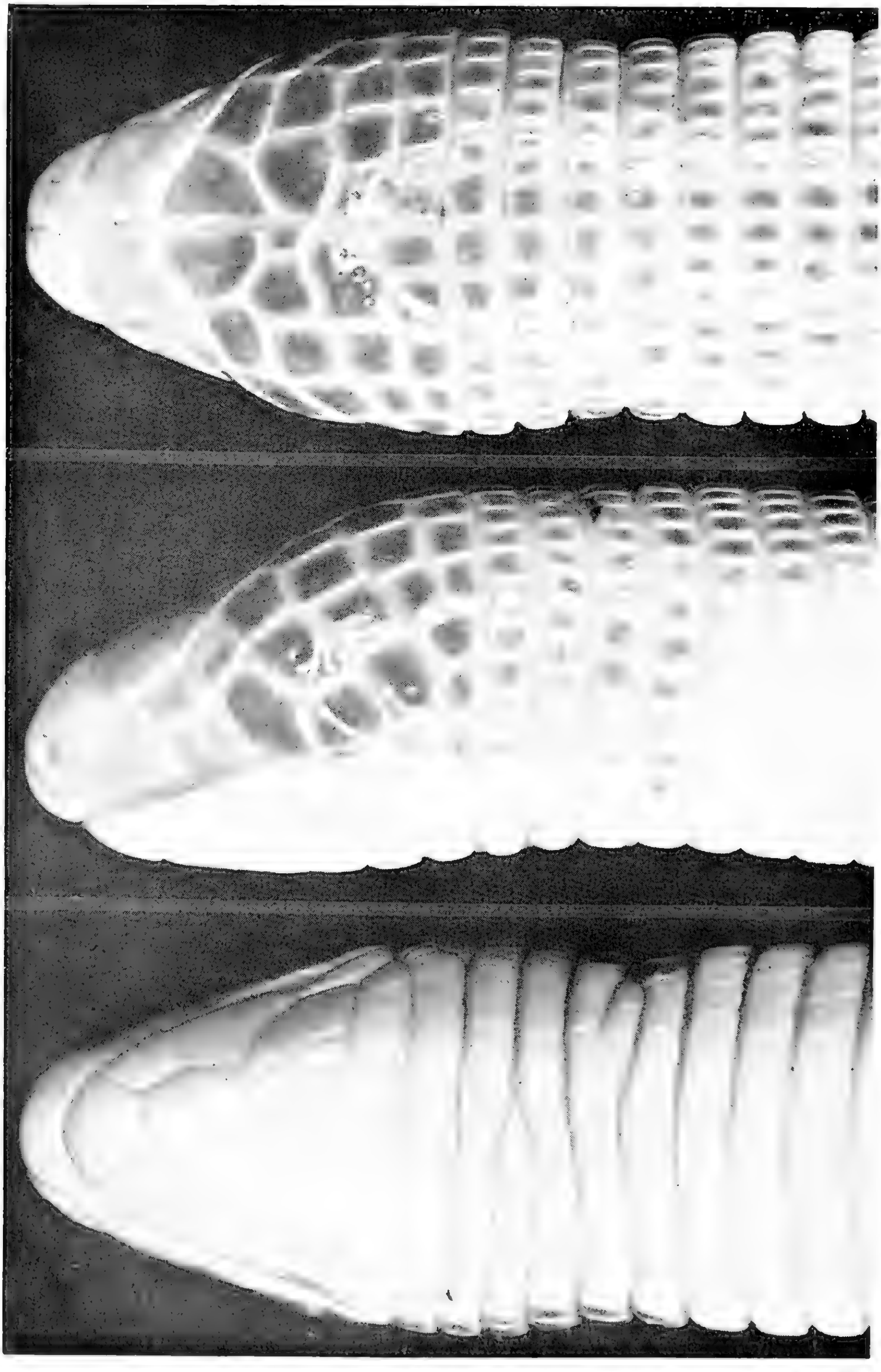
TABLE 1. *Continued.*

Collection No.	*Body, Lateral, and Caudal Annuli*	*Dorsal and Ventral Segments*	*Chin Segments*	*Labials*	*Cloaca*	*Total Length*
DZ 6621	232+3+(5)x	21–2+24	2+(2)+10	4+3	4+8+15	235+x
DZ 6673	243+4+(6)29	22+24	3+8	4+3	5+8+14	227+35
AMNH 90268	227+¾+(6)x	23–5+21	2+9	4+3	4+8+12	299+x
AMNH 90269	233+3+(6)26	24+22	2+8	4+3	4+8+14	281+42
AMNH 92916	229+3+(6)x	20–2+21	2+8	4+3	4+8+14	271+x
DZ 6500	225+4+(6)25	22+23	2+9	4+3	4+7+12?	240+35
DZ 2526	223+¾+(6)x	22–3+23–4	2+9	4+3	4+8+13	266+x
MPEG 194	229+4+(6)29	20+20	2+8	4+3	4+8——	173+27
MPEG 225	225+3+(6)x	20+20–1	2+7	4+3	4+8+14	325+x
MPEG 576	228+4+(5)x	20+21–2	2+8	4+3	4+8+14	307+x
MN 1766A	229+3+(5)24	22–3+22–3	2+10	4+3	4+8+14	225+29
MN 1766B	226+4/3+(7)25	22–3+22	2+10	4+3	4+8+14	180+22
VM 12331-1	230+5+(6)28	22–4+23	2+10	4+3	4+6+13	298+51
VM 12331-2	246+4+(6)24	19–20+20–3	4+8	4+3	4+8+13	197+26
VM 12331-3	245+3+(7)25	19–20+20	5+9	4+3	4+8+16	212+27
VM 12331-4	237+4+(5–6)24	18+19–20	3+9	4+3	4+9+14	188+25
VM 16735-1	237+3+(6)27	21–2+22	3+7	4+3	4+8+15	192+27
VM 16735-2	236+3+(7)25	18–20+20	3+9	4+3	4+6+13	190+27
VM 12332-1	229+4+(6)26	19+21	3+8	4+3	4+6+14	286+44
VM 12332-2	234+¾+(6)26	19–20+22	4+8	4+3	4+8+13	212+31
VM 12332-3	229+3+(6)27	18+20–1	2+9	4+3	4+6——	228+35
MN 1777A	234+5+(6)22	20–1+21–2	5+11	4+3	4+8+15	94+12
MN 1777B	238+4+(7)24	20–1+20–1	3+6	4+3	4+8+14	258+36
ZSM 226/33	238+3+(6)28	18+20	3+8	4+3	4+8+12	230+37

midline. The segment pigmentation in these zones is accentuated in the segmental center, yielding a markedly different pigmentation pattern.

A certain number of specimens (see Geographic Variation) have the anterior edge of the segments more densely pigmented or accentuated. This arrangement is generally combined with an overall darkening of the pigmentation. In such specimens there is often a roughly diagonal pigment dropout across each annulus, and the anterior edge of the ventral segments may also be accentuated by a series of posteriorly fading half-moons.

The head segmentation is characterized by lack of major fusions, by the very large prefrontals, and generally by the absence of parietal enlargement (see Geographic Variation). The parietal region commonly shows irregularities involving fusions within annuli and between adjacent annuli. The tip of the snout is relatively blunt and slightly produced; however, the bulging temporal area



in adults is expressed by a considerable widening posterior to the eye. This yields a more pointed impression. The snout is almost as deep at the level of the nares as at the eye; it rises over the temporal bulges. The lateral projection of the lower jaw is triangular. The nuchal constriction is faintly indicated and there is only a very gradual increase in body diameter to a thickness equivalent to that of the head. The trunk is faintly oval in cross section continuing with a constant diameter until the level of the cloaca, where it is often reduced approximately one-third its former proportions.

The rostral is slightly larger than the first supralabial; it shows only a small triangular tip in dorsal view. Pairs of large, rectangular nasals, equal-sized prefrontals, and variously polygonal frontals, follow in sequence along the dorsal midline of the head. The nasal–prefrontal, and prefrontal–frontal sutures are always posteriorly concave. The posterior sutures of the frontals may be angled or form a continuous line. When the parietals are enlarged they are generally smaller than the prefrontals. The posterior edge of the frontals lies at a level approximately equivalent to the level of the suture between third and fourth supralabials. There are four supralabials; the first of these is the longest, the second the tallest, and the fourth the smallest in all dimensions. Only three specimens have the third supralabial split by a diagonal suture forming a small triangular supralabial and a large infraocular (rather than a large supralabial as in *A. pretrei*). The angulus oris, which ordinarily lies after the fourth supralabial, sometimes lies slightly anterior to this point, but it always lies along the posterior half of this segment. The supralabial sutures run anteriorly at angles of 45°, 70°, 60°, 60°, and 70° to the edge of the mouth. The ocular is diamond-shaped; its anterior tip is more acute than its posterior. Ventrally it contacts the posterior half of the second and all of the third supralabials' superior edges, and dorsally the posterior half of the prefrontal's lateral edge. Posteriorly the ocular contacts the entire anterior edge of the top and the dorsal tip of the next lower temporals; these are two approximately equal-sized, or two large and one smaller, segments that lie between the superior edge of the fourth supralabials and the lateral edges of the frontals. The ocular may also be in point contact with the frontal. The eye is large and clearly apparent.

The mental corresponds to the rostral in extent along the edge of the mouth. Centrally it sends back a broad, short, posteriorly convex process, that inserts into the anterior aspect of the large shield-shaped postmental. The anterior aspect of the postmental is flanked by the medium-sized first and the three times as large second infralabials. Its sides are contacted, along their posterior third,

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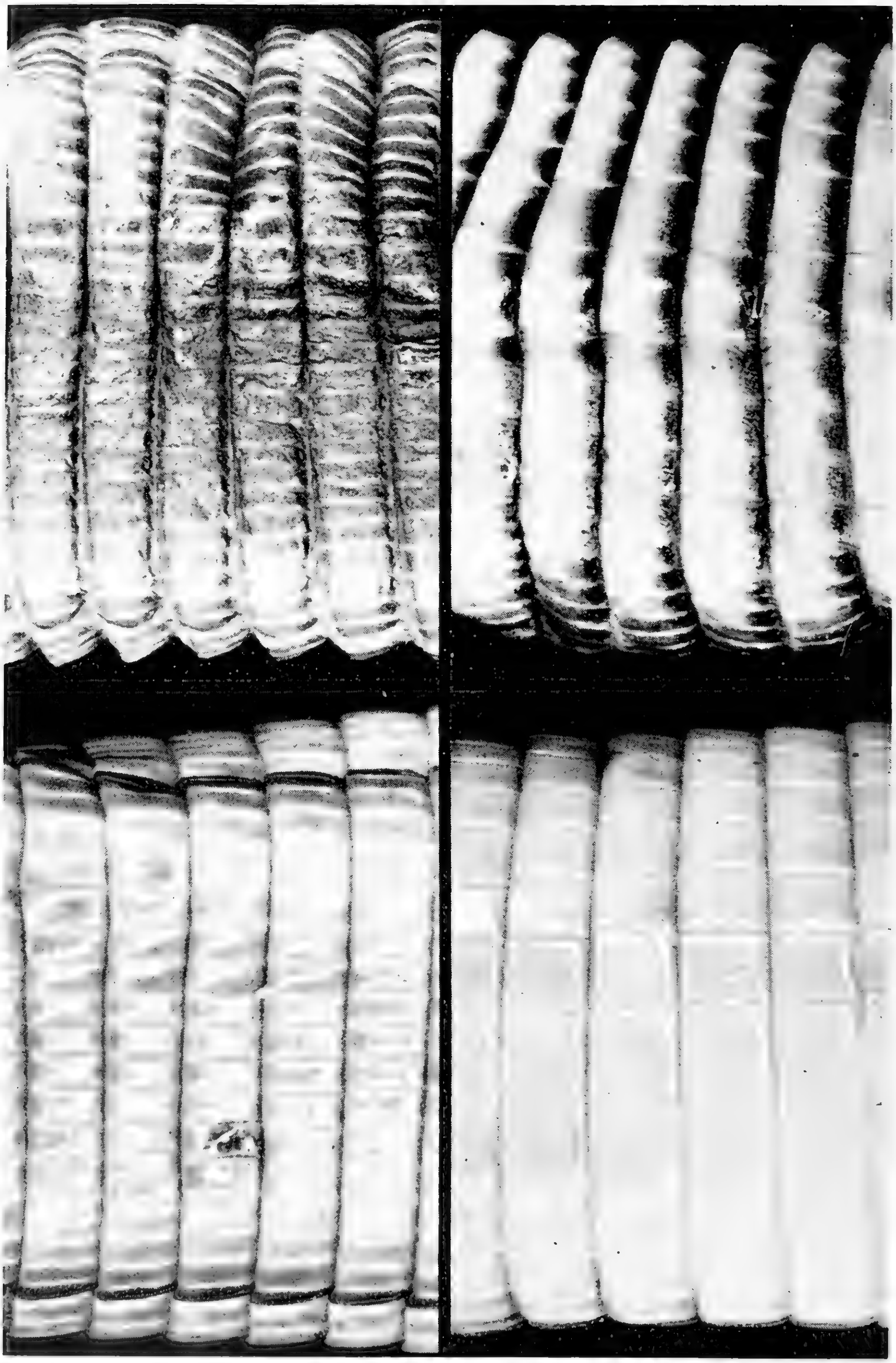
Figure 6. *Amphisbaena vermicularis*. Dorsal, lateral, and ventral views of the head of MN R 2087 from Afogados, south of Recife, Pernambuco, Brazil. Note the asymmetrical parietals (fewer than 10 per cent of the samples have symmetrical nuchal shields) and the light margins of the head shields.



by the anterior tips of the large triangular malars, though either or both of a pair of smaller triangular segments, seemingly divided off their medial edges, may reduce the contact distance. Between these, and embracing the obtusely angled posterior aspect of the postmental, are the two larger central elements of the first, generally the only postgenial row. From one to four smaller segments occasionally form an irregular second postgenial row. The third infralabials are elongate and narrow. A row of 7 to 11, generally 8 or 9, irregularly shaped postmalar segments lies between the third infralabials; the lateralmost members of this row may or may not be faintly widened.

The first, second, or third body annuli split at or above the level of the angulus oris to provide two, one, or part of one dorsal intercalated half-annulus. The first, or second body annulus, or the intercalated half-annulus provide the segments of the parietal region. The interannular raphe between first and second generally, that between second and third always, lies in a position normal to the long axis of the trunk.

There are 211 to 254 body annuli (*cf.* fig. 2A) from the back of the fourth supralabial up to and including the pore-bearing precloacals. The first four to five body annuli are narrower than the succeeding ones, and the interannular raphes are deeper and wider than those between more caudad annuli. There is no significant complexing in the ventral region of the first body annuli, though annular asymmetries frequently occur here. The annular pattern is regular along the trunk and only shows modification in the postcephalic region and in the zone immediately anterior to the cloaca. There are no dorsal intercalated half-annuli. There are 18 to 26 dorsal and 18 to 25 ventral segments to a mid-body annulus (one specimen has 26 and another has 27, though these values cannot be checked since the specimens have already been returned). There is but little alignment of intersegmental raphes.

The cloacal region is characterized by a row of four, rarely and irregularly five or six, clearly marked, round to suboval precloacal pores in both sexes. Six to nine segments form the segment-shaped precloacal shield, but only the central six of these are generally of significant size. The postcloacals number 10 to 16; they are tiny slit-shaped segments that enter the cloaca in parallel with the interannular sutures, and only the central pair are widened. There are three to five, generally three or four, lateral annuli, and four to seven, generally five or six, caudal annuli up to and including the markedly narrowed autotomy annulus at which autotomy had taken place in 33 out of 144 specimens. Caudal annuli

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Figure 7. *Amphisbaena vermicularis.* Dorsal (left) and ventral (right) views at mid-body of AMNH 90269 from Santa Isabel, Goiás (top) and MN R 1765 from Afogados, south of Recife, Pernambuco, Brazil (bottom). The heads point to the right. Note the denser pigmentation of the Goiás specimen and the accenting of the anterior portions of the annuli on the ventral surface.

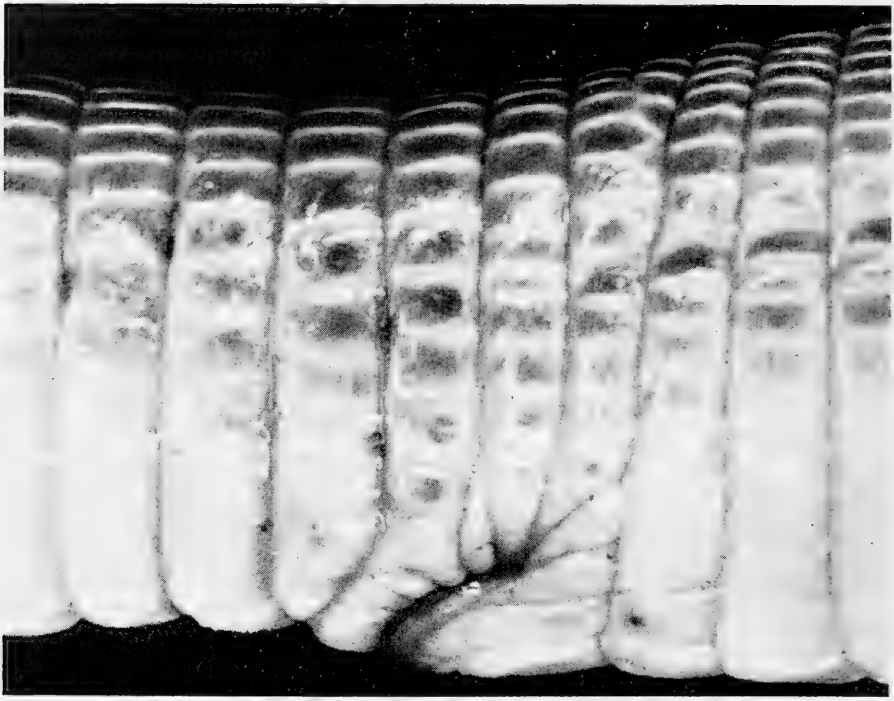

Figure 8. *Amphisbaena vermicularis.* Right lateral view of cloaca of MN R 2114 from Joazeiro, Bahia, Brazil, to show termination of lateral sulcus, and dot pattern on the lateral segments in the cloacal region.

number 24 to 30, all but the terminal pair separated from each other by well-defined and markedly inserted raphes, that often separate even the last ring of segments on the faintly compressed, rounded, caudal tip. The tail is horizontally oval in cross section; at the autotomy annulus it is markedly constricted, and thereafter it swells so that the distal portion is of significantly greater diameter.

The lateral annuli are clearly marked after the twenty-fifth to fiftieth body annulus; at mid-body they are about the width of one of the fringing segments and divided from these by a pair of diagonal lines that divide off their corners. Dorsal sulci are indicated in the neck region by a faint alignment of intersegmental raphes; they are absent at mid-body. There are no ventral sulci, though the median intersegmental sutures are aligned.

The middorsal segments vary from two and one-half to three times as long as wide. The midventral segments are slightly wider than long.

Anatomy. The structure of the palate and of certain groups of head muscles is discussed by Lakjer (1926, 1927). Comments on the remnants of appendicular nerve plexi are included in Carlsson (1887), while details of the visceral circula-

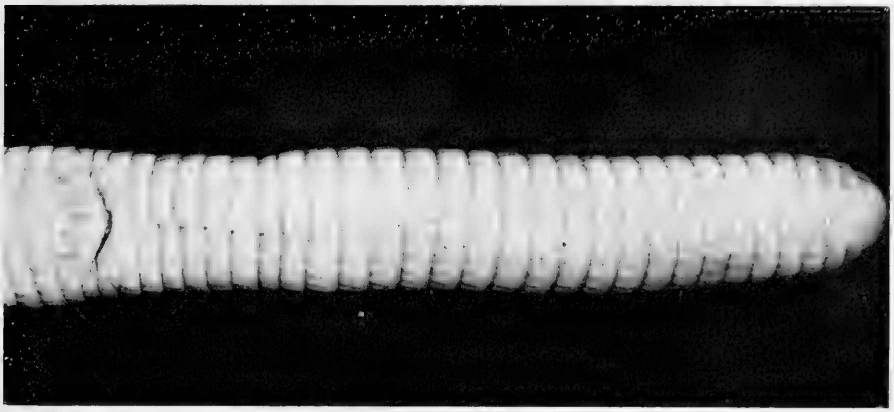

Figure 9. *Amphisbaena vermicularis*. Ventral view of cloaca and tail of MN R 1765 from Afogados, south of Recife, Pernambuco, Brazil.

tion are included in Hochstetter (1898) and Rathke (1857, 1863). Rosenberg (manuscript) describes the hemipenes.

Range. Brazilian lowlands, south of the Amazonian forest and west of the coast, inland into Bolivia, south into Minas Gerais, and Central Mato Grosso.

Distribution records. BRAZIL: —: (Burt and Burt, 1931; Duméril and Bibron, 1839; Schmidt, 1936; Schmidt and Inger, 1951; Strauch, 1881); AMNH 1096; CAS 49896 (paratype *spixi*); MSNUP 109; SMF 11820 (?Mendoza); ZMU 1381. "St. Thomas": MHNP 1077. *Pará*: —: (Burt and Burt, 1930); USNM 6035A-6035B. Cametá, Rio Tocantins: (26 I 1911, no. 83) VM 19A-19B. Tajapura: MCZ 4658. *Maranhão*: Vitoria do Baixo Mearim: DZ 7053. Barra do Corda: DZ 6377–6383. *Piauí*: Piripiri: DZ 6458–6460. Sierra de Parnagua: VM 12335-1. *Ceará*: (Vanzolini, 1949); DZ 6447. Fortaleza: DZ 3571. Mucuripe, Fortaleza: MN 2101–2104. Russas: MN 2090. Limoeiro do Norte: SMF 57919. *Rio Grande do Norte*: Ceará Mirim: (Schmidt, 1936; Schmidt and Inger, 1951); CAS 49423; CNHM 64421–64422. *Paraíba*: Açude Soledade: (Amaral, 1935a, 1935b); DZ 6474 (mentioned by Amaral, but not paratype of *A. centralis*). *Pernambuco*: —: BM 87.9.5.4–87.9.5.5; GM 983: 59; MCZ 1464; SMNS 3662A–3662B; USNM 59067, 59068. Recife: (Vanzolini, 1949); DZ 2670–2671. Recife, Afogados (south of): MN 1765, 2087–2088. Recife, Ypiringa: MN 2083–2086. Pesqueira: (Vanzolini, 1949); MN 2089. Dois Irmãos: MN 2091–2092. *Alagoas*: Barra do Penedo: (Griffin, 1917); CM 1046. *Sergipe*: Cotinguiba: KM R-4462. *Bahia*: —: (Vanzolini, 1949); ZMU 9387A. Salvador: DZ 6446. Salvador, environs: (Wagler, 1824; Hellmich, 1960); ZSM 660/0 (holotype *vermicularis*). Joazeiro: MN 2110–2114; UMMZ 103073A–103073E; VM 12330. Barinha, near Joazeiro: VM 20A–20C. Barra, Cobre de Cabezas, Joazeiro: VM 12. Barrieras: MN 2109;

UMMZ 103072. Bom Jesus de Lapa: MN 2108, 2115; UMMZ 103071A–103071C. Carinhanha: MN 2107. *Minas Gerais*: Manga: UMMZ 103070. Januária: MCZ 3724; UMMZ 103068A–103068B. Rio Pandeiro: (Amaral, 1935b; Vanzolini, 1949); DZ 6575, 6622. Pirapora: MN 2105–2106; UMMZ 103069A–103069B. Lagoa Santa: (Lütken, 1892; Reinhardt and Lütken, 1861; Vanzolini, 1949); KM R-4444–R-4447, R-4449–R-4461, R-4463; MN 1425–1426. *São Paulo*: —: MCZ 20651. *Rio de Janeiro*: —: VM 12335-2. *Goiás*: Cana Brava: (Amaral, 1935b; Vanzolini, 1949); DZ 1925, 6588, 6618 (holotype *centralis*), 6619–6621, 6673 (type series). Santa Isabel, Ilha do Bananal: AMNH 90268–90269, 92916; DZ 6500. Aruana: DZ 2526. Aragançаs: (Cunha, 1961); MPEG 194, 225, 576. *Mato Grosso*: Barra do Tapirape: (Vanzolini, 1949); MN 1766a–1766b. ?Borba, Cuyaba: (Steindachner, 1867; *cf.* Gans, 1955); VM 12331-1–12331-4. Cuyaba: (Steindachner, 1867; *cf.* Gans, 1955); VM 16735-1–16735-2. Rio Branco and Borba: (Steindachner, 1867, *cf.* Gans, 1955); VM 12332-1–12332-3. São Luiz de Caceres: (Vanzolini, 1949); MN 1777a–1777b.

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 6, pp. 91–112; 10 figs.; 1 table January 31, 1966

THE LIMITS OF THE FISH FAMILY SERRANIDAE, WITH NOTES ON OTHER LOWER PERCOIDS

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A satisfactory phylogenetic classification of the families of percoid fishes has yet to be worked out. One of the many problems is to determine what characters they inherited from the proto percoid stock. The serranid fishes lie near the heart of this problem. There has been a tendency to place the serranids at the base of the percoids and all basal percoids in the serranids. As a result, Serranidae can only be defined, to misquote slightly a fellow student of the group, as containing all of those percoid fishes that do not belong in some other family. More briefly, it forms a wastebasket for lower percoids.

Here, the family Serranidae is restricted to the subfamilies Serraninae, Epinephelinae, and Anthiinae (except *Callanthias*), of Jordan and Eigenmann (1890). Such limitation greatly improves the coherence and definability of the family. Thus shorn of accretions, Serranidae, together with its specialized offshoot, Grammistidae, comprises, I think, a group of related fishes somewhat specialized in a number of respects.

A major problem, of course, is what to do with the excluded accretions. Some of these, *e.g., Centrogenys* and *Ostracoberyx,* are made up of poorly known fishes that can be at best dubiously allocated. One excluded group, however, contains such well known forms as *Roccus* and *Lateolabrax.* The osteology and relationships of this group, here united under Percichthyidae, will be considered at some length. The importance of the group lies not only in the fame of some of its members but also in the fact that they seem to be among the most generalized of percoids.

Materials and Acknowledgments

The opercular spines of serranids and other lower percoids were checked on a rather large number of specimens in the collections of the University of Hawaii, the Stanford Natural History Museum, and the California Academy of Sciences. For courtesies extended at the latter two institutions I wish to thank Drs. G. S. Myers and W. C. Freihofer at Stanford and Mr. W. I. Follett and Mrs. Lillian Dempster at the California Academy. Specimens of the following species have been stained in alizarin and more or less completely skeletonized: from the University of Hawaii collections—*Epinephelus quernus, Cephalopholis urodelus, Pteranthias longimanus*, and *Caesioperca thompsoni* (all Serranidae), *Apogon snyderi, Paramia quinquelineata*, and *Gymnapogon gracilicauda* (Apogonidae); from the U. S. Fish and Wildlife Service—*Howella* sp. (usually placed in the Apogonidae); from the University of Michigan Museum of Zoology—*Centropomus viridis* (Centropomidae); from the Stanford Natural History Museum—*Roccus saxatilis* (Percichthyidae) and *Archoplites interruptus* (Centrarchidae); and from the California Academy of Sciences—*Diplectrum pacificum* (Serranidae), *Percichthys trucha, P. melanops*, and *Percilia gillissi* (Percichthyidae). For these specimens I wish to thank Drs. D. W. Strasburg (U. S. Fish and Wildlife Service), R. M. Bailey (University of Michigan), W. C. Freihofer (Stanford), and Mrs. Lillian Dempster and Mr. W. I. Follett (California Academy). I am also indebted to the last named for the photographs of the opercles of *Paralabrax* (fig. 1). Finally I wish to thank W. C. Freihofer, C. L. Smith, and W. I. Follett for advice regarding various aspects of the manuscript.

What will have to pass for drawings were made from wet specimens. As is well known, cartilaginous and membranous areas shrink considerably when such specimens are dried.

Definition of the Family Serranidae

The family Serranidae (together with Grammistidae) as here restricted is based on a number of features. One of these—the presence of a (third) lower opercular spine (fig. 1)—appears to be almost unique among percoids and, as its presence is usually though not always verifiable by superficial examination, will be dealt with first.

In the Serranidae and Grammistidae there is, below the main opercular spine and separated from it, a flat opercular point that extends out over the distal end of the subopercle (fig. 3a). (In the serranids and grammistids there is usually, perhaps always, a flat opercular point above the main opercular spine as well.)

One or two opercular spines are quite frequent among percoid fishes. When one is present, it projects from the posterior border of the opercle about at the level of the hyomandibular-opercular articulation. A ridge generally runs along

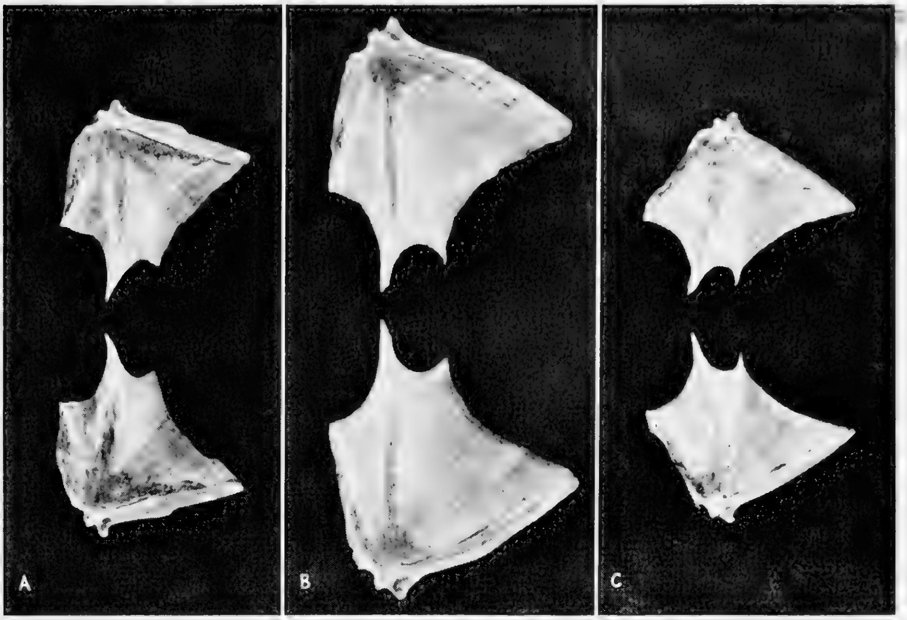


Figure 1. Opercles, external view, right above and left below. a. *Paralabrax macculatofasciatus.* b. *P. nebulifer.* c. *P. clathratus.*

the inner surface of the opercle between the spine and the hyomandibular articulation; not only does this add structural support to the spine, but its upper face provides a surface of attachment for the levator operculi muscle.

Such other spines as may be present on the opercular border appear to be supplementary. The usual secondary spine, *e.g.,* in the Mullidae, is one directed upward and backward toward the upper limit of the gill opening; it corresponds to the uppermost opercular point of the Serranidae. A supplementary spine on the opercle below the main one occurs among percoids, to my knowledge, only in the Serranidae and Grammistidae, and in *Niphon.* (*Niphon,* see below, differs immediately from the Serranidae as recognized here in the presence of a serrated preorbital.) Sometimes, as in the centrarchid *Archoplites* or the apogonidlike *Howella,* the opercle splays out posteriorly into a whole series of small points, but these are all immediately adjacent to one another.

The use of any single, minor character as a marker for a taxon is, of course, a dangerous procedure. In the present instance the danger seems to lie less in creating an artificial assemblage, for the fishes considered here as the serranid group have always been united on other grounds, than in the possible exclusion of fishes which properly belong in the group but which have secondarily lost the usual serranid opercular armature. Boulenger (1895, p. 271), for example, states in the account of his expanded genus *Serranus*: "Opercle with one, two

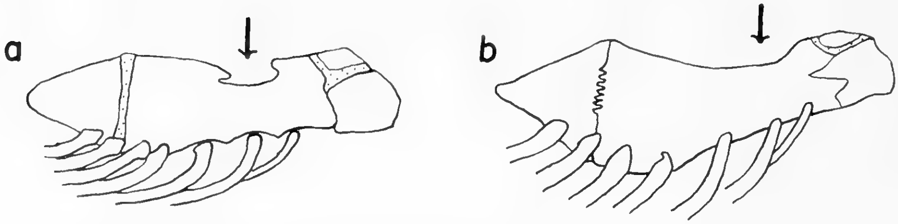
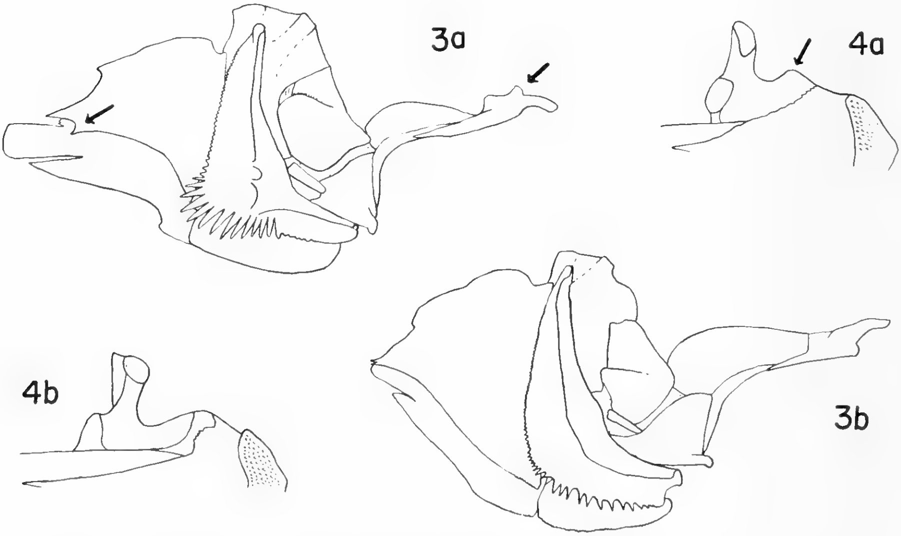


Figure 2. Right half of hyoid arch (interhyal not shown) with upper portions of branchiostegal rays, external view. a. *Percichthys trucha.* b. *Diplectrum pacificum.* Dotted areas indicate cartilage. Arrows point to excavated area in a, and to the same region in b.

of three spines." In his description of individual species he frequently says that the upper and lower opercular spines are "small or absent"; indeed, he (1895, pp. 278–280) makes this statement about all three species of *Paralabrax* illustrated in figure 1. Though the distal portion of the bony opercle is sometimes so flimsy that no lower point can be seen or felt, in all instances observed by me one appears with alizarin staining or careful maceration (figs. 1 and 3; see also



Figures 3 and 4. Fig. 3. Suspensoria and opercular bones, right side, external view. a. *Diplectrum pacificum.* b. *Percichthys trucha.* Dotted areas represent membrane. On Fig. 3a the left hand arrow points to the lower opercular spine of serranids, the right arrow to the anterior articular facet of the palatine. Fig. 4. Left side of the anterior portion of the cranium, from below. a. *Diplectrum pacificum.* b. *Percichthys trucha.* Dotted areas posterior to the vomerine teeth in 4b represent cartilage (I can find no cartilage in this portion of the cranium of *Diplectrum*). The arrow in 4a points to the anterior lateral ethmoid facet for articulation with the palatine.

Katayama, 1959, p. 115, figs. 6–9 and Gosline, 1960, pp. 32–33, fig. 5). Dr. W. J. Courtenay has, however, clearly demonstrated that the third (lower) opercular spine is consistently absent in a new species of *Rypticus* he will shortly describe.

Using this lower opercular spine as a touchstone, it is possible to exclude from the Serranidae–Grammistidae certain fishes generally included there. Thus the subfamilies of Serranidae recognized by Katayama (1960, pp. 3–5) in his revision of Japanese forms would be allotted as follows:

Included	*Excluded*
Niphoninae	Acropomatinae
Diploprioninae	Doderleiniinae
Grammistinae	Malakichthyinae
Epinephelinae	Macculochellinae
Giganthiinae	Polyprioninae
Liopropomatinae	Ostracoberycinae
Serraninae	Callanthiinae
Anthiinae	*Symphysanodon* (which is not allocated to a subfamily by Katayama)

Of Katayama's subfamilies with a (third) lower opercular spine, only Niphoninae seems, on the basis of a host of other osteological characters described by Katayama (1959), not to belong there. Its systematic allocation will be discussed below.

In addition to Katayama's subfamilies, a number of other groups, sometimes placed in Serranidae, are here excluded. These include Theraponinae and Pseudochromidinae, recognized as serranid subfamilies by Norman (1957); Centrogenysinae of Weber and de Beaufort (1931, p. 86); and Priacanthinae and Latinae of Boulenger (1895). On the other hand Pinguilabrinae of McCully (1961) should apparently be included, though nothing is known about its osteology.

A diagnosis of the SERRANID–GRAMMISTID GROUP as here restricted, drawn largely from the literature but partly from the subsequent portion of this paper, may be written as follows:

Opercle with a spine or flat point below and separated from the main opercular spine (as well as one above). Preorbital (lacrimal) without serrations. Adults without a single, greatly enlarged preopercular spine. Subocular shelf present. Metapterygoid lamina present (Katayama, 1959). Supraoccipital crest with a low flange extending out along either side of it (fig. 9). Baudelot's ligament (fig. 5) small or lacking, so far as known, the lateral wall of the basioccipital forming a surface of attachment for a portion of the body musculature. Parietal crests, if present, not continued forward onto frontals; body musculature extending forward on top of head about to the level of the front

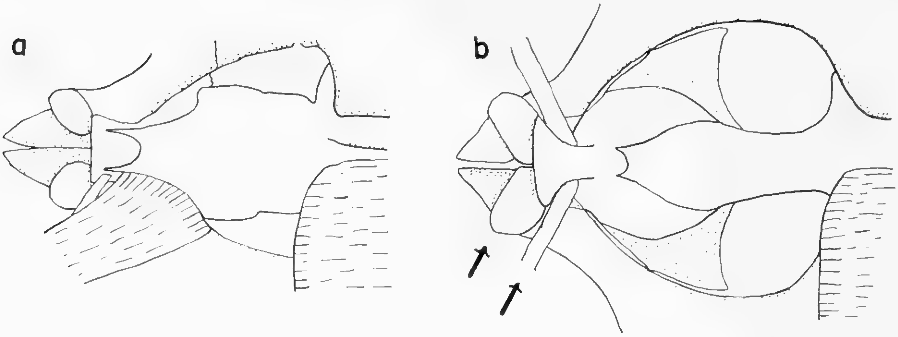


FIGURE 5. Rear of cranium, from below, head of fish to the right. a. *Diplectrum pacificum*. b. *Percichthys trucha*. Evenly dotted areas represent membrane, dashed areas musculature (which has been removed from the right side of the fishes' skulls). The left hand arrow points to the exoccipital condyle for articulation with the first vertebra; the right arrow to Baudelot's ligament (which is shown only on the left side of the fish's skull in 5a).

of the supraoccipital. Upper border of ceratohyal distinctly concave (Katayama, 1959); branchiostegal rays 7. Lateralis accessorius nerve, if present, showing pattern 9 of Freihofer (1963). One and a half or two actinosts borne on the coracoid. Postpelvic process relatively small (Katayama, 1959); pelvic fin with a spine and five soft rays, without a scaly axillary process. Caudal skeleton with autogenous hypurals, and a single uroneural (fig. 10); the caudal fin either rounded or lunate, rarely forked (bilobed). Scales belonging to types II, III, and IV of McCully (1961). Fishes hermaphroditic, though the two sexes usually do not develop synchronously (Smith, 1965).

The serranid–grammistid lineage seems to be represented by three main groupings, represented by the old subfamily categories Serraninae, Anthiinae, and Epinephelinae (*cf.* Jordan and Eigenmann, 1890; Smith, 1965). "Serraninae" appears to be made up mostly of small, large-scaled, functionally hermaphroditic fishes; "Anthiinae" of deeper-water, often reddish or yellowish forms; and "Epinephelinae" of small-scaled, large-mouthed, predaceous forms. The last group can also be characterized by an increased fleshiness of its members, *e.g.*, in the nape region where the number of predorsal bones is reduced (Katayama, 1959), which reaches its epitome in the Grammistidae (Gosline, 1960). This last family contains a series of specialized offshoots of the Epinephelinae that hold in common the following characters by which they may be separated from the Serranidae (Gosline, 1960):

GRAMMISTIDAE. Nasal rosette expanded dorsoventrally (Gosline, 1960, fig. 2b), to an extent that appears highly exceptional if not unique among percoids. Opercle joined to the skull above by a membrane for its full length. Upper portion of preopercular border usually with one or a few spines. Inner pelvic ray attached to the abdomen by a membrane.

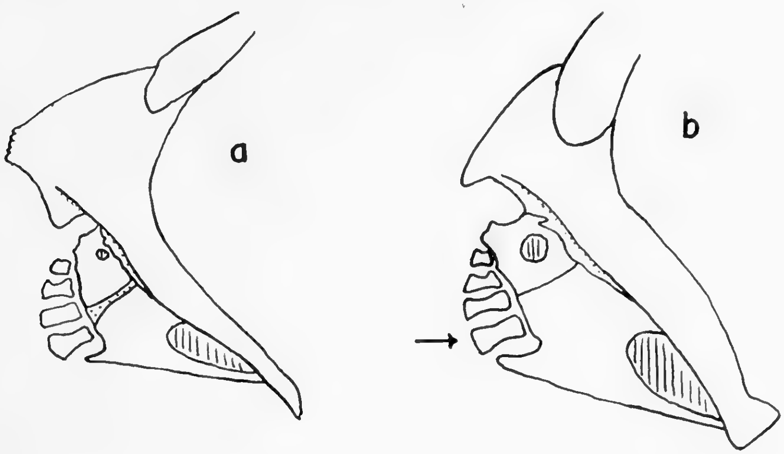


Figure 6. Lower portion of the pectoral girdle, right side, external view. a. *Percichthys trucha*. b. *Diplectrum pacificum*. The dashed areas represent open spaces, the dotted area between the scapula and the coracoid in 6a represents cartilage. The arrow points to the lowermost actinost.

Some of the grammistids, *e.g., Pseudogramma,* have an interrupted lateral line. Others, *e.g., Rypticus*, have one anal spine and only three dorsal spines. With the grammistids removed, three anal spines and a continuous and complete lateral line can, I believe, be added to the list of characters held in common by all members of the Serranidae.

Groups Here Excluded from Serranidae

The serious problem remains of what to do with the groups usually placed in Serranidae but here excluded from that family. With the exception of the percichthyids, which will be dealt with in some detail below, I have made no thorough study of these, and the suggestions that follow as to their allocation are purely tentative.

Therapon and its relatives are included in the Serranidae by Regan (1913) and Norman (1957), but no intensive study of their systematic position seems ever to have been made. Fraser-Brunner (1945) and Freihofer (1963, p. 147) have pointed out similarities with the Scorpididae.

Callanthias, to which *Grammatonotus* seems closely related (Gilbert, 1905), has generally been placed in the Serranidae, but Katayama (1959) has pointed out its many distinctive characters, and Böhlke (1960, p. 5) has suggested a possible affinity with the pseudochromid–plesiopid–acanthoclinid group of families. This area of percoid classification has generally been treated as a sort of trailing appendage to the family Serranidae (*e.g.,* Regan, 1913; Gosline, 1960). Much remains to be done with this series of families. However, on the

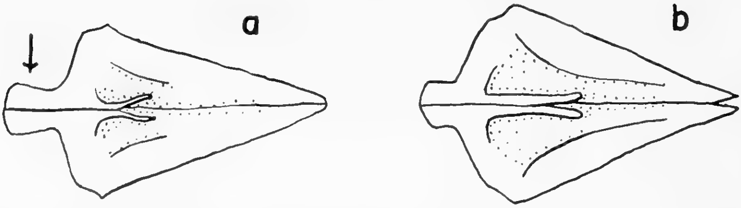


FIGURE 7. Pelvic girdle, from below, head of fish to the right. a. *Percichthys trucha.* b. *Diplectrum pacificum.* The arrow points to the postpelvic process.

basis of a comparison of a skeleton of *Pseudochromis tapeinosoma* with Katayama's account of *Callanthias,* two comments seem worth making. First, both *Callanthias* and *Pseudochromis* lack the major specializations of the Serranidae (as here defined). Thus, neither of the two genera named has the (third) lower opercular spine; *Pseudochromis* has Baudelot's ligament well developed but no body musculature attaching to the basioccipital; there is no metapterygoid lamina (Katayama, 1959); the postpelvic process is short; and some of the dorsal and anal pterygiophores have three sections in *Pseudochromis.* It seems impossible therefore to treat at least *Callanthias* and *Pseudochromis* as direct serranid derivatives. Second, if *Callanthias* and *Pseudochromis* are any criteria, the fishes in this whole general area are quite diverse (at least by percoid

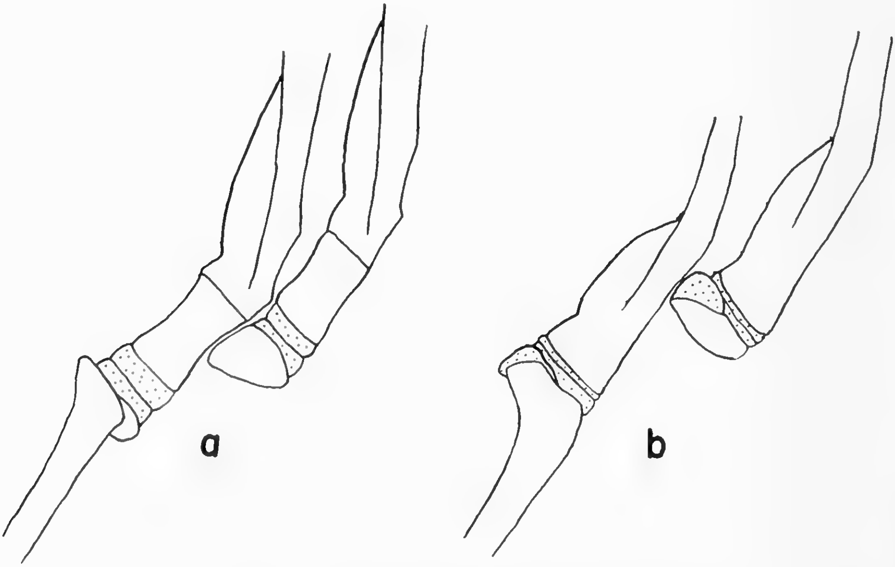
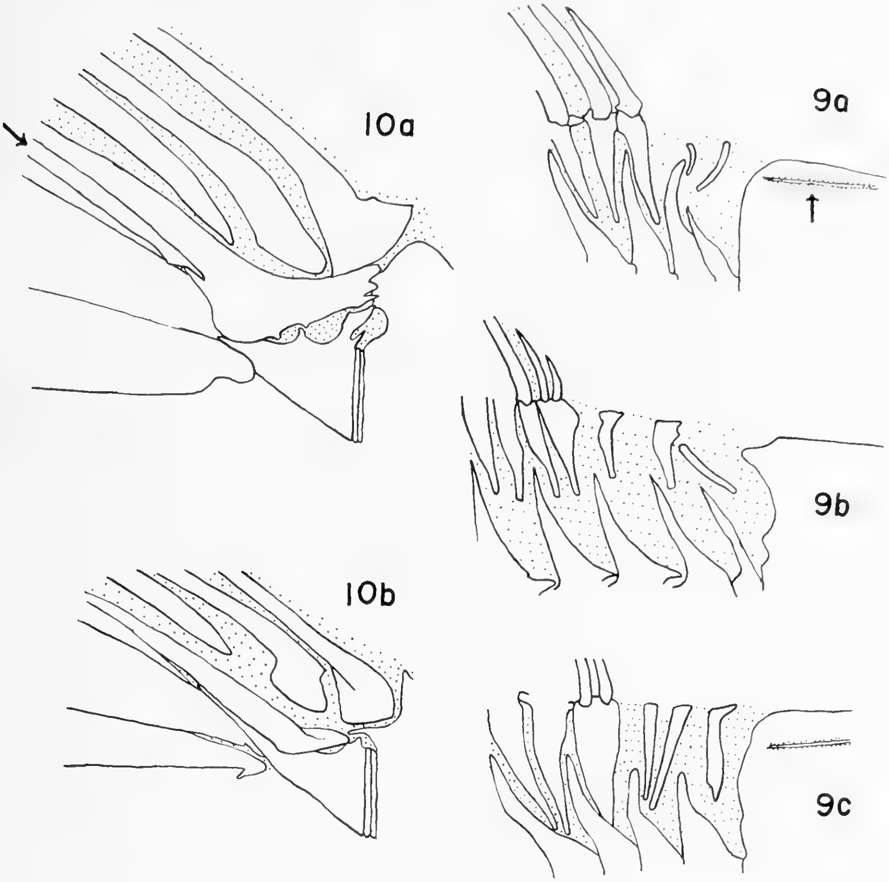


FIGURE 8. Pterygiophores of the penultimate and antepenultimate anal rays, with the base of the penultimate ray shown, lateral view, head of fish to the right. a. *Percichthys trucha.* b. *Diplectrum pacificum.* Dotted areas indicate cartilage.



Figures 9 and 10. Fig. 9. Posterior portion of supraoccipital, predorsal bones, and anterior neural spines, dorsal pterygiophores and dorsal spines, lateral view, head of fish to right. a. *Cephalopholus urodelus.* b. *Roccus saxatilis.* c. *Pseudanthias* (? = *Zalanthias*) *kelloggi.* Dotting indicates interspaces between bony areas. Arrow points to ridge running along each side of the supraoccipital. Fig. 10. Upper portion of caudal skeleton, only the upper hypurals shown, lateral view, head of fish to the right. a. *Percichthys melanops.* b. *Diplectrum pacificum.* Dotting indicates interspaces between bony areas. Arrow points to the second uroneural in 10a.

standards). *Callanthias* has very long supraoccipital–frontal and parietal crests on the top of the head. *Pseudochromis* has a very short, low supraoccipital crest and no parietal crest. It, however, has at least two areas of specialization. One is the increased number of branched caudal rays (17) and the rather highly fused caudal skeleton (with only 2 epurals and 3 or 4 hypurals). The other is in the very curious jaw structure, with the palatine far more firmly attached to the lateral ethmoid by ligaments than to the rest of the suspensorium (Gosline, 1960). Indeed this jaw structure represents the same basic type of specialization found in the Congrogadidae (Regan, 1912) and Haliophidae (Smith, 1952).

Apparently as an addendum, Katayama (1960) placed *Symphysanodon* in the Serranidae; in any event he did not even allocate it to a subfamily. However, *Symphysanodon* has a well developed scaly process in the axil of the pelvics, parietal crests (personal observation), and fin counts that fit better with the Lutjanidae than the Serranidae (as do the other two characters).

Ostracoberyx, placed by Katayama (1960) and others in the family Serranidae, seems to be a percoid fish *sui generis.* Norman (1939, p. 57), followed by Katayama (1959, fig. 39), placed it next to *Niphon.* The two genera have in common the greatly enlarged preopercular spine and the serrate lacrimal, but that would seem to be about all.

Perhaps equally aberrant is the genus *Centrogenys,* for which Weber and de Beaufort (1931, p. 87) recognize a separate subfamily. The genus is said to have a number of peculiar characters, *e.g.,* "lower pharyngeals united into a triangular bone, but separated by suture," and the caudal "with 12 divided rays." The fish has a fringed nasal flap, and bears a superficial resemblance to the Cirrhitidae.

The remaining of Katayama's (1960) subfamilies that are here excluded from Serranidae may be provisionally grouped together in the family Percichthyidae.[1] As here understood this family comprises, of Japanese forms, Katayama's (1960) subfamilies Acropomatinae, Doderleiniinae, Malakichthyinae, Polyprioninae, Niphoninae, and Maccullochellinae. As Katayama's numerous divisions of a rather small family would indicate, it is far from homogeneous. In mode of life it contains three different categories: an apparently oceanic group—*Acropoma*, *Doderleinia*, *Synagrops*, *Neoscombrops*, and *Malakichthys*; a benthonic marine series—*Stereolepis*, *Polyprion*, and *Niphon*; and an estuarine and freshwater lot. This last seems to have representatives in most of the temperate and subtropical regions of the world (in the tropics it is to some extent replaced by the Centropomidae, including *Lates*): *Roccus* in North America, Europe, and North Africa; *Percichthys* and *Percilia* in South America; *Coreoperca*, *Siniperca*, and *Lateolabrax* in Asia; and *Percalates*, *Ctenolates*, *Macquaria*, and *Maccullochella* (*Oligorus*) in Australia. The relationships of these genera to one another would seem to require rather intensive investigation on a worldwide basis; at least, the American genera examined by me—*Roccus*, *Percichthys*,

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[1] The family name here used for this group of fishes is based on the assumption that Jordan and Eigenmann's (1890, p. 330) subfamily term Percichthynae represents the oldest available name for this family. Jordan and Eigenmann (1890, p. 335) place *Roccus* and *Kuhlia* with *Lates* in the subfamily Latinae, but various authors have since shown that *Lates*, of which Jordan and Eigenmann had no specimen, belongs in a family quite different from *Roccus* or, for that matter, from *Kuhlia*. According to Katayama (1960, p. 6), the oldest available name should be Acropomidae Gill (1872), but I have not been able to find any such name in Gill's 1872 paper, and Gill (1893, p. 134) attributes the name "Acropomidae" to "Gill, 1891."

Percilia—do not seem to fit into the subfamily framework supplied by Katayama (1960) on the basis of Japanese material. Furthermore, there are certain forms included herewith in the Percichthyidae whose pertinence to that family is subject at least to question. One of the more aberrant members is certainly *Acropoma* (Acropomatinae), which has frequently been allotted a separate family principally because of the forward position of the anus (Goode and Bean, 1895) and the light-organs. Again *Niphon* (Niphoninae) in certain respects, *e.g.*, opercular spines, is more like a serranid than a percichthyid. In the great majority of features (Katayama, 1959), however, it appears to belong with the latter. Finally, Katayama (1959 and 1960) has based his account of the Polyprioninae on *Coreoperca* and *Stereolepis ischinagi*; however, figures of *Polyprion, e.g.*, Goode and Bean, 1895, fig. 236, indicate a rather different sort of fish. With the above caveats, the Percichthyidae, comprising, in Japan, Katayama's subfamilies mentioned above, will be accepted here. This family, based upon Katayama's (1959) account of Japanese forms, plus my own dissections of *Percichthys trucha, P. melanops, Percilia gillissi,* and *Roccus saxatilis*, may be contrasted with the Serranidae as shown in table 1.

The features listed in table 1 differ greatly from one another in their biological significance and in the extent to which they have been investigated in the serranid and percichthyid fishes. By far the most thoroughly tested characters are those which Katayama (1959) has checked in some 8 genera of Japanese Percichthyidae and 20 of Serranidae. My own work with the features listed in table 1 has for the most part been limited to three serranid genera (*Diplectrum, Pteranthias*, and *Caesioperca*) and three percichthyid genera (*Percichthys, Percilia*, and *Roccus*) not available to Katayama; it is thus essentially a supplement to his work.

Brief comments on each of the characters seem warranted.

I. *The number of opercular spines* (figs. 1 and 3). This feature has already been discussed.

II. *The upper border of the ceratohyal* (fig. 2). A nerve runs forward in the epi- and ceratohyal. The degree to which it is bone-enclosed in the percichthyid–serranid fishes varies greatly. In some percichthyids (Katayama, 1959, fig. 10) there is merely a window in the upper part of the ceratohyal; in this area the nerve runs along without bony protection; in others (fig. 2a and Katayama, 1959, fig. 11) the window breaks through more or less narrowly to the upper surface of the ceratohyal. In the Serranidae this break has broadened out to form a broad-bottomed indentation in the upper surface of the ceratohyal (fig. 2b and Katayama, 1959, figs. 12–13).

III. *The lateral ledge along the supraoccipital crest* (fig. 9). In *Percichthys* and *Percilia* the front of the supraoccipital crest is somewhat expanded above into a roof which lies just under the skin of the nape, but there are no lateral flanges below this. In *Roccus* the supraoccipital crest forms a simple flat

Table 1

	Percichthyidae	Serranidae
I.	Opercle without a spine or point below the main spine (except *Niphon*) (fig. 3b).	Opercle with a spine or flat point below the main spine (figs. 1, 3a).
II.	Upper border of ceratohyal either approximately straight or with an oblong hollow excavated in it (fig. 2a).	Upper border of ceratohyal smoothly concave (fig. 2b).
III.	Supraoccipital crest without a longitudinal ridge extending laterally along its mid-sides (except Polyprioninae) (fig. 9b).	Supraoccipital crest with a longitudinal ridge running along its mid-sides for most or all of its length (fig. 9a, c).
IV.	Lower surface of lateral ethmoid with only two articular facets, one for the lacrimal and one for the palatine (fig. 4b).	Lower surface of the lateral ethmoid with three articular facets, one for the lacrimal and two for the palatine (fig. 4a).
V.	Exoccipital facets for articulation with the first vertebra adjacent or nearly so (fig 5b).	Exoccipital facets for articulation with the first vertebra well separated from one another (fig. 5a).
VI.	No body musculature running forward below Baudelot's ligament to an attachment along the lateral walls of the basioccipital (fig. 5b).	Baudelot's ligament small, body musculature extending forward below and around it to an attachment along the lateral walls of the basioccipital (fig. 5a).
VII.	Usually ½ or 1 actinost articulating with the coracoid (fig. 6a).	1½ or 2 actinosts articulating with the coracoid (fig. 6b).
VIII.	Postpelvic process relatively long (fig. 7a).	Postpelvic process relatively short (fig. 7b).
IX.	Vertebrae 25, frequently more.	Vertebrae 24 in most, more in some Anthiinae.
X.	Some of the dorsal and anal soft ray pterygiophores divided into three parts (fig. 8a).	None of the dorsal and anal soft ray pterygiophores divided into three parts (fig. 8b).
XI.	Three or four predorsal bones (except *Niphon*), the last interdigitating behind the second neural spine (fig. 9b).	One to three predorsal bones, the last, except in Serraninae (fig. 9c), interdigitating between the first and second neural spines (fig. 9b).
XII.	Caudal skeleton with two uroneurals (fig. 10a).	Caudal skeleton with a single uroneural (fig. 10b).
XIII.	Caudal fin usually forked.	Caudal fin rounded, truncate, or lunate, rarely forked (*i.e.*, bilobed).
XIV.	Gas bladder tending to produce a pair of anterior lobes and/or a posterior projection into the first interhemal spine.	Gas bladder rounded at both ends.
XV.	Fishes belong to McCully's (1961) scale group I.	Fishes belonging to McCully's (1961) scales groups II or III.
XVI.	Fishes belonging to Freihofer's (1963) ramus lateralis accessorius patterns 8 or 9, or the ramus absent.	Fishes belonging to Freihofer's (1963) ramus lateralis accessorius pattern 9, or the ramus absent.
XVII.	Fishes not hermaphroditic (Smith, 1965).	Fishes hermaphroditic, though the two sexes are usually not developed synchronously (Smith, 1965).

vertical lamina throughout. *Epinephelus, Cephalopholis* (fig. 9a), *Diplectrum, Pseudogramma, Pteranthias, Caesioperca,* and *Pseudanthias* (fig. 9c), among Hawaiian serranids all have a low ridge running along either side of the supraoccipital crest well below its top. Judging from Katayama's illustrations (1959, figs. 15–23), all serranids have this type of lateral ridge developed to some extend, but so also do certain other lower percoids including apparently some percichthyids (*Coreoperca, Stereolepis*; Katayama, 1959, fig. 17).

IV. *The palatine-lateral ethmoid articulation* (figs. 3, 4). In *Diplectrum* and *Epinephelus,* and less markedly in *Pteranthias,* the palatine and lateral ethmoid articulate with one another at two distinct points. The posterior of these is the usual one located just inside the lacrimal–lateral ethmoid facet on the lower surface of the front bony border to the orbit. Additionally, there is anteriorly a distinct knob on the palatine (fig. 3a) which articulates with a marked lateral flange on the lateral ethmoid (fig. 4a). In the percichthyids *Percichthys, Percilia,* and *Roccus,* the usual posterior articular facet is present; anterior to this the palatine extends along under and in close association with the lateral ethmoid, but has no particular point of articulation with it.

V. *The exoccipital–vertebral column articulation* (fig. 5). This character is discussed and illustrated by Katayama (1959). Among the percichthyids (fig. 5b and Katayama, 1959, figs. 15–17) the surfaces of vertebral articulation on the two exoccipitals either adjoin one another or are narrowly separated. In the Serranidae (fig. 5a) these two articular surfaces are well separated. Katayama's illustrations and my own observations on *Percilia* and *Epinephelus* suggest that, although this differentiation is valid in general, there is so much gradation between Katayama's described types as to make them of little value as criteria for distinguishing families.

VI. *Muscle and ligament attachment to the basioccipital* (fig. 5). Since this character lies in an area of the fish that is quite difficult to investigate without damaging the specimen, the account here is based largely on *Epinephelus, Diplectrum, Pteranthias, Percichthys,* and *Percilia.* In *Percichthys* (fig. 5b) and *Percilia* there is a strong ligament (Baudelot's) running from the top of the cleithrum to the lateral wall of the basioccipital just ahead of the basioccipital–vertebral articulation. In *Diplectrum* (fig. 5a) Baudelot's ligament is very slight and a portion of the body musculature runs forward below it to an attachment along the whole lateral surface of the basioccipital. *Epinephelus merra* duplicates *Diplectrum* in the above respects. *Pteranthias* seems to differ in that at least part of the musculature to the basioccipital appears to come from the cleithrum.

VII. *The primary pectoral girdle* (fig. 6). Katayama (1959, p. 155, figs. 29, 30) has described and figured two (probably associated) features in the primary pectoral girdle that would seem to separate the Percichthyidae from the Serranidae. Of these the relationship between the actinosts and the coracoid would seem to be the more reliable and easier to use, even though the percichthyid genus *Percilia* seems to have 1½ actinosts on the coracoid.

VIII. *The postpelvic process* (fig. 7). The postpelvic process, according to Katayama's account and illustration (1959, pp. 161–163, fig. 3) forms a more or less graded series—from long in the Percichthyidae to short in most Serranidae.

IX. *Number of vertebrae.* Vertebral counts in the Serranidae and Percichthyidae have been given by Boulenger (1895, p. 115) and Katayama (1959, pp. 146, 147). Among the genera of Percichthyidae for which they give counts six have 25 vertebrae and eight have more. Among the genera of Serranidae, thirteen have 24 vertebrae and fourteen have more; within the Serranidae the Epinephelinae and Serraninae have 24 vertebrae, whereas the Anthiinae tend to have 26.

X. *Dorsal and anal soft ray pterygiophores* (fig. 8). Bridge (1895) has shown that the normal dorsal and anal pterygiophore of lower teleosts consists of three parts, and that this condition is retained in a few of the lower percoids, though in most the two lower portions have fused. In the serranids, *Diplectrum* and *Epinephelus* at least have the two-part pterygiophores of higher percoids. In *Percichthys*, *Percilia*, and *Roccus*, however, at least some of the pterygiophores retain the three-part structure.

XI. *The number and position of predorsal bones* (fig. 9). This character has been described for serranid and percichthyid fishes in somewhat different ways by Katayama (1959, pp. 148, 149, figs. 25–28) and by Smith and Bailey (1961). In the Percichthyidae (fig. 9b) there are usually three predorsal bones (two in *Niphon* according to Katayama, 1959, p. 149, and four in *Percilia* and *Percichthys trucha*). Except for *Niphon,* which has both predorsals before the first neural spine, the percichthyids have the last predorsal bone ending behind the second (in *Percilia* and *Percichthys trucha* behind the third) neural arch. The first pterygiophore bears two spines wherever investigated. In the Serranidae the number and configuration of the predorsal bones and first pterygiophore differ according to subfamilies. In the Epinephelinae (fig. 9a) there are one or two predorsal bones the last of which interdigitates ahead of the second neural spine, and the first pterygiophore bears a single spine (Smith and Bailey, 1961, p. 358). In the Anthiinae (fig. 9c) there are three predorsals; the last interdigitates ahead of the second neural spine; and the first pterygiophore seems to bear two spines. Finally, in the Serraninae there are usually three, but sometimes two, predorsals, the last interdigitating between the second and third neural arches so far as known; the first pterygiophore bears two spines. Thus, *Niphon* in this character seems to resemble the serranid Epinephelinae. Among the Serranidae the Epinephelinae and Anthiinae can apparently be distinguished from the Percichthyidae, but the Serraninae cannot.

XII. *Caudal skeleton* (fig. 10). As with the three-part pterygiophore, two separate uroneurals would seem to represent the primitive condition in percoid fishes (Gosline, 1961). Among the percichthyids available, *Roccus* and *Percichthys* (fig. 10a) definitely have two separate uroneurals; *Percilia,* in which the single specimen examined shows a rather large amount of fusion elsewhere in the caudal skeleton, has only a single uroneural. In the Serranidae investigated (fig. 10b) only one uroneural is present.

XIII. *Caudal fin.* There can be no doubt that a forked caudal is basic to the teleosts in general and the percoids in particular. One finds it in almost all strong swimmers. Nevertheless, various other tail shapes have been adopted especially by those fishes that habitually maneuver in rather close quarters, *e.g.,* around a coral reef. At all events the caudal fin of the percichthyids is often more or less forked whereas among the serranids it may be of various shapes, *e.g.,* rounded or lunate, but is rarely if ever forked (bilobed).

XIV. *Gas bladder.* Katayama (1959, pp. 164–166, figs. 33–35) has shown that whereas the gas bladder of the Japanese Serranidae is rather normally shaped, that of the Percichthyidae tends to have a pair of projections anteriorly or to extend posteriorly into the first interhemal. The anterior extensions are most pronounced in *Doderleinia* and *Synagrops* (Katayama, 1952), where they project into a basioccipital fossa of the skull. Genera in which the gas bladder enters the first interhemal are *Acropoma, Lateolabrax,* and *Malakichthys.* Though my gas bladder dissections are so inadequate as to make the following observation quite unreliable, I have been unable to find either forward prongs or a backward extension of the gas bladder into the interhemal in *Roccus, Percichthys,* or *Percilia.*

XV–XVII. For a discussion of these characters, the reader can best be referred to the papers cited.

DISCUSSION OF PERCICHTHYID–SERRANID DIFFERENCES

Of the various differences between the Serranidae and the Percichthyidae that have been discussed in the preceding paragraphs several strongly suggest evolutionary advances in the Serranidae. Some of these serranid features represent losses as compared to the generalized teleostean or percoid type, *e.g.,* the disappearance of the tripartate pterygiophore (X) and of the posterior uroneural (XII). Another group of characters, *e.g.,* the separation of the exoccipital condyles (V), the pectoral actinost articulations (VII), and the length of the postpelvic process (VIII), represent slight shifts in position or shape for which transitional stages between the serranid and percichthyid condition are either known or can be expected. Still other characters, in varying degrees of certainty, represent specializations. In this category fall the rounded or lunate caudal of the serranids (XIII) and the lower spine on the opercle (I). Indeed, as already noted, this lower opercular spine seems to be developed among the percoids only in the serranids and grammistids.

Of the seventeen listed differences between the serranids and percichthyids, I think the working hypothesis might be suggested that in all, the serranids are either the more specialized or that they and the percichthyids have both evolved in different directions from a proto percoid ancestor. Stated negatively, this hypothesis would postulate that in no one of the seventeen characters listed have the percichthyids evolved from the serranid condition. Some discussion of this idea is needed.

It is generally considered that 24 is a basal number of vertebrae in the percoid fishes. The reason for such a belief is that in a fairly large number of the lower percoid families 24 is at least a frequently recurring and in some families constant figure. An alternate possibility that would seem worth considering is that percoids have no fixed basal number of vertebrae. Circumstantial evidence for such a suggestion can be marshalled from several sources. One is that certain of the more generalized percoid families seem to have no basal number of vertebrae at all, *e.g.,* the Centrarchidae (Boulenger, 1895, p. 5) and Percidae (Bailey and Gosline, 1955). Another is that even in many of the families that have a frequently repeated vertebral number, *e.g.,* the Serranidae, there are often members with other counts. Finally, there are lower percoid families with other basal numbers, *e.g.,* the Percichthyidae, with 25, or the Priacanthidae with 22–23 (Boulenger, 1895, p. 352). Perhaps with the trend toward reduction and specialization of vertebrae (Williston's law) brought pretty well to completion in the percoids, some groups settled on one number in the general vicinity of 24 and others on another.

A second feature that requires comment is the gas bladder peculiarities in many Percichthyidae. There can be no doubt that the tendency for the gas bladder to extend backward into a hollow interhemal (*Acropoma*, *Lateolabrax*, and *Malakichthys* according to Katayama, 1959, p. 164, fig. 34) or forward as a pair of prongs to the wall of the internal ear (*Doderleinia* and *Synagrops*) is a departure from the normal gas bladder type and must be considered a specialization in the percichthyids. Nevertheless, both of the features mentioned occur time and again in the percoid fishes. The extension of the gas bladder into an interhemal, for example, occurs in the Gerreidae (Gerridae) and Sparidae. The connection between the gas bladder and the cranium in some percichthyids deserves somewhat more discussion.

Among the berycoid and lower percoid fishes a gas bladder-ear connection occurs at least three times: in the berycoid family Holocentridae (*cf.* Nelson, 1955) and in the percoid families Kuhliidae (*Kuhlia,* personal observation) and Percichthyidae (Katayama, 1952 and 1959). In *Kuhlia* the anterior prongs of the gas bladder pass forward above Baudelot's ligament whereas in the Holocentridae they pass below it. In *Doderleinia* and *Synagrops* Katayama

(1952) does not mention (at least in the English resumé) the relationship between the prongs of the gas bladder and Baudelot's ligament, but he does describe and figure for these fishes (1952, fig. 1) a pair of basioccipital fossae for the accommodation of the anterior prongs of the gas bladder. These fossae seem to be somewhat different from the gas bladder-auditory bulla association of either the Holocentridae or Kuhliidae. The implication is that a connection between the gas bladder and the cranium has occurred independently at least three times: in the Holocentridae, Kuhliidae, and Percichthyidae.

In the Serranidae examined, as previously noted (VI), Baudelot's ligament is small or has completely disappeared and a portion of the body muscle extends forward to an attachment along the lateral walls of the basioccipital. Part of this muscular attachment is on that forward portion of the basioccipital which forms a part of the wall of the auditory bulla. Under such circumstances the lateral basioccipital walls necessarily form a strong, rigid structural support. It would seem that a firm muscle-supporting basioccipital would preclude the development of a gas bladder–inner ear connection (which to be functionally successful would seem to require a highly flexible intervening wall between these two structures). In short, with regard to this character the serranids appear to have evolved in one direction while the percichthyids show at least tendencies to develop in a quite different one.

Percichthyid Relationships

The serranids as here defined have certain specializations, especially the presence of a lower opercular spine, that will distinguish them from other basal percoid families. By contrast the Percichthyidae has, as a group, only the gas bladder tendencies that I am aware of in this category of characters. The question thus arises of how to distinguish the Percichthyidae from other lower percoid groups. For the moment at least, this must be done by a process of elimination. The remainder of the present paper will be devoted to this matter. The percoid families to be considered are Centropomidae, Percidae, Kuhliidae, Centrarchidae, Scorpididae, and Apogonidae.

As with the Serranidae, it would seem that at least some of these last-named families have peculiarities (perhaps markers would be a more appropriate word) by which they may be distinguished. Thus the PERCIDAE, in addition to the characters usually used to define the family (see Collette, 1963, pp. 620–621), seem to have dropped out the normal connection between the preopercular and temporal sensory canals of the head (Hubbs and Cannon, 1935, p. 10; Disler, 1950). This, however, is a by no means unusual feature.

In the CENTRARCHIDAE, judging from an examination of *Archoplites*, *Pomoxis*, and *Micropterus*, the largely bone-enclosed supraorbital commissure of the lateral line forms a cross-ridge on the frontals. The posterior face of this ridge provides the anteriormost surface of attachment for the body musculature running forward over the skull.

Among the CENTROPOMIDAE, *Centropomus* (personal observation) and *Lates* (Katayama, 1956) have the second neural spine anteroposteriorly expanded into a somewhat bladelike structure. Unlike the other groups mentioned previously they also have a well developed scaly process in the axil of the pelvics.

At this point, a brief discussion of this scaly process in the pelvic axils of many percoids seems advantageous. It is on the basis of the presence or absence of this feature that Regan (1913) and Norman (1957) made their primary division of percoid families. There can be no doubt that the character forms a convenient and valid marker for certain groups. On the other hand, it is an open question, to say the least, whether it will bear the weight that Regan and Norman have placed on it. There are two problems here.

One is whether the percoid families without an axillary process form one phylogenetic group and those with it another. I do not have enough information on this topic to discuss the matter intelligently. The other regards the consistency of the presence or absence of an axillary scale within percoid families. Certainly in some well known families the consistency breaks down. According to Norman (1957, p. 219) this happens in the Sciaenidae. In the Chaetodontidae (*vide* Fraser-Brunner, 1945, p. 466), the Chaetodontinae possess a well developed axillary process but the Pomacanthinae do not. Part of the difficulty lies in the fact that the axillary process is not an all or none character; it can be and frequently is rudimentary or practically transitional between a ridge and a process.

Nevertheless in the great majority of percoid families the scaly axillary process in the pelvics is either consistently absent or consistently present. Consequently the presence of a well developed axillary scale in *Symphysanodon* would argue rather strongly against its inclusion in the serranid-percichthyid group. Similarly, the well developed axillary process shown in Starks' (1899) figure of *Dinolestes* would indicate that this fish is not a member of the Apogonidae, despite its almost invariable allocation to that family.

Among the generalized percoids, *i.e.,* those with the characters listed for the Percichthyidae in table 1, but with an axillary scale, I have dissected only two—*Microcanthus* and *Centropomus*. *Microcanthus,* a scorpidid, differs further from the Percichthyidae in the small mouth and twisted maxillary that usually goes with it; also the premaxillary has only one ascending process. *Centropomus* has already been mentioned.

The two remaining basal percoid families to be differentiated from the Percichthyidae present more difficulty.

KUHLIIDAE, according to Norman (1957, p. 249) contains the Pacific-wide *Kuhlia* and two poorly known Australian freshwater genera—*Nannatherina* and *Nannoperca*. Regan (1940, p. 174), in assigning *Nannatherina* to Kuhliidae, stated: "In *Nannatherina* the pelvic bones are remote from the cleithra and connected to them by a rather long ligament." If Regan's allocation and statement are correct, Kuhliidae is a very primitive percoid family indeed. Until more is known about *Nannatherina* and *Nannoperca,* a comparison of the Kuhliidae with other families must be based largely on *Kuhlia.* For the present, suffice it to say that *Kuhlia* is very like the percichthyids, differing only in such minor osteological characters as the absence of a subocular shelf.

The final family to be compared with the Percichthyidae is APOGONIDAE. This is another lower percoid family that has been stretched into almost protean form. The absence of information on the internal characters of many apogonid genera makes any final attempt to define the family premature. However, two peculiarities of *Apogon* are worth noting as a possible basis of family definition. One is that the intercalar is included in the convex wall of the greatly expanded auditory bulla; hence the lower prong of the posttemporal is attached to the bulla wall. Second, the single uroneural is reduced to a single weak splint without the anterior expansion usual in percoids.

In light of the foregoing discussion, an attempt can be made to define the basically generalized Percichthyidae in such a way as to exclude at least those other families that have been considered in this paper.

PERCICHTHYIDAE. Percoid fishes with the lateral line canals of head at least partially enclosed in bone; preopercular sensory canal usually joining the temporal canal; supraorbital commissure not enclosed in a raised ridge of bone that forms the anterior level of attachment for the body musculature; lateral line of the body complete and continuous. Premaxillary with two ascending processes; maxillary expanded posteriorly. Opercle with two rounded protrusions or spines (three in *Niphon*), the main one below. A subocular shelf. Expanded auditory bulla, if present, not including the intercalar. Vertebrae 25 or more; 2nd neural spine not anteroposteriorly expanded. Three predorsal bones. No scaly process in the axil of the pelvics; pelvics thoracic, of a spine and five soft rays, the outer the longest. Two uroneurals, the larger expanded anteriorly.

Summary

A preliminary attempt has here been made to unravel the taxonomic confusion that has accumulated around certain of the lower percoid families. Lower percoid groups with a scaly process in the pelvic axis—the Centropomidae, *Symphysanodon, Dinolestes*—have barely been mentioned; they do not seem to belong with the serranids and their associates dealt with here. The family Serranidae itself has been restricted and redefined. As here restricted, the Serranidae form a somewhat specialized offshoot of the basal percoid stock. In addition to the Grammistidae, which have been treated previously (Gosline, 1960), the groups here removed from the Serranidae of older authors fall into two categories. One is made up of apparently specialized fishes of dubious affinities—the Callanthiinae and Ostracoberycinae of Katayama (1960); the

Centrogenysinae of Weber and de Beaufort (1931); and the pseudochromids, etc., of Regan (1913). The other category—formed by the Acropomatinae, Doderleiniinae, Malakichthyinae, Maccullochellinae, Polyprioninae, and Niphoninae of Katayama (1960)—is here provisionally considered as a single, separate family of basal percoid fishes. This family, Percichthyidae, is briefly compared with a number of other lower percoid groups and provisionally defined.

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 7, pp. 113–196; 1 table January 31, 1966

INSECTS OF THE GALÁPAGOS ISLANDS[1]

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Introduction

When Charles Darwin visited the Galápagos Islands in September and October of 1835, he was impressed with the small size and dull colors of the insects he encountered, and of the insect fauna in general he commented that "excepting Tierra del Fuego, I never saw . . . so poor a country." G. R. Waterhouse, upon examining the insects which Darwin collected, reported that there was nothing in their appearance which would have led him to imagine that they had come from under the equator. Darwin described them as having a desert character, along with the plants and the birds.

Few entomologists who have visited the Archipelago would disagree with the generalization that the insect fauna is more desert than tropical in aspect, a fact in keeping with the arid nature of the islands, but tropical species are present, especially, but by no means exclusively, in the mangrove swamps along the shores and in the moist forests of middle elevations of the larger islands. The fauna is depauperate, as would be expected of oceanic islands populated by chance. For example, the continental British Isles have currently known more than three times as many families, ten times as many genera and thirty-two times as many species of insects as the Galápagos (table I). Although this differential will no doubt be reduced as the Galápagos fauna becomes better known, there is no reason to believe that it will ever be eliminated. However, although the fauna is poor in taxonomic entities, in favorable seasons it is rich in individuals, and the entomologists of the Galápagos International Expedition of 1964 brought back thousands of specimens.

In connection with our own studies we attempted to assemble as much as possible of the literature relevant to Galápagos insects prior to the Expedition, and to organize it in a systematic manner upon our return. The result gave us,

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[1] Contribution No. 27 from the Charles Darwin Foundation for the Galápagos Islands.

TABLE I *Comparison of recorded insect fauna of the Galápagos Archipelago with that of the British Isles.*

Insect Orders	*Galápagos Archipelago*			*British Isles**		
	Families	*Genera*	*Species*	*Families*	*Genera*	*Species*
Collembola	2	2	2	9	62	261
Protura	–	–	–	2	4	17
Thysanura	1	2	2	2	6	11
Diplura	1	1	1	1	1	12
Orthoptera	3	11	18	5	27	38
Blattaria	1	7	9	4	5	8
Mantodea	1	1	1	–	–	–
Dermaptera	1	2	2	3	7	9
Phasmida	–	–	–	–	–	–
Isoptera	2	2	6	–	–	–
Embioptera	–	–	–	–	–	–
Plecoptera	–	–	–	6	15	32
Odonata	3	6	7	9	21	42
Ephemerida	–	–	–	8	19	46
Corrodentia	–	–	–	11	33	68
Mallophaga	2	25	61	7	58	252
Anoplura	1	2	2	4	15	34
Thysanoptera	–	–	–	3	42	183
Hemiptera	14	34	41	30	221	499
Homoptera	3	27	38	19	252	912
Megaloptera	–	–	–	2	3	6
Neuroptera	3	4	6	5	18	54
Coleoptera	39	107	192	80	947	3,690
Strepsiptera	–	–	–	4	5	17
Mecoptera	–	–	–	2	2	4
Trichoptera	–	–	–	13	70	188
Lepidoptera	16	71	97	64	657	2,187
Diptera	27	68	102	75	1,132	5,199
Siphonaptera	–	–	–	5	24	47
Hymenoptera	9	23	31	52	1,071	6,191
TOTALS	129	395	618	425	4,717	20,007

* From Kloet, G. S., and W. D. Hincks, 1945, A Check List of British Insects. 483 pp. Stockport, England.

hopefully, a fairly complete list of the insects which have been reported from the Islands and a partially annotated bibliography of Galápagos entomology. We have been encouraged by entomologists interested in the Galápagos to publish this material, even though we realize that it is incomplete and has some obvious deficiencies. Among the latter are the fact that we have passed no independent taxonomic judgment on the validity of published records and unless we were aware of subsequent revisions, or unless the specialists who have so kindly examined our list have independently evaluated the references, with few exceptions they appear in the form in which they were treated in the most recent Galápagos publication. Nevertheless, we hope that our provisional faunal list and provisional bibliography will be useful, and it is in this spirit that we offer it, whatever its shortcomings.

Acknowledgments

This bibliography was prompted by the authors' participation in the Galápagos International Scientific Project, supported in part by Grant GE-2370 from the National Science Foundation and in part by the following: Belvedere Scientific Fund; California Academy of Sciences; California Maritime Academy; Charles Darwin Foundation; Government of Ecuador; Pacific Science Board, National Academy of Sciences; Shell Oil Company; the United States Army, Navy, and Air Force; the University of California Extension Division; and the Associates in Tropical Biogeography, University of California. Many specialists have reviewed sections and made valuable corrections and additions. Acknowledgment is made of this kind assistance in the introductory remarks under each order.

ECUADORIAN NAMES OF GALÁPAGOS ISLANDS WITH THEIR ENGLISH SYNONYMS

Baltra = South Seymour
Chávez = Santa Cruz = Indefatigable
Española = Hood
Fernandina = Narborough
Floreana = Santa María = Charles
Genovesa = Tower
Isabela = Albemarle
Marchena = Bindloe
Pinzón = Duncan
Pinta = Abingdon
Rábida = Jervis
San Cristóbal = Chatham
Santa Cruz = Chávez = Indefatigable
Santa Fé = Barrington
Santa María = Floreana = Charles
Santiago = James

A BRIEF HISTORY OF ENTOMOLOGICAL EXPLORATION IN THE GALÁPAGOS ISLANDS

Charles Darwin collected the first specimens of insects in the Galápagos Islands for scientific purposes. A surprising number of others have followed him in the 130 years since the *Beagle*'s visit in 1835. We realize that the following list is incomplete, but it is offered mainly as an aid in locating collections of Galápagos insects and in finding detailed accounts of entomological work, islands visited, collecting, dates, field notes, etc. In some cases the information presented was difficult to find, and we hope that the list may save others unnecessary searching of the literature.

The general pattern of presentation is: first a list of individual collectors, in chronological order, followed by a list of expeditions, also in chronological order. In each case, where known, the name of the collector (or expedition and vessel) is given, then the dates and islands visited. Usually the place of publication of entomological results is indicated by reference to the bibliography or by mention of the most important journal articles or book. The best general account for each expedition is also cited, as is the current location of Galápagos collections. The information presented is as complete as we could make it up to the time of the Galápagos International Scientific Project (January, 1964).

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FÖRSTER, JUAN—March, April, May, 1959. San Cristóbal, Floreana, and Santa Cruz islands. *Collection*: Zool. Sammlgn. Bayerischen Staates, München. *Publication*: Kernbach (1962).

SEKIGUCHI, KOICHI—December—January, 1959–1960. Floreana and San Cristóbal islands. *Publication*: Asahina (1961).

GALÁPAGOS EXPEDITIONS

Voyage of the Beagle. Charles Darwin. H.M.S. *Beagle*. September 16 to October 19, 1835. Chatham, Charles, Albemarle, and James islands. *Re-*

sults published: Butler, *et al.* 1877; Walker, 1848–1873, etc. *Insect collections*: British Museum (Natural History). *General account*: Darwin, C. 1839. Narrative of the surveying voyages of His Majesty's ships *Adventure* and *Beagle*, between the years 1826 and 1836, describing their examination of the southern shores of South America, and the *Beagle*'s circumnavigation of the globe. London, Henry Colburn. Vol. III. Journal and Remarks. 1832–1836. pp. xiv + 629, maps. Darwin, C. 1845. Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. *Beagle* round the world, under the command of Capt. FitzRoy, R.N. 2d ed. London, John Murray, pp. viii + 519, 12 figs.

Kongliga Svenska Fregatten Eugenies Resa Omkring Jorden under befäl af C. A. Virgin, Åren 1851–3. (Royal Swedish frigate *Eugenie* voyage around the world under the command of C. A. Virgin, years 1851–3). Eugenie. Dr. J. G. M. Kinberg. May 9, 1852 to May 20, 1852. Chatham, Indefatigable, Charles, James, Albemarle islands. *Results published*: Svenska Vetenskaps-academien, Stockholm. *Insect collections*: Naturhistoriska Riksmuseum, Stockholm. *General account*: Skogman, C. 1854–1855. Fregatten Eugenies Resa Omkring Jorden Åren 1851–1853, under befäl of C. A. Virgin. Stockholm, Adolf Bonnier, Förra Delen. pp. vi + 250; sednare delen, pp. v + 224, col. pls. maps, and text figs.

"Agassiz Expedition." Alexander Agassiz. Steamer *Hassler*. June 10, 1873 to June 20, 1873. Charles, Albemarle, James, Jervis, and Indefatigable islands. *Insect collections*: Museum of Comparative Zoology, Harvard. *General account*: Elizabeth Agassiz, "A cruise through the Galapagos." Atlantic Monthly, 1873 (May), pp. 579–584.

Voyage of the Peterel. Commander W. E. Cookson. H.M.S. *Peterel*. June 1875. Abingdon, Charles, and Albemarle islands. *Results published*: Proc. Zool. Soc. Lond. 1877. *General account*: Gunther, A. 1877. "Account of the zoological collection made during the visit of H.M.S. "Peterel" to the Galapagos Islands." Proc. Zool. Soc. Lond., pp. 64–91.

"Albatross" Expedition—1888. (U. S. Fish Commission). Leslie A. Lee, Charles H. Townsend. Steamer *Albatross*. April 4 to 16, 1888. Chatham, Hood, Gardner, Albemarle, James, Duncan, Indefatigable, and Abingdon islands. *Results published*: Proc. U. S. National Museum, vol. XII, 1889. *Insect collections*: U. S. National Museum. *General account*: Howard, L. O. 1890. Scientific results of explorations by the U. S. Fish Commission Steamer *Albatross*. No. V. Annotated catalogue of the insects collected in 1887–88. Proc. U. S. National Museum, vol. 12, pp. 185–207.

"Albatross" Expedition—1891. (U. S. Fish Commission). Alexander Agassiz. Steamer *Albatross*. March 28–April 4, 1891. Chatham, Charles, Duncan, James, Hood, and Albemarle islands. *Results published*: Bulletin Museum of Comparative Zoology, vol. 23, p. 25. *General account*: Agassiz, Alexander. 1892. Reports on the dredging operations off the west coast of Central America to the Galápagos to the west coast of Mexico, and in the Gulf of California in charge of Alexander Agassiz, carried on by the U. S. Fish Commission Steamer "Albatross," Lieut. Commander Z. L. Tanner, U.S.N., Commanding. II. General sketch of the expedition of the "Albatross," from February to May, 1891. Bull. Mus. Comp. Zool., 23:1–89, 22 pls. (insects, pp. 68–69). Scudder, S. H. 1893. No. 1. Reports on the dredging operations off the west coast of Central America to the Galápagos . . . VII. The Orthoptera of the Galápagos Islands. Bull. Mus. Comp. Zool., vol. 25, pp. 1–25, 3 pls.

Hopkins Stanford Galápagos Expedition, 1898–1899. R. E. Snodgrass and Edmund Heller. Schooner *Julia E. Whalen.* December 8, 1898 to June 23, 1899. Visited all large and many small islands. *Results published*: Proc. Washington Academy of Sciences, vols. 4 and 5. *Insect collections*: Stanford University; mostly destroyed. *General account*: Proc. Wash. Acad. Sci., vol. 3, pp. 363–364, 1901.

California Academy of Sciences Expedition. F. X. Williams. Schooner *Academy.* Sept. 24, 1905 to Sept. 25, 1906. Visited all the islands. *Results*: Proc. Calif. Acad. Sci. *Insect collections*: Calif. Acad. Sci., San Francisco. *General account*: Slevin, J. R. 1931. Log of the schooner Academy, on a voyage of scientific research to the Galápagos Islands, 1905–1906. Occ. papers, Calif. Acad. Sci., no. 17, 162 pp.

Harrison Williams Galápagos Expedition. Wm. Beebe and Wm. Morton Wheeler. Yacht *Noma.* March 28, 1923, for 21 days (100 hours on land). San Cristóbal, Santa Cruz, Santiago, Isabela, and Tower islands. *Results*: Zoologica—New York Zoological Society and "Galapagos, World's End." *Insect collections*: American Museum of Natural History. *General account*: Beebe, Wm. 1923. Williams Galapagos Expedition, Zoologica, vol. 5, no. 1, pp. 1–20, figs. and maps.

St. George Expedition. C. L. Collenette, Cynthia Longfield, E. Cheesman. Steam Yacht *St. George.* July 24, 1924—arrived. James, Indefatigable, Eden, Charles, Albemarle, and Narborough islands. *General account*: Collenette, C. L. 1925. Sea Girt Jungles. London, pp. 72–116.

Arcturus Oceanographic Expedition, 1925. Wm. Beebe. Steam Yacht *Arcturus.* April 4 to April 28, 1925. South Seymour, Albemarle, Tower, and Hood islands. *Results published*: Zoologica, vols. 7 and 8. Beebe, Wm.

1926. Zoologica, vol. 8, pp. 1–45. *General account*: Beebe, Wm. 1926. "Arcturus Adventure" with "Log of the Arcturus." Also Beebe, Wm. 1925. "Logging the Arcturus, a visit to the Galápagos." Bull. N. Y. Zool. Soc., no. 4, July, pp. 103–116; N. Y. Zool. Soc., vol. 28, pp. 119–129.

The Norwegian Zoological Expedition. 1925. Alf Wollebaek. Cutter *Monsunen.* August to December, 1925. Floreana, Chatham, and Santa Cruz islands. *Results published*: Med. Zool. Mus., Oslo. *Insect collections*: Zoologiske Museum, Oslo. *General account*: Mielche, Hakon, 1938. Let's see if the world is round. London, 330 pp.

Cornelius Crane Pacific Expedition (Field Museum of Natural History, Chicago). Karl P. Schmidt. Brigantine Yacht *Illyria.* January 6, 1929–January 16, 1929. Albemarle, Narborough, Indefatigable, S. Seymour, Eden, and Charles islands. *Collections*: Chicago Museum of Natural History. *Results*: Publ. Field Museum, Zool. Series under heading: Scientific results of the Crane Pacific Expedition. *General account*: Shurcliff, S. N. 1930. Jungle Islands. The "Illyria" in the South Seas. New York, G. P. Putnam's Sons, pp. xv + 298, illus.

Gifford Pinchot Expedition. Dr. A. K. Fisher. Yacht *Mary Pinchot.* June and July, 1929 (5 weeks). Chatham, Charles, Albemarle, Tower, Indefatigable, Seymour, Duncan, Hood, Daphne Major, Barrington, and Narborough islands. *Collections*: U. S. National Museum. *General account*: Pinchot, G. 1929. "To the South Seas, the cruise of the Mary Pinchot to the Galápagos, the Marquesas, and the Tuamotu islands, and Tahiti. Philadelphia, The John C. Winston Co., xiii + 500 pp., 1 plate.

Vincent Astor Expedition. C. H. Townsend, Kermit Roosevelt, and Henry K. Svenson. *Nourmahal.* March 31 to April 15, 1930. Indefatigable, Albemarle, Tower, and Charles islands. *General account*: Townsend, C. H. 1930. The Astor Expedition to the Galápagos Islands. Bull. N. Y. Zoological Society, vol. 33, pp. 135–172.

Hancock Galápagos Expeditions. J. S. Garth. R/V *Velero III. 1.* December 31, 1931 to January 24, 1932. Chatham, Charles, Albemarle, James, Indefatigable, S. Seymour, and Tower islands. *2.* January 24, 1933 to February 26, 1933. Hood, Charles, Chatham, Barrington, Indefatigable, Albemarle, James, Duncan, S. Seymour, Abingdon, and Tower islands. *3.* January 11 to January 31, 1934. Wenman, Albemarle, Narborough, Charles, Indefatigable, Chatham, S. Seymour, James, and Hood islands. *4.* December 2, 1934 to December 19, 1934. Bindloe, Charles, Indefatigable, Albemarle, James, S. Seymour, Chatham, and Hood islands. *5.* January 16 to January

30, 1938. Tower, Chatham, S. Seymour, James, Albemarle, Charles, Indefatigable, and Hood islands. *Results published*: Richards, A. G., Jr. The noctuid moths of the Galapagos from the collections of the Allan Hancock Foundation. Report of the Allan Hancock Pacific Exped., vol. 5, pp. 233–251, 4 pls. *General account*: Fraser, C. McLean. 1943. Allan Hancock Pacific Exped., vol. 1, 445 pp., 115 charts, 128 pls.

Templeton Crocker Expedition of the California Academy of Sciences. Mr. Maurice Willows. Schooner *Zaca*. April 15 to June 16, 1932. Thirteen islands including all main islands. *Results*: Proc. Calif. Acad. Sci., series 4, vols. 21 and 22. *Insect collections*: California Academy of Sciences. *General account*: Crocker, Templeton. 1933. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 2. Introductory statement. Proc. Calif. Acad. Sci., ser. 4, vol. 21, no. 2, pp. 3–9, 1 pl.

Templeton Crocker Expedition to Polynesia in 1934–35. Templeton Crocker. Schooner *Zaca*. March 9–25, 1935. Albemarle, Tower, and Santa Cruz islands. *Results*: Proc. Calif. Acad. Sci., ser. 4, vols. 21 and 22. *Insect collections*: American Museum of Natural History and (Hemiptera) Calif. Acad. Sciences. *General account*: Van Duzee, E. P. 1937. No. 33. The Hemiptera of the Templeton Crocker Expedition to Polynesia in 1934–1935. Proc. Calif. Acad. Sci., ser. 4, vol. 22, pp. 111–126. See also: Chapin, J. P. 1936. Jour. Amer. Mus. Nat. Hist., vol. 37, pp. 31–38.

Darwin Memorial Expedition. Wolfgang Von Hagen. September 1935 to February 1936. Chatham, Santa Cruz, Barrington, Hood, Seymour, Duncan, Jervis, James, Abingdon, and Albemarle islands. *Insect collections*: Termites. American Museum of Natural History? *General accounts*: *1.* Von Hagen, Victor Wolfgang, 1940. Ecuador the Unknown. Two and a half years' travels in the Republic of Ecuador and the Galápagos Islands. New York, Oxford Univ. Press, 296 pp., many plates. *2.* Von Hagen, Victor Wolfgang, 1949. Ecuador and the Galápagos Islands. Norman, Oklahoma, Univ. of Oklahoma Press, 290 pp., plates and maps.

Hans Hass Expedition. Irenäus Eibl-Eibesfeldt. Yacht *Xarifa*. November, 1953 to January, 1954. Tower, Santa Cruz, Hood, Narborough, Albemarle, Barrington, San Cristóbal, and Floreana islands. *Specimens*: Senckenberg Museum. *General account*: I. Eibl-Eibesfeldt, 1961. Galápagos, The Noah's Ark of the Pacific (Transl. by A. H. Brodrick). New York, Doubleday and Company, Inc. 192 pp. 21 plates, 4 colored.

Deutschen Galápagos-Expedition. 1962/63. Eberhard Curio. December, 1962–1963. Santa Cruz, Isabela, Fernandina, Wenman, Abingdon, Tower and Hood. *Publication*: Curio, E., 1964. Über das Nächtigen von *Nocticanace galapagensis* Curran. Zeit. für Tierpsychologie, Band 21, Heft 7, pp. 794–797.

INSECTS RECORDED FROM THE GALÁPAGOS ISLANDS

Order COLLEMBOLA

Family Entomobryidae

Genus **Lepidocyrtus**

intermixtus Folsom, 1924, Zoologica, vol. 5, p. 75, pl. 5, figs. 27–29.	Baltra

Family Neanuridae

Genus **Anurida**

maritima Guerin, 1836, Icon. règne animal de Cuvier, vol. 7, no. 3, p. 11 (*Achorutes*).	Floreana

Order THYSANURA

Principal references to Galápagos fauna: Banks (1901), Folsom (1924), Stach (1932), Paclt (1959).

Family Lepismatidae

Genus **Heterolepisma**

insulare Banks, 1901, Proc. Washington Acad. Sci., vol. 3, p. 543, figs. 51–52 (*Lepisma*). *intermedia* Folsom, 1924, Zoologica, vol. 5, p. 67, pl. 3, figs. 1–8.	Genovesa, Fernandina, Isabela, Santa Cruz, Baltra, Floreana

Genus **Stylifera**

galapagoensis Banks, 1901, Proc. Washington Acad. Sci., vol. 3, p. 541, figs. 47–50 (*Lepisma*).	Santiago, Pinzón, Daphne Major, Santa Cruz, Baltra, Floreana, Española

Order DIPLURA

Family Campodeidae

Genus **Lepidocampa**

juradoi seclusa Condé, 1960, Bull. Mus. Nat. Hist. Paris, ser. 2, vol. 32, p. 172.	Santa Cruz

Order ORTHOPTERA

The principal references for the Galápagos Islands are Butler (1877), Scudder (1893), McNeill (1901), Snodgrass (1902), Hebard (1920), and Caudell (1932). The treatments of *Sphingonotus* and *Schistocerca* by Snodgrass (1902) are followed rather than those of Hebard (who synonymized most subspecies) because Snodgrass was familiar with the insects in the field. Also, McNeill's (1901) treatment of *Liparoscelis* is adopted in preference to Hebard (1920). The list was reviewed for overall classification but not for completeness of Galápagos references by Grant (personal communication).

Family Acrididae

Genus **Closteridea**

bauri Scudder, 1893, Bull. Mus. Comp. Zool., vol. 25, p. 9, figs.	Isabela, San Cristóbal

Genus **Sphingonotus**

tetranesiotis Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 444 (synonym of *fuscoirroratus* Stål, *fide* Hebard, 1920).	
subsp. **tetranesiotis** Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 444 (as var. *charlesensis*).	Floreana
fuscoirrorata Stål. 1860, Freg. Eugenies Resa, Zool. 1, Ins. p. 345 (type locality first restricted to Puna I., Ecuador, by Snodgrass).	
subsp. **barringtonensis** Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 445 (as variety)	Santa Fé
subsp. **hoodensis** Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 446 (as variety)	Española
subsp. **indefatigabilensis** Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 447 (as variety)	Santa Cruz, Seymour
trinesiotis Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 439 (synonym of *fuscoirroratus* Stål, *fide* Hebard, 1920).	
subsp. **trinesiotis** Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 439 (as var. *chathamensis*).	San Cristóbal
subsp. **indefatigabilensis** Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 441 (as variety)	Seymour, Santa Cruz
subsp. **albemarlensis** Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 443 (as variety)	Isabela

Genus **Schistocerca**

intermedia Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 431.	Pinzón
literosa Walker, 1870, Cat. Derm. Salt. Brit. Mus., vol. 4, p. 620.	
subsp. **literosa** Walker, 1870, Cat. Derm. Salt.	San Cristóbal

Brit. Mus., vol. 4, p. 620.	
discoidalis Scudder, 1893, Bull. Mus. Comp. Zool., vol. 25, p. 16 (as subspecies).	
subsp. **hyalina** Scudder, 1893, Bull. Mus. Comp. Zool., vol. 25, p. 16.	Genovesa
subsp. **punctata** Scudder, 1893, Bull. Mus. Comp. Zool., vol. 25, p. 16.	Española
melanocera Stål, 1861, Freg. Eugenies Resa, Zool. 1, Ins. p. 326 (*Acridium*) (all subspecies synonymized by Hebard, 1920).	Genovesa
subsp. **immaculata** Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 223 (as variety)	Santa Cruz, Baltra
subsp. **lineata** Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 423 (as variety)	Isabela
subsp. **melanocera** Stål, 1861, Freg. Eugenies Resa, Zool. 1, Ins., p. 326.	Floreana
subsp. **minor** Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 421 (as variety)	Isabela
subsp. **pallida** Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 422 (as variety)	Santa Fé

Genus **Halmenus**

eschatus Hebard, 1920, Proc. Calif. Acad. Sci., ser. 4, vol. 2, no. 2, p. 329.	Wenman I.
robustus Scudder, 1893, Bull. Mus. Comp. Zool., vol. 25, p. 18.	
subsp. **choristopterus** Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 450 (as species).	Floreana
subsp. **cuspidatus** Snodgrass, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 450 (as species).	Isabela
subsp. **robustus** Scudder, 1893, Bull. Mus. Comp. Zool., vol. 25, p. 18.	Santa Cruz, Santiago

Family TETTIGONIIDAE

Genus **Anaulocomera**

darwinii Scudder, 1893, Bull. Mus. Comp. Zool., vol. 25, p. 19, figs.	San Cristóbal, Santa Cruz

Genus **Liparoscelis**

cooksonii Butler, 1877, Proc. Zool. Soc. London, p.	Floreana, Isabela,

87 (*Agraecia*).	Genovesa
cooksoni ensifer McNeill, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 498, fig. 39 (synon. *fide* Hebard, 1920).	Hood, Santa Cruz
pallidus McNeill, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 500, fig. 41 (synon. *fide* Hebard, 1920).	Barrington
paludicola McNeill, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 499, fig. 40 (synon. *fide* Hebard, 1920).	Isabela

Genus **Conocephalus**

exitiosus McNeill, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 501, fig. 42 (*Xiphidium*).	Santa Cruz, Santiago

Genus **Neoconocephalus**

triops Linnaeus, 1758, Systema Naturae, Ed. 10, p. 430 (*Gryllus-Tettigonia*).	San Cristóbal
insulanus Scudder (not Redtenbacher), 1893, Bull. Mus. Comp. Zool., vol. 25, p. 21, pl. III, figs. 2, 3 (*Conocephalus*).	
insularum Karny, 1907, Revisio Conocephalidarum, p. 38 (*Conocephalus*).	

Family Gryllidae

Genus **Cryptoptilum**

erraticum Scudder, 1893, Bull. Mus. Comp. Zool., vol. 25, p. 23, pl. III, figs. 6, 7 (*Cycloptilum*).	Floreana, Isabela, Hood, Abingdon
lepismoide McNeill, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 505 (*Cycloptilum*).	Isabela, Genovesa

Genus **Hygronemobius**

speculi McNeill, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 503, figs. 43, 44 (*Nemobius*).	Isabela

Genus **Gryllus**

assimilis Fabricius, 1775, Syst. Ent., p. 280 (*Acheta*). *galapageius* Scudder, 1893, Bull. Mus. Comp. Zool., vol. 25, p. 22, pl. III, fig. 8.	Isabela, Floreana, San Cristóbal, Santa Cruz, Hood

Order BLATTARIA

Family Blattidae

Genus **Anisopygia**

snodgrassii McNeill, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 493, figs. 35–37 (*Temnopteryx*).	Isabela

Genus **Blattella**

germanica Linnaeus, 1767, Systema Naturae, Ed. 12, p. 668 (*Blatta*).	Hood

Genus **Symploce**

lita Hebard, 1916, Trans. Am. Ent. Soc., vol. 42, p. 354, figs.	San Cristóbal

Genus **Leurolestes**

pallidus Brunner, 1865, Nouv. Syst. Blatt., p. 286 (*Nauphoeta*).	San Cristóbal

Genus **Periplaneta**

americana Linnaeus, 1758, Systema Naturae, ed. 10, pp. 1:424 (*Blatta*).	Floreana, San Cristóbal
australasiae Fabricius, 1775, Syst. Ent., p. 271 (*Blatta*).	San Cristóbal, Floreana
brunnea Burmeister, 1838, Handb. Ent. 2; Abt. 2, pt. 1, p. 503.	San Cristóbal

Genus **Pycnoscelus**

surinamensis Linnaeus, 1767, Systema Naturae, Ed. 12, p. 687 (*Blatta*).	Isabela, San Cristóbal, Floreana

Genus **Nauphoeta**

cinerea Olivier, 1789, Encycl. Method., Ins., vol. 4, p. 314 (*Blatta*). *circumvagans* Scudder (not Burmeister), 1893, Bull. Mus. Comp. Zool., vol. 25, p. 7.	San Cristóbal, Floreana

Order MANTODEA

Family Mantidae

Genus **Galapagia**

solitaria Scudder, 1893, Bull. Mus. Comp. Zool., vol. 25, p. 8, figs.	Isabela, Floreana, Seymour

Order DERMAPTERA

Family Forficulidae

Genus **Anisolabis**

bormansi Scudder, 1893, Bull. Mus. Comp. Zool., vol. 25, p. 5.	San Cristóbal

Genus **Euborellia**

annulipes Lucas, 1847, Bull. Soc. Ent. France, ser. 2, vol. 5, p. lxxxiv (*Forficula*).	Isabela, San Cristóbal

Order ISOPTERA

Primary references for the Galápagos are Banks (1901) and Light (1935).

Family Kalotermitidae

Genus **Kalotermes**

darwini Light, 1935, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 242, pl. 9, figs. 1, 2, 7, 8 (subg. *Cryptotermes*).	Santiago, Santa Cruz, Gardner, Floreana

galapagoensis Banks, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 544, figs. 55, 56 (*Calotermes*).	Wenman, Genovesa
immigrans Snyder, 1922, Proc. U. S. Nat. Mus., vol. 61, no. 20, pp. 2–4. (*Kalotermes* s. str.).	Fernandina, Santiago, Rábida, Santa Cruz, Baltra, San Cristóbal, Isabela, Genovesa
fatulus Light, 1935, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 245, pl. 9, figs. 4, 6 (subg. *Cryptotermes*).	Isabela, Santiago
pacificus Banks, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 555, fig. 57 (*Calotermes*).	Fernandina, Baltra, Isabela, Santiago

Family RHINOTERMITIDAE

Genus **Heterotermes**

orthognathus Light, 1933, Univ. Calif. Publ. Entom., vol. 6, p. 113.	Santa Cruz

Order ODONATA

The principal references are Currie (1901), Calvert (1901–08), and Asahina (1961). The list was checked by Lieftinck (personal communication).

Family COENAGRIONIDAE

Genus **Anomalagrion**

hastatum Say, 1839, Jour. Acad. Nat. Sci. Philadelphia, vol. 8, p. 38 (*Agrion*).	San Cristóbal, Isabela

Family AESHNIDAE

Genus **Aeshna**

galapagoensis Currie, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 382, figs. 29, 30.	San Cristóbal, Isabela

Genus **Anax**

amazili Burmeister, 1839, Handb. d. Ent., vol. 2, p. 841 (*Aeschna*).	San Cristóbal, Floreana

Family LIBELLULIDAE

Genus **Pantala**

flavescens Fabricius, 1798, Ent. Syst. Suppl., p. 285 (*Libellula*).	Santa Cruz, Baltra, Floreana
hymenaea Say, 1839, Jour. Acad. Nat. Sci. Philadelphia, vol. 8, p. 18 (*Libellula*).	Floreana

Genus **Tramea**

cophysa darwini Kirby, 1889, Trans. Zool. Soc. London, vol. 12, p. 315, pl. 51, fig. 1.	Isabela, Floreana, San Cristóbal, Española

Genus **Cannacria**

fumipennis Currie, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 387, figs. 31–34.	Isabela

Order MALLOPHAGA

The principal references to Galápagos species are Kellogg and Kuwana (1902), Kellogg (1906), and Ewing (1924). Dr. Theresa Clay has kindly reviewed the manuscript and checked or corrected many of the names after studying types and other specimens in the Kellogg collection. Mr. B. C. Nelson assisted Dr. Clay by locating Galápagos slides in the Kellogg collection at Berkeley and sending them to London. New synonymy and confirmed or corrected identifications by Dr. Clay are marked with an asterisk [*]. The synonymy of *Actornithophilus milleri* is from Timmermann (1954), and generic placement of *Philopterus domesticus* and *P. insulicola* is by Carriker (1957). *Menopon rusticum*, Kellogg, 1896 (not Giebel, 1874), is a *Colpocephalum* (Clay, *in litt.*). For interpretation of the species of *Bruecelia* see Hopkins (1951). Synonymy of *Nirmus curvilineatus* Kellogg & Kuwana is given by Clay (1958), that of *Lipeurus limitatus* (*Halipeurus*) by Edwards (1961), and that of *Docophorus peristictus* by Ward (1953).

Suborder AMBLYCERA

Family MENOPONIDAE

Genus **Actornithophilus**

grandiceps Piaget, 1880, Pédiculines, p. 558, pl. 46, fig. 7 (*Colpocephalum*)*	Santa Cruz
incisus Piaget, 1880, Pédiculines, p. 569, pl. 47, fig. 9 (*Colpocephalum*)	Wolf, Marchena, Fernandina, Isabela, Daphne, Baltra
funebris Kellogg, 1906 (not Kellogg, 1896), Trans. Amer. Ent. Soc., vol. 32, p. 320 (*Colpocephalum*)*	
milleri Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 483, pl. 30, fig. 6 (*Colpocephalum*)*	

Genus **Austromenopon**

albemarlei Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 488, pl. 31, fig. 5 (*Menopon*)	Isabela
becki Kellogg, 1906, Trans. Amer. Ent. Soc., vol. 32, p. 322 (*Menopon*)*	Daphne
narboroughi Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 485, pl. 31, fig. 2 (*Menopon*).	Darwin, Marchena, Fernandina, Baltra
numerosum Kellogg, 1906 (not Kellogg, 1896), Trans. Amer. Ent. Soc., vol. 32, p. 321 (*Menopon*)*	
navigans Kellogg, 1896, Proc. Calif. Acad. Sci., ser. 2, vol. 6, p. 156, pl. 14, figs. 4, 5 (*Menopon*)	Galápagos Islands

Genus **Colpocephalum**

flavescens Haan, 1829, Mem. Mus. Hist. Nat. Paris, vol. 18, p. 309 (*Liotheum*).	Wolf, Santa Cruz
heterosoma Piaget, 1880, Pédiculines, p. 572, pl. 48, figs. 3, 4.*	Santa Cruz
spineum Kellogg, 1899, Occ. Pap. Calif. Acad. Sci., no. 6, p. 38, pl. 4, fig. 1.*	Wolf, Isabela
unciferum Kellogg, 1896, Proc. Calif. Acad. Sci., ser. 2, vol. 6, p. 140, pl. 12, figs. 1–3.	Galápagos Islands

Genus **Cuculiphilus**

snodgrassi Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 486, pl. 31, fig. 3 (*Menopon*). *galapagensis* Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 487, pl. 31, fig. 4 (*Menopon*).	San Cristóbal, Española

Genus **Eidmanniella**

aurifasciata Kellogg, 1899, Occ. Pap. Calif. Acad. Sci., vol. 6, p. 43, pl. 4, fig. 5 (*Menopon*). *fuscofasciatum* Kellogg, 1906 (not Piaget, 1880), Trans. Amer. Ent. Soc., vol. 32, p. 321.*	Wolf, Marchena, Daphne, Baltra, Santa Cruz
singularis Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 485, pl. 31, fig. 1 (*Menopon*).*	Wolf

Genus **Myrsidea**

incerta Kellogg, 1896, Proc. Calif. Acad. Sci., ser. 2, vol. 6, p. 553, pl. 73, fig. 2 (*Menopon*).	Wolf, Marchena, Fernandina, Isabela, Santiago, Santa Cruz, Santa Fé, San Cristóbal, Española

Genus **Trinoton**

lituratum Burmeister, 1838, Handbuch Ent., vol. 2, p. 441 (*Trinotum*).	Santa Cruz
querquedulae Linnaeus, 1758, Systema Naturae, Ed. 10, p. 612 (*Pediculus*). *luridum* Kellogg, 1906 (not Burmeister, 1838), Trans. Amer. Ent. Soc., vol. 32, p. 320.*	Santa Cruz

Family Ricinidae

Genus **Ricinus**

angulatus Kellogg, 1896, Proc. Calif. Acad. Sci., ser. 2, vol. 6, p. 515, pl. 70, fig. 5 (*Physostomum*).	Fernandina

Suborder Ischnocera

Family Philopteridae

Genus **Anatoecus**

icteroides Nitzsch, 1818, Germar's Mag. Ent., vol. 3, p. 290 (*Philopterus*).	Santa Cruz

Genus **Brueelia**

chelydensis Hopkins, 1951, Ann. Mag. Nat. Hist., ser. 12, vol. 4, p. 377. *galapagensis* Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., 4:474 (*Nirmus vulgatus* var.).	Fernandina, Isabela, San Cristóbal, Española
galapagensis Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 464, pl. 28, fig. 4 (*Docophorus*). *galapagensis* Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 471, pl. 29, fig. 5 (*Nirmus*).	Fernandina, Isabela, San Cristóbal
interposita Kellogg, 1896, Occ. Pap. Calif. Acad. Sci., no. 6, p. 23, pl. 2, fig. 7 (*Nirmus*).	Fernandina, Isabela
vulgata Kellogg, 1896, Occ. Pap. Calif. Acad. Sci., no. 6, p. 495, pl. 67, fig. 5 (*Nirmus*).	Isabela

Genus **Columbicola**

?**macrourae** Wilson, 1941, Jour. Parasitol., vol. 27, no. 262, figs. 5–8 (*Esthiopterum*). *baculus* Kellogg & Kuwana, 1902 (not Nitzsch, 1818), Proc. Wash. Acad. Sci., vol. 4, p. 478 (*Lipeurus*).*	Wolf, Marchena, Isabela

Genus **Craspedorrhynchus**

taurocephalus Kellogg, 1896, Proc. Calif. Acad. Sci., ser. 2, vol. 6, p. 471, pl. 65, fig. 1 (*Docophorus*).	Baltra

Genus **Degeeriella**

regalis Giebel, 1866, Zeitschr. Ges. Naturwiss., vol. 28, p. 364 (*Nirmus*). *curvilineata* Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 470, pl. 29, fig. 4 (*Nirmus*). *fusca* Kellogg, 1906 (not Denny, 1842), Trans. Amer. Ent. Soc., vol. 32, p. 318 (*Nirmus*).*	Fernandina, Isabela, Marchena

Genus **Docophoroides**

?**brevis** Dufour, 1835, Ann. Soc. Ent. France, vol. 4, p. 674, pl. 21, fig. 3 (*Philopterus*).	Fernandina
irroratae Timmerman, 1962, Zeitschr. f. Parisitenk., vol. 21, p. 435.	Galápagos Islands
levequei Timmerman, 1963, Bonn. zool. Beitr., vol. 14, p. 158.	Española

Genus **Halipeurus**

attenuatus Edwards, 1961, Jour. Parasitol., vol. 47, p. 148, figs. 3–7 M.	nr. Galápagos Islands
diversus Kellogg, 1896, Proc. Calif. Acad. Sci., ser. 2, vol. 6, p. 123, pl. 8, figs. 3, 4 (*Lipeurus*).	Darwin, Wolf, Isabela
limitatus Kellogg, 1906, Trans. Amer. Ent. Soc., vol. 32, p. 319 (*Lipeurus*).	
intermedius Edwards, 1961, Jour. Parasitol., vol. 47, p. 151, figs. 3–7 S.	Galápagos Islands
major Kellogg & Kuwana, 1902 (not Piaget, 1880), Proc. Wash. Acad. Sci., vol. 4, p. 447 (*Lipeurus diversus* var.).	
pelagicus Denny, 1842, Mon. Anopl. Brit., vol. 58, p. 173, pl. 14, fig. 2 (*Lipeurus*).	Darwin, Wolf, Isabela
exiguus Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 479, pl. 30, fig. 2 (*Lipeurus*).	
languidus Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 475, pl. 28, fig. 8 (*Lipeurus*).	

Genus **Pectinopygus**

annulatus Piaget, 1880, Pédiculines: p. 340, pl. 27, fig. 10 (*Lipeurus*).	Darwin, Wolf, Isabela, Daphne, Baltra, Santa Cruz
fuscomarginatus, Kellogg, 1906 (not Denny, 1842), Trans. Amer. Ent. Soc., vol. 32, p. 318 (*Nirmus*).*	
minor Ewing, 1924, Zoologica, vol. 5, p. 84 (*Esthiopterum potens* var.).*	
potens Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 477, pl. 30, fig. 1 (*Lipeurus*).	
fregatiphagus Eichler, 1843, Zool. Anz. (*Epifrega*).*	Wolf
major Kellogg, 1899, Occ. Pap. Calif. Acad. Sci., no. 6, p. 30, pl. 3, fig. 3 (*Lipeurus gracilicorne* var.).	

nannopteri Ewing, 1924, Zoologica, vol. 5, p. 82, fig. 12 (*Esthiopterum*).*	Galápagos Islands
sulae Rudow, 1869, Beitr. Kenntn. Malloph., p. 43 (*Lipeurus*).	Darwin, Wolf, Marchena, Isabela
helleri Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 479, pl. 30, fig. 3 (*Lipeurus*).*	

Genus **Perineus**

miriceps Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 480, pl. 30, fig. 4 (*Lipeurus*).	Isabela
oblongus Kéler, 1957, Beitr. Ent., vol. 7, p. 523, figs. 27–28.	Galápagos Islands

Genus **Philoceanus**

becki Kellogg, 1903, Biol. Bull. Woods Hole, vol. 5, p. 88, figs. 1, 2.*	Wolf

Genus **Philopterus**

breviformis Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 463, pl. 28, fig. 3 (*Docophorus*).*	Isabela, Santa Cruz
communis Nitzsch, 1818, Germar's Mag. Ent., vol. 3, p. 290.	Fernandina, Española
domesticus Kellogg, 1896, Proc. Calif. Acad. Sci., ser. 2, vol. 6, p. 475, pl. 65, fig. 4 (*Docophorus*).	Santa Cruz
insulicola Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 466, pl. 28, fig. 6 (*Docophorus*).	Isabela

Genus **Physconelloides**

galapagensis Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 481, pl. 30, fig. 5 (*Goniocotes*).*	Wolf, Marchena, Fernandina, Isabela

Genus **Quadraceps**

birostris Giebel, 1874, Insecta Epizoa, p. 174 (*Nirmus*).	Isabela, Baltra, Santa Fé
gloriosa Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 467 (*Nirmus*).*	
paludicola Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 469, pl. 29, fig. 3 (*Nirmus*).*	Isabela
ridgewayi Kellogg, 1906, Trans. Amer. Ent. Soc., vol. 32, p. 317 (*Nirmus*).*	Santa Cruz
separatus Kellogg & Kuwana, 1902, Trans. Wash. Acad. Sci., vol. 4, p. 472, pl. 29, fig. 6 (*Nirmus*).*	Wolf, Marchena, Isabela, Española

strepsilaris Denny, 1842, Mon. Anopl. Brit., pp. 52, 135, pl. 11, fig. 4 (*Nirmus*). *lepidus* Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 473, pl. 29, fig. 7 (*Nirmus*).*	Fernandina, Santa Fé

Genus **Saemundssonia**

albemarlensis Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 465, pl. 28, fig. 5 (*Docophorus*). *melanocephalus* Kellogg & Kuwana, 1902 (not Burmeister, 1838), Proc. Wash. Acad. Sci., vol. 4, p. 462 (*Docophorus*).*	Darwin, Wolf, Fernandina, Isabela, Baltra, Gardner
lari O. Fabricius, 1780, Fauna Groenlandia, p. 219 (*Pediculus*).*	Darwin
minor Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 460 (*Docophorus validus* var.).	Darwin, Fernandina, Isabela, Santa Fé
platygaster Denny, 1842, Mon. Anopl. Brit., pp. 43, 83, pl. 2, fig. 5 (*Docophorus*). *peristicta* Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 462, pl. 28, fig. 2 (*Docophorus*).	Darwin, Isabela, Santa Fé
phaetona Osborn, 1890, Proc. U. S. Nat. Mus., vol. 12, p. 189 (*Docophorus*).*	Wolf, Daphne, Santa Cruz
platycephalus Kellogg & Kuwana, 1902, Proc. Wash. Acad. Sci., vol. 4, p. 461, pl. 8, fig. 1 (*Docophorus*).*	

Genus **Trabeculus**

mirabilis Kellogg, 1896, Proc. Calif. Acad. Sci., ser. 2, vol. 6, p. 138, pl. 11, fig. 7, 8 (*Giebelia*).*	Wolf, Isabela

Order ANOPLURA

Family HAEMATOPINIDAE

Genus **Hoplopleura**

nesoryzomydis Ferris, 1921, Stanford Univ. Publ., Biol. Ser., vol. 2, no. 2, p. 90. *quadridentata* Ferris, 1916 (not Neumann), Psyche, vol. 23, p. 116.	Galápagos Islands

Genus **Polyplax**

spinulosa Burmeister, 1839, "*Rhynchota*" Gen. Ins., p. 8 (*Pediculus*).	Floreana

Order HEMIPTERA

The principal references to Galápagos Hemiptera–Heteroptera are by Stål (1859), Butler (1877), Heidemann (1901), Barber (1925, 1934), and Van Duzee (1933, 1937). Changes since Barber's comprehensive list (1934) are *Dallasiellus* (Froeschner, 1960), *Dicranocephalus* (Scudder, 1957), *Liorhyssus* and *Rhopalus* (Harris, 1943, Iowa State College Jour. Sci., vol. 17, pp. 197–204), *Pentacora sphacelata* (Drake, 1954), *Trigonotylus* (Carvalho and Wagner, 1957), *Polymerus nigritulus* and *Cyrtopeltis modesta* (Carvalho, 1957–1960), and *Halobates* (Herring, 1961). *Trichocorixa* (Hutchinson, 1931) was not identified to species. It is here recorded as *Trichocorixa reticulata* Guerin (Usinger).

Family Cydnidae

Genus **Dallasiellus**

murinus Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 26 (*Geotomus*).	Isabela, San Cristóbal

Family Pentatomidae

Genus **Acrosternum**

viridans Stål, 1859, Fregatten Eugenies Resa, Zool., vol. 1, p. 228 (*Rhaphigaster*).	San Cristóbal, Isabela, Santa Cruz, Santiago

Genus **Thyanta**

setigera Ruckes, 1957, Pan-Pac. Ent., vol. 33, p. 179. *perditor* Heidemann, 1901 (not Fabricius, 1794), Proc. Wash. Acad. Sci., vol. 3, p. 365.	Santa Cruz, Isabela, San Cristóbal, Floreana, Jervis, Gardner, James, N. Seymour
similis Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 26.	Rábida, Floreana

Genus **Podisus**

sordidus Stål, 1859, Fregatten Eugenies Resa, Zool., vol. 1, p. 221 (*Arma*).	Santa Cruz, Isabela, San Cristóbal, Floreana

Genus **Trincavellius**

galapagoensis Butler, 1877, Proc. Zool. Soc. London, 1877, p. 88 (*Sciocoris*).	Floreana

Genus **Alcaeorrhyncus**

grandis Dallas, 1851, List Hemipt. Brit. Mus., vol. 1, p. 91 (*Canthecona*).	Floreana

Family Coreidae

Genus **Anasa**

obscura Dallas, 1852, List Hemipt. Brit. Mus., vol. 2, p. 505.	San Cristóbal

Genus **Dicranocephalus**

insularis Dallas, 1852, List Hemipt. Brit. Mus., vol.	Santa Cruz, Santiago,

2, p. 482 (*Stenocephalus*).	Isabela, Santiago, Santa Cruz
Genus **Harmostes**	
disjunctus Barber, 1925, Zoologica, vol. 5, p. 241. *serratus* Heidemann (not Fabricius), 1901, Proc. Wash. Acad. Sci., vol. 3, p. 365.	Santa Cruz, Isabela
Genus **Liorhyssus**	
hyalinus Fabricius, 1794, Ent. Syst., vol. 4, p. 168 (*Lygaeus*).	Genovesa, Daphne Major
Genus **Rhopalus**	
lugens Signoret, 1859. Ann. Soc. Ent. France, ser. 3, vol. 7, p. 92 (*Corizus*).	Galápagos
Genus **Jadera**	
sanguinolenta Fabricius, 1775, Syst. Ent., p. 721 (*Cimex*).	Wenman
Family Neididae	
Genus **Aknisus**	
galapagensis Barber, 1934, Meded. Zool. Mus., Oslo, vol. 42, p. 284. *tenellus* Heidemann, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 366 (not Stål) (*Jalysus*).	San Cristóbal
Family Lygaeidae	
Genus **Nysius**	
naso Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 27 (*Nysius-Ortholomus*).	Floreana
marginalis Dallas, 1852, List Hemipt. Brit. Mus., vol. 2, p. 556 (? *Nysius*). *galapagensis* Stål, 1860, Freg. Eugenies Resa, Ins., p. 252 (*Cymus*).	Floreana, Santiago, Daphne Major
Genus **Heraeus**	
pacificus Barber, 1925, Zoologica, vol. 5, p. 245.	Santiago
Genus **Orthaea**	
insularis Barber, 1925, Zoologica, vol. 5, p. 246.	Baltra, Santiago, Isabela, Santa Cruz
Family Pyrrhocoridae	
Genus **Dysdercus**	
concinnus Stål, 1861, Öfv. Vet. Akad. Förh., p. 198.	Santa Cruz
Family Tingidae	
Genus **Corythaica**	
cytharina Butler, 1877, Proc. Zool. Soc. Lond., 1877,	Santiago, Daphne

p. 90 (*Monanthia*).	Major
renormata Barber, 1925, Zoologica, vol. 5, p. 251.	

Family REDUVIIDAE

Genus **Ghilianella**

galapagensis Heidemann, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 367.	Isabela, Española

Genus **Repipta**

annulipes Barber, 1925, Zoologica, vol. 5, p. 250.	Santa Cruz, Isabela
species? Heidemann, 1901. Proc. Wash. Acad. Sci., vol. 3, p. 366 (nymph) (*Cosmoclopius-Harpactor*).	

Family NABIDAE

Genus **Nabis**

punctipennis Blanchard, 1852, Gay, Hist. de Chili, Zool., vol. 7, p. 161.	Isabela, Floreana, Santiago

Family CIMICIDAE

Genus **Cimex**

lectularius Linnaeus, 1758, Syst. Nat., 10th ed., p. 441.	Floreana

Family MIRIDAE

Genus **Trigonotylus**

lineatus Butler, 1877, Proc. Zool. Soc. Lond., 1877, p. 89 (*Miris*).	Isabela, Floreana, Seymour

Genus **Psallus**

insularis Barber, 1925, Zoologica, vol. 5, p. 250.	Santiago

Genus **Fulvius**

geniculatus Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 29.	Rábida, San Cristóbal, Santiago, Fernandina, Floreana

Genus **Diaphnidia**

crockeri Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 29.	Santiago

Genus **Dagbertus**

darwini Butler, 1877, Proc. Zool. Soc. Lond., 1877, p. 89 (*Capsus*).	Floreana
quadrinotatus Walker, 1873, Cat. Hem. Heter. Brit. Mus., vol. 6, p. 113 (*Capsus*).	Floreana, Santiago
spoliatus Walker, 1873, Cat. Hem. Heter. Brit. Mus., vol. 6, p. 112 (*Capsus*).	Floreana, Santiago

Genus **Polymerus**

nigritulus Walker, 1873, Cat. Hem. Heter. Brit. Mus., vol. 6, p. 112 (*Capsus*).	Floreana
vegatus Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 28 (*Poeciloscytus*).	Isabela

Genus **Creontiades**

castaneum Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 27.	San Cristóbal
fucosus Barber, 1925, Zoologica, vol. 5, p. 248.	Santiago, Santa Cruz
willowsi Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 28.	Santiago, Santa Cruz, Rábida

Genus **Cyrtopeltis**

modesta Distant, 1893, Biol. Centr.-Amer. Rhynch., vol. 1, p. 447 (*Neosilia*).	Santa Cruz
geniculatus Reuter, 1876, Öfv. K. Vet. Akad. Förh., vol. 36, no. 2, p. 83 (*Engytatus*).	

Genus **Europiella**

mella Van Duzee, 1937, Proc. Calif. Acad. Sci., ser. 4, vol. 22, p. 117.	Santa Cruz

Family SALDIDAE

Genus **Pentacora**

sphacelata Uhler, 1877, Bull. U. S. Geol. Geogr. Survey, vol. 3, p. 434 (*Salda*).	Isabela
rubromaculata Heidemann, 1901, Proc. Wash. Acad. Sci., vol. 3, p. 368 (*Salda*).	

Family GERRIDAE

Genus **Halobates**

micans Eschscholtz, 1822, Entomographien, p. 107	near Santiago, Galápagos
wüllerstorffi Frauenfeld, 1867, Verh. K. K. Zool. Bot. Ges. Wien, vol. 17, p. 458.	
robustus Barber, 1925, Zoologica, vol. 5, p. 253.	Santa Cruz, Floreana, Isabela
sobrinus White, 1883, Voy. Challenger, Rpt. Zool., vol. 7, no. 19, p. 46.	near Galápagos

Family CORIXIDAE

Genus **Trichocorixa**

reticulata Guerin, 1857, *in* Sagra, Hist. Cuba, Ins., p. 423 (*Corisa*).	Galápagos

Order HOMOPTERA

The leading publications on Galápagos Homoptera are Walker (1851), Stål

(1859), Butler (1877), Morrison (1924), Osborn (1924), and Van Duzee (1933, 1937). Reclassification of the Walker and Butler species was by Muir (1919) and W. E. China (*in* Champion, 1924). The most recent placement of Fulgoridae is given in Metcalf (1943, 1954, 1958). Fennah (personal communication) placed *Issus varius* Walker in *Philatis*. Linnavuori (1959) is the authority for generic placement of *Deltocephalus*, *Scaphytopius*, *Amplicephalus*, and *Exitianus*. W. E. China (personal communication) corrected the name *Jassus* of Van Duzee and Osborn. D. A. Young (personal communication) examined the Van Duzee types of Cicadellidae and his generic assignments have been followed. The modern classification of Coccidae is after Ferris (Atlas of Scale Insects of North America, Stanford University). H. L. McKenzie kindly reviewed the manuscript on Coccidae.

Family FULGORIDAE

Sub-family CIXIINAE

Genus **Nymphocixia**

unipunctata Van Duzee, 1923, Proc. Calif. Acad. Sci., ser. 4, vol. 12, p. 189.	Isabela, Santa Cruz

Genus **Oliarus**

galapagensis Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 33.	Isabela, Santa Cruz

Sub-family ISSINAE

Genus **Philatis**

breviceps Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 33.	Floreana
cinerea Osborn, 1924, Zoologica, vol. 5, p. 78.	Genovesa
major Osborn, 1924, Zoologica, vol. 5, p. 79.	Santa Cruz
producta Stål, 1859, Fregatten Eugenies Resa, Ins., p. 278 (*Mycterodus*).	Isabela, Seymour, Genovesa, Santa Cruz
serva Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 34.	Isabela, ? Santiago
varia Walker, 1851, List Homopt. Brit. Mus., vol. 2, p. 372 (*Issus*). New combination.	Santiago
vicina Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 34.	Rábida

Genus **Euthiscia**

crockeri Van Duzee, 1937, Proc. Calif. Acad. Sci., ser. 4, vol. 22, p. 119.	Santa Cruz

Genus **Galapagosana**

rostrifer Butler, 1877, Proc. Zool. Soc. Lond., 1877, p. 90 (*Issus*).	Floreana

Sub-family DELPHACINAE

Genus **Delphacodes**

substitua Walker, 1851, List Homopt. Brit. Mus., vol. 2, p. 354 (*Delphax*).	Floreana, Santiago
vicaria Walker, 1851, List Homopt. Brit. Mus., vol. 2, p. 355 (*Delphax*).	Floreana, Santiago

Genus **Ilburnia**

simulans Walker, 1851, List Homopt. Brit. Mus., vol. 2, p. 355 (*Delphax*).	Santiago, Floreana

Family CICADELLIDAE

Genus **Deltocephalus**

insularis Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 30 (possibly an *Amplicephalus* Linnavuori, 1959).	San Cristóbal, Floreana

Genus **Scaphytopius**

aequinoctialis Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 30 (*Platymetopius*).	Isabela, ? Santiago
retusus Van Duzee, 1937, Proc. Calif. Acad. Sci., ser. 4, vol. 22, p. 123 (*Platymetopius*).	Santa Cruz

Genus **Sanctonus**

discalis Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 31 (*Scaphoideus*).	San Cristóbal

Genus **Exitianus**

digressus Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 32 (*Athysanus*).	San Cristóbal, Santiago, Seymour, Rábida

Genus **Agalliopsis**

mera Van Duzee, 1937, Proc. Calif. Acad. Sci., ser. 4, vol. 22, p. 123.	Santa Cruz

Genus **Agallia**

planus Butler, 1877, Proc. Zool. Soc. Lond., 1877, p. 91 (*Jassus*).	Floreana
striolaris Butler, 1877, Proc. Zool. Soc. Lond., 1877, p. 91. (*Jassus*).	Floreana

Genus **Coelidia**

infesta Van Duzee, 1937, Proc. Calif. Acad. Sci., ser. 4, vol. 22, p. 124 (*Jassus*).	Santa Cruz
galapagoensis Osborn, 1924, Zoologica, vol. 5, no. 6, p. 77 (*Jassus*).	Santiago, Santa Cruz

Genus **Mesamia**

obliquus Walker, 1851, List Homopt. Brit. Mus., vol. 3, p. 851 (*Acrocephalus*).	

Genus **Balclutha**

lucidus Butler, 1877, Proc. Zool. Soc. Lond., 1877, p. 91 (*Jassus*).	Santiago

Family Coccidae

Genus **Margarodes**

similis Morrison, 1924, Zoologica, vol. 5, p. 143, fig. 33.	Santa Cruz, Eden, Baltra

Genus **Orthezia**

galapagoensis Kuwana, 1902, Jour. New York Ent. Soc., vol. 10, p. 28.	Isabela, Santa Cruz, Duncan

Genus **Eriococcus**

papillosus Morrison, 1924, Zoologica, vol. 5, p. 145.	Santa Cruz

Genus **Asterolecanium**

pustulans Cockerell, 1892. Jour. Inst. Jamaica, vol. 1, p. 143 (*Asterodiaspis*).	Isabela

Genus **Saissetia**

hemisphaerica Targioni-Tozzetti, 1867. Studii sul. Cocc., vol. 11, p. 26 (*Lecanium*).	Isabela, San Cristóbal

Genus **Coccus**

hesperidum var. **pacificum** Kuwana, 1902, Jour. New York Ent. Soc., vol. 10, p. 30 (*Lecanium*).	Abingdon, Isabela, Baltra

Genus **Melanaspis**

obtusa Ferris, 1941, Atlas of Scale Ins. N. America, S III, p. 362.	Isabela
smilacis Kuwana, 1902. Jour. N. Y. Ent. Soc., vol. 10, p. 32 (not Comstock).	

Genus **Hemiberlesia**

lataniae Signoret, 1869, Ann. Soc. Ent. France, ser. 4, vol. 9, p. 124 (*Aspidiotus*).	Abingdon

Genus **Phenacoccus**

parvus Morrison, 1924, Zoologica, vol. 5, p. 147.	Tower

Genus **Pseudococcus**

galapagoensis Morrison, 1924, Zoologica, vol. 5, p. 148.	Santa Cruz, (Eden)
insularis Morrison, 1924, Zoologica, vol. 5, p. 150.	Baltra

Genus **Ceroplastes**

sp. Morrison, 1924, Zoologica, vol. 5, p. 152.	Santa Cruz, (Eden), Baltra

Order Neuroptera

The principal references are Banks (1924) and Esben-Petersen (1934).

The list was checked by D. E. Kimmins (personal communication).

Family Myrmeleonidae

Genus **Myrmeleon**

perpilosus Banks, 1924, Zoologica, vol. 5, p. 177.	Santa Cruz
sp., Esben-Petersen, 1934, Nyt Mag. f. Naturvidensk., vol. 74, p. 293, fig. 3 (larva).	Floreana

Genus **Dimares**

formosus Banks, 1908, Proc. Ent. Soc. Washington, vol. 9, p. 31.	S. Elena
nummatus Navas, 1912, Ann. Soc. Sci. Bruxelles, vol. 36, p. 229, fig. 16.	

Family Chrysopidae

Genus **Chrysopa**

nigripilosa Banks, 1924, Zoologica, vol. 5, p. 177.	Baltra
galapagoensis Banks, 1924, Zoologica, vol. 5, p. 179.	Baltra
wollbaeki Esben-Petersen, 1934, Nyt Mag. f. Naturvidensk., vol. 74, p. 291, figs. 1–2.	Floreana

Family Hemerobiidae

Genus **Megalomus**

darwini Banks, 1924, Zoologica, vol. 5, p. 179.	Santa Cruz

Order COLEOPTERA

The major contributors to our knowledge of the Galápagos Coleoptera have been G. R. Waterhouse (1845), Boheman (1859), C. Waterhouse (1877), Mutchler (1925, 1938), Blair (1928, 1933), and Van Dyke (1953). The present summary is based largely on Van Dyke, supplemented by descriptions or taxonomic treatment of Galápagos beetles appearing since 1953. Three of the most doubtful of the records reported by Blair (1933), *Doryphora guerina* Stål, *Diabrotica ventricosa* Jacoby, and *Physonota alutacea* Boheman, were excluded by Van Dyke and we have not restored them to the list. However, other dubious records remain and these are indicated with a question mark in front of the recorded Galápagos locality. R. F. Smith (personal communication) examined the type of *Diabrotica limbata* Waterhouse and found that it belongs to the genus *Acalymma*. This altered generic assignment is indicated below and the new combination should be credited to him.

Family Cicindelidae

Genus **Cicindela**

galapagoensis W. Horn, 1915, Genera Insectorum, Fasc. 82, p. 402.	Isabela
vonhageni Mutchler, 1938, Amer. Mus. Nov., no. 981, p. 2, pl. 1, fig. 1.	Santa Cruz

Family CARABIDAE

Genus **Calosoma**

darwiniana Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 10, pl. 1, f. 3.	Isabela
galapageium Hope, 1838, Trans. Ent. Soc. London, vol. 2, p. 130.	Santiago
howardi Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 251.	Darwin, Isabela, Santiago, Pinzón, Santa Cruz, Baltra, San Cristóbal, Floreana
galapagoum Howard (not Hope), 1889, Proc. U. S. Nat. Mus., vol. 12, p. 191.	
galapageium Breuning (not Hope), 1927, Koleopt. Rundschau, vol. 13, p. 140.	
linelli Mutchler, 1925, Zoologica, vol. 5, p. 221.	San Cristóbal
galapageium Linell (not Hope), 1898, Proc. U. S. Nat. Mus., vol. 21, p. 250.	

Genus **Scarites**

galapagoensis Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 253.	San Cristóbal
williamsi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., vol. 22, p. 13, pl. 2, fig. 3.	Isabela

Genus **Bembidion**

equatoriale Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 15.	San Cristóbal
galapagoensis G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 23 (*Notaphus*).	Pinta, Santiago

Genus **Tachys**

beebei Mutchler, 1925, Zoologica, vol. 5, p. 223, fig. 42.	Baltra

Genus **Feronia**

becki Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 24.	Santiago
blairi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 19.	Santiago
calathoides G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 21.	San Cristóbal
duncani Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 21, pl. 2, fig. 4.	Pinzón
galapagoensis G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 21.	Santiago
insularis Boheman, 1858, Fregatten Eugenies Resa, vol. 1, p. 14.	Isabela

mutchleri Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 20.	Isabela
waterhousei Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 17.	Floreana
williamsi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 21.	Santa Cruz

Genus **Agonum**

albemarli Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 27.	Isabela
chathami Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 26, pl. 2, fig. 9.	San Cristóbal
darwini Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 25, pl. 2, figs. 7, 8.	San Cristóbal

Genus **Selenophorus**

galapagoensis G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 22.	San Cristóbal, Floreana, Española, Gardner
obscuricornis G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 22 (*Amblygnathus*).	Isabela
wenmani Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., vol. 22, p. 29.	Wolf

Family DYTISCIDAE

Genus **Copelatus**

galapagoensis G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 23.	Isabela, San Cristóbal

Genus **Rhantus**

sp. (*signatus* Fabricius?) Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 32.	San Cristóbal

Genus **Thermonectes**

basillaris galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 33. *incisus* var. C. Waterhouse, 1877, Proc. Zool. Soc. London, vol. 5, p. 79, 82 (*Acilius*). *basillaris* Mutchler (not Harris), 1925, Zoologica, vol. 5, p. 225.	Isabela, Baltra, San Cristóbal, Floreana

Genus **Eretes**

sticticus Linnaeus, 1767, Systema Naturae, ed. 12, p. 666 (*Dytiscus*). *occidentalis* C. Waterhouse (not Erickson), 1877, Proc. Zool. Soc. London, vol. 5, p. 77 (*Eunectes*).	Santa Cruz, San Cristóbal, Floreana

Family Gyrinidae

Genus **Gyrinus**

galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 34.	San Cristóbal

Family Hydrophilidae

Genus **Ochthebius**

batesoni Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 473.	San Cristóbal ?

Genus **Tropisternus**

lateralis Fabricius, 1775, Systema Entomologia, p. 28 (*Hydrophilus*).	Santiago, San Cristóbal, Floreana

Genus **Enochrus**

obscurus Sharp, 1882, Biologia Centr.-Americana, Coleoptera, vol. 1, no. 2, p. 69 (*Philhydrus*).	San Cristóbal, Floreana
waterhousei Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 473.	? San Cristóbal

Genus **Galapagodacnum**

darwini Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 474 (*Coelostoma*).	Pinta, Brattle, Genovesa

Family Staphylinidae

Genus **Bledius**

aequatorialis Mutchler, 1925, Zoologica, vol. 5, p. 225, fig. 43.	Baltra

Genus **Criophilus**

villosus Gravenhorst, 1802, Coleopt. Microptera Brunsvicensis, p. 160.	Isabela, San Cristóbal

Family Histeridae

Genus **Carcinops**

galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 38.	Pinta, Genovesa, Santa Cruz
tenellus Erickson, 1834, *in* King, Jahrb. Ins., vol. 1, p. 170 (*Paramalus*).	Isabela, Santiago

Genus **Saprinus**

batesoni Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 475.	Eden, ? San Cristóbal
modestior Marseul, 1845, Mon., p. 493, pl. 19, fig. 110.	Pinta

Family Lycidae

Genus **Calocladon**

testaceum Gorham, 1881, Biologia Centr.-Americana, Coleoptera, vol. 3, no. 2, p. 28, pl. 2, fig. 20.	? San Cristóbal

Family Cantharidae

Genus **Chauliognathus**

sulphureus C. Waterhouse, 1878, Trans. Ent. Soc. London, 1878, p. 331.	? San Cristóbal

Family Melyridae

Genus **Ablechrus**

flavipes C. Waterhouse, 1877, Proc. Zool. Soc. London, p. 79.	San Cristóbal
darwinii C. Waterhouse, 1877, Proc. Zool. Soc. London, p. 81.	

Family Cleridae

Genus **Pelonium**

longfieldae Blair, 1928, Ann. Mag. Nat. Hist., ser. 10, vol. 1, p. 677.	Isabela, Santiago, San Cristóbal, Floreana

Genus **Necrobia**

rufipes De Geer, 1775, Mem., vol. 5, p. 165, pl. 15, fig. 4.	Cosmopolitan

Family Oedemeridae

Genus **Oxacis**

galapagoensis Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 266.	Isabela, Santiago, San Cristóbal, Floreana, Española
pilosa Champion, 1890, Biologia Centr.-Amer., Coleoptera, vol. 4, no. 2, p. 156, pl. 7, fig. 15.	Santiago

Genus **Alloxacis**

collenettei Blair, 1928, Ann. Mag. Nat. Hist., ser. 10, vol. 1, p. 673.	Isabela, Santiago, Santa Cruz, Baltra
hoodi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 43.	Española
seymourensis Mutchler, 1925, Zoologica, vol. 5, p. 226.	Baltra

Family Mordellidae

Genus **Mordellistena**

galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 44.	Genovesa

Family Meloidae

Genus **Cissites**

maculata Swederus, 1787, Svenska Vetensk. Avhandl. Natursk., p. 199, pl. 8, fig. 8 (*Cucujus*).	Santa Cruz, Baltra, San Cristóbal

Family Elateridae

Genus **Conoderus**

galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 45, pl. 6, fig. 4.	Isabela, San Cristóbal, Floreana

Genus **Physorinus**

batesoni Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 51.	Isabela
blairi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 50.	Santiago
chathami Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 51.	San Cristóbal
dichroa Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 47.	Santiago
hoodi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 49.	Española
quirsfeldi Mutchler, 1938, Amer. Mus. Novitates, no. 981, p. 4.	Santa Cruz
ruficeps Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 48.	Isabela

Genus **Anchastus**

galapagoensis G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 25 (*Physorhinus*).	Galápagos Islands
williamsi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 53.	Santa Cruz

Genus **Heterocrepedius**

puberulus Boheman, 1858, Fregatten Eugenies Resa, vol. 1, p. 66.	Galápagos Islands

Genus **Aeolus**

fuscatus Steinhal, 1875, Coleopt. Hefte, vol. 14, p. 125.	Santa Cruz, Floreana

Genus **Grammophorus**

galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., ser. 4, vol. 22, p. 55.	Pinzón, Santa Cruz

Genus **Coptostethus**

williamsi Mutchler, 1925, Zoologica, vol. 5, p. 227, fig. 44.	Pinta, Marchena, Baltra

Family Buprestidae

Genus **Chrysobothris**

williamsi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 56, pl. 6, fig. 6.	Isabela, Pinzón, San Cristóbal

Genus **Mastogenius**

cuneaticollis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 58.	Pinzón, Santa Cruz
galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 57.	Gardner

Family Dermestidae

Genus **Dermestes**

carnivorus Fabricius, 1775, Syst. Ent., p. 55.	Isabela, San Cristóbal
maculatus De Geer, 1774, Mem. Ins., vol. 4, p. 223.	Santiago

Family Ostomidae

Genus **Temnochila**

galapagoensis Mutchler, 1938, Amer. Mus. Novitates, no. 981, p. 5, fig. 4.	Isabela, Santiago, Santa Cruz

Genus **Tenebroides**

sp., Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 61.	Isabela

Family Nitidulidae

Genus **Stelidota**

insularis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 61.	Santa Cruz, San Cristóbal

Genus **Haptonchus**

luteolus Erickson, 1843, Zeitschr. f. Ent., vol. 4, p. 272 (*Epuraea*).	Isabela

Family Cucujidae

Genus **Silvanus**

tropicalis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 62.	Santa Cruz

Family Monotomidae

Genus **Bactridium**

insularis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 63.	Santa Cruz

Family Discolomidae

Genus **Fallia**

colorata John, 1959, Senckenbergiana Biol., vol. 40, p. 295, pl. 35, figs. 2a–2e.	Santa Cruz

galapagana John, 1959, Senckenbergiana Biol., vol. 40, p. 295, fig. 2.	Santa Cruz

Family Colydiidae

Genus **Bitoma**

exarata Pascoe, 1866, Jour. Ent., vol. 2, p. 91, pl. 5, fig. 8 (*Coniophaea*).	Isabela

Family Languriidae

Genus **Comptocarpus**

longicollis Motschulsky, 1860, *in* Schrenck, Reisen u. Forschungen im Amurlande, vol. 2, no. 2, p. 244.	San Cristóbal

Family Coccinellidae

Genus **Scymnus**

galapagoensis G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 41.	Fernandina, Santa Cruz

Genus **Cycloneda**

sanguinea Linnaeus, 1763, Centurea Ins., p. 10.	Genovesa, Santa Cruz, Floreana

Genus **Olla**

abdominalis Say, 1824, Jour. Acad. Nat. Sci., Philadelphia, vol. 4, p. 95.	Santa Cruz

Genus **Adalia**

galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 65.	Isabela, Floreana

Genus **Psyllobora**

bisigma Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 66.	Isabela

Family Alleculidae

Genus **Lobopoda**

galapagoensis Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 266.	Floreana
Allecula sp., Howard, 1889, Proc. U. S. Nat. Mus., vol. 12, p. 191.	

Genus **Allecula**

galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., vol. 22, p. 67.	Santiago, Santa Cruz
insularis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 68.	Isabela, Santa Cruz

Genus **Ctesia**

pedinoides Mäklin, 1875, Acta Soc. Sci. Fennica, vol. 10, p. 681.	? San Cristóbal

Family Tenebrionidae

Genus **Stomion**

cribricollis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 75, pl. 3, fig. 3.	Darwin, Wolf
galapagoensis G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 29.	San Cristóbal, Floreana, Española
carinipenne Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 262.	
carinatipenne Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 477.	
piceum Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 262.	
punctipennis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 72 (*galapagoensis* subsp.).	
helopoides G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 30.	Genovesa, San Cristóbal, Floreana, Española, Gardner
laevigatum G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 30.	Santiago, Floreana
bauri Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 263.	
linelli Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 478.	Genovesa, Eden, Santa Cruz
laevigatum Linell (not Waterhouse), 1898, Proc. U. S. Nat. Mus., vol. 21, p. 263.	
mutchleri Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 477.	
longicornis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 79, pl. 3, fig. 7.	Española
longulum Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 76, pl. 3, fig. 4.	Isabela, Santa Cruz
obesum Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 74.	Pinzón, Brattle, Santa Fé
rugosum Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 80.	Pinta

Genus **Perepitragus**

fuscipes Latreille, 1833, Humb. et Bonpl. Voy., vol. 2, p. 64, pl. 34, fig. 5.	San Cristóbal

Genus **Ammophorus**

abingdoni Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 96, pl. 4, fig. 7.	Pinta
antennatus Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 90.	Santa Fé
bifoveatus bifoveatus G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 31.	Santiago
bifoveatus barringtoni Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 96.	Santa Fé
cooksoni C. Waterhouse, 1877, Proc. Zool. Soc. London, vol. 5, p. 80.	Brattle, San Cristóbal, Floreana
caroli Linell, 1892, Proc. U. S. Nat. Mus., vol. 21, p. 264.	
denticollis Boheman, 1858, Fregatten Eugenies Resa, vol. 1, p. 89.	? Galápagos Islands
galapagoensis G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 30.	San Cristóbal
laevis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 86, pl. 4, fig. 2 (*galapagoensis* subsp.).	
subpunctatus Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 86, pl. 4, fig. 2 (*galapagoensis* subsp.).	
insularis Boheman, 1858, Fregatten Eugenies Resa, vol. 1, p. 89.	Isabela, San Cristóbal
obscurus G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 32.	Isabela, Pinzón, Eden, Santa Cruz
simplex Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 87.	San Cristóbal

Genus **Pedonoeces**

apicalis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 105.	Genovesa
barringtoni Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 109, pl. 5, fig. 9.	Santa Fé
batesoni Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 479.	Eden
blairi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 103.	Floreana
bauri Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 265.	San Cristóbal
caudatus Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 104, pl. 5, fig. 2.	Española

costatus G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 35.	Santiago
duncani Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 110.	Pinzón
galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 107.	Santiago
lugubris Boheman, 1858, Fregatten Eugenies Resa, vol. 1, p. 91, pl. 1, fig. 5 (*Tessaroma*).	Pinta, Isabela, Eden, Santa Cruz, Española
morio Boheman, 1858, Fregatten Eugenies Resa, vol. 1, p. 92 (*Tessaroma*).	Santiago, Santa Cruz
opacus Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 114.	Rábida
pubescens G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 36.	San Cristóbal
spatulus Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 108, pl. 5, fig. 5.	Española, Gardner
uniformis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 105.	San Cristóbal
wenmani Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 100, pl. 5, fig. 1.	Wolf
williamsi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 112.	Santa Cruz

Genus **Phaleria**

manicata Boheman, 1858, Fregatten Eugenies Resa, vol. 1, p. 92.	Isabela, Floreana, Española

Genus **Gnathocerus**

cornutus Fabricius, 1798, Entom. Syst., Suppl., p. 51 (*Trogosita*).	Isabela, Santiago

Genus **Alphitobius**

laevigatus Fabricius, 1781, Species Ins., vol. 1, p. 304.	Floreana

Genus **Rhacius**

costipennis Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 480.	Santiago

Genus **Prateus**

dentatus Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 119.	Santa Cruz

Family Anobiidae

Genus **Trichodesma**

denticollis Blair, 1928, Ann. Mag. Nat. Hist., ser. 10, vol. 1, p. 675.	Floreana

Genus **Thaptor**

galapagoensis Blair, 1928, Ann. Mag. Nat. Hist., ser. 10, vol. 1, p. 676.	Isabela, Santiago, Santa Cruz, Floreana

Genus **Eupactus**

alutaceus Blair, 1928, Ann. Mag. Nat. Hist., ser. 10, vol. 1, p. 677.	Santiago
georgicus Blair, 1928, Ann. Mag. Nat. Hist., ser. 10, vol. 1, p. 676.	Floreana

Family Bostrichidae

Genus **Tetrapriocera**

longicornis Olivier, 1795, Entomologie, vol. 4, no. 77, p. 15, pl. 3, fig. 18 (*Apate*).	Pinzón, Santa Cruz

Genus **Micrapate**

scabratus Erickson, 1847, Wiegm. Arch. f. Naturg., vol. 13, no. 1, p. 87 (*Rhizopertha*).	San Cristóbal

Genus **Amphicerus**

cornutus galapaganus Lesne, 1910, Bull. Mus. Hist. Nat. d'Hist. Naturelle, vol. 16, p. 184 (*Schistoceros*).	Wolf, Pinta, Isabela, Pinzón, Santa Cruz, Española
sp., G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 36 (*Apate*).	
unicantus C. Waterhouse, 1877, Proc. Zool. Soc. London, p. 82 (*Bostrichus*).	
punctipennis Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 256.	

Family Scarabaeidae

Genus **Copris**

lugubris Boheman, 1858, Fregatten Eugenies Resa, vol. 1, p. 42.	? Galápagos Islands

Genus **Ataenius**

aequatorialis Petrovitz, 1961, Entomologische Arb., vol. 12, p. 355.	Santa Cruz
arrowi Hinton, 1936, Ann. Mag. Nat. Hist., ser. 10, vol. 17, p. 414.	Pinta, Isabela, Santa Cruz
cribrithorax, Blair, 1933 (not Bates, 1887), Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 476.	
dampieri Petrovitz, 1961, Entomologische Arb., vol. 12, p. 356.	Floreana
scutellaris Harold, 1867, Coleopterologische Hefte, vol. 18, p. 82.	Pinta, Isabela, San Cristóbal, Floreana

Genus **Trox**

galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 124, pl. 6, fig. 7.	Darwin
suberosus Fabricius, 1775, Systema Ent., p. 31.	Pinta, Isabela, Santiago, Santa Cruz, San Cristóbal, Floreana, Española
seymourensis Mutchler, 1925, Zoologica, vol. 5, p. 229.	Pinta, Isabela, Baltra

Genus **Neoryctes**

galapagoensis G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 26 (*Oryctes*).	Isabela, San Cristóbal, Floreana
linelli Mutchler, 1938, Amer. Mus. Novitates, no. 981, p. 10, figs. 10–12.	San Cristóbal
sp., Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 126.	Santa Cruz

Family PASSALIDAE

Genus **Passalus**

interruptus Linnaeus, 1767, Systema Naturae, ed. 12, p. 560 (*Lucanus*).	Floreana
tlascala Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 257.	

Family CERAMBYCIDAE

Genus **Parandra**

galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 127.	Isabela, Santiago, Santa Cruz

Genus **Stenodontes**

galapagoensis Mutchler, 1925, Amer. Mus. Novitates, no. 981, p. 11, fig. 6.	Santa Cruz
molarius Bates, 1879, Biol. Centr.-Americana, vol. 5, p. 9 (*Mallodon*).	Santa Cruz, San Cristóbal, Floreana

Genus **Strongylaspis**

kraepelini Lameere, 1903, Mem. Soc. Ent. Belgique, vol. 11, p. 28.	Santiago

Genus **Achryson**

galapagoensis Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 259.	Baltra, San Cristóbal

Genus **Eburia**

amabilis Boheman, 1859, Fregatten Eugenies Resa, vol. 1, p. 150.	? Galápagos Islands

lanigera Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 259. *amabilis* Howard, 1890, Proc. U. S. Nat. Mus., vol. 12, p. 192.	Isabela, Santiago, Rábida, Pinzón, Eden, San Cristóbal, Floreana, Española, Gardner
proletaria Erickson, 1847, Arch. f. Naturgesch., vol. 13, p. 140. *bauri* Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 260.	Santiago, San Cristóbal
Genus **Compsa**	
apicalis Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 481.	Santiago
Genus **Desmiphora**	
hirticollis Olivier, 1795, Entomologie, vol. 4, no. 68, p. 11, pl. 4, fig. 37 (*Saperda*).	Santiago
Genus **Estoloides**	
galapagoensis Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, no. 11, p. 482 (*Estola*).	Isabela, Santa Cruz
Genus **Estola**	
cribrata Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 483.	Isabela
duncani Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 135.	Pinzón
insularis Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, no. 11, p. 483.	Isabela, Santiago, Santa Cruz
Genus **Acanthoderes**	
galapagoensis Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 261. *vonhageni* Mutchler, 1938, Amer. Mus. Novitates, no. 981, p. 14 (*galapagoensis* var.).	Isabela, Santiago, Santa Cruz, San Cristóbal
Genus **Leptostylus**	
galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 136, pl. 7, fig. 1.	Isabela, Santiago
williamsi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 137.	Santiago, Rábida, Santa Cruz
Genus **Taeniotes**	
hayi Mutchler, 1938, Amer. Mus. Novitates, no. 981, p. 13, fig. 3.	? Galápagos Islands
Family CHRYSOMELIDAE	
Genus **Metachroma**	
labrale Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 484.	Isabela, Santiago, Santa Cruz

Genus **Gynandrobrotica**

ventricosa Jacoby, 1887, Biol. Centr.-Amer., Coleoptera, vol. 6, p. 543, pl. 32, fig. 1 (*Diabrotica*).	? San Cristóbal

Genus **Acalymma**

limbata C. Waterhouse, 1877, Proc. Zool. Soc. London, 1877, p. 81 (*Diabrotica*).	? Galápagos Islands

Genus **Docema**

darwini Mutchler, 1924, Zoologica, vol. 5, p. 230.	Genovesa, Eden
galapagoensis G. R. Waterhouse, 1845, Ann. Mag. Nat. Hist., vol. 16, p. 39 (*Haltica*).	Isabela, Rábida, Floreana

Genus **Longitarsus**

galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 140.	Santa Cruz, San Cristóbal, Floreana
lunatus C. Waterhouse, 1877, Proc. Zool. Soc. London, 1877, p. 81.	

Family Bruchidae

Genus **Spermophagus**

galapagoensis Blair, 1928, Ann. Mag. Nat. Hist., ser. 10, vol. 1, p. 678.	Santiago, Española

Genus **Bruchus**

fuscomaculatus Blair, 1928, Ann. Mag. Nat. Hist., ser. 10, vol. 1, p. 679.	Santiago

Family Anthribidae

Genus **Ormiscus**

variegatus G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 37.	Pinta, Isabela, Gardner, Floreana

Family Curculionidae

Genus **Amphideritus**

cuneiformis G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 38 (*Otiorhynchus*).	San Cristóbal, Floreana

Genus **Pantomorus**

blairi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 146.	Santiago
caroli Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 147.	Floreana
conwayensis Mutchler, 1938, Amer. Mus. Novitates, no. 981, p. 15.	Santa Cruz
crockeri Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 147.	Genovesa

galapagoensis Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 268.	San Cristóbal
williamsi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 150.	Isabela

Genus Gerstaeckeria

galapagoensis barringtoni Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 152.	Santa Fé
galapagoensis galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 151, pl. 7, fig. 8.	Pinta
galapagoensis hoodensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 153.	Española
galapagoensis seymourensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 153.	Baltra

Genus Gerais

batesoni Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 9, p. 485.	San Cristóbal

Genus Lembodes

subcostatus Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 154, pl. 7, fig. 2.	Isabela, Pinzón

Genus Anchonus

galapagoensis G. R. Waterhouse, 1845, Ann. Nat. Hist., vol. 16, p. 39.	Santiago

Genus Dryotribus

mimeticus Horn, 1873, Proc. Amer. Philos. Soc., 13: 433.	Fernandina

Genus Micrancylus

gracilis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 156.	Pinta

Genus Neopentarthrum

cunicollis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 157.	Isabela, Pinzón
glabrum Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 158.	Pinta, Española
mutchleri Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 158.	Pinta
towerensis Mutchler, 1925, Zoologica, vol. 5, p. 231, fig. 45.	Genovesa

Family PLATYPODIDAE

Genus Platypus

santacruzensis Mutchler, 1925, Zoologica, vol. 5, p. 232, fig. 24.	Isabela, Santa Cruz

Family Scolytidae

Genus **Pycnarthrum**

insulare Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 478.	Genovesa, Isabela, Española

Order LEPIDOPTERA

Comprehensive works on Galápagos Lepidoptera are by Williams (1911) for butterflies and hawk moths and Schaus (1923) for other moths. Meyrick (1926) described additional Microlepidoptera, some of which have been revised by Clark (1958). Richards (1941) dealt with the Noctuidae collected on Hancock expeditions. Beebe (1923) gives field notes for his collections of Lepidoptera. Burns (1964) clarifies the Van Duzee record of *Erynnis* (Hesperiidae). Kernbach (1962) gives the most recent review of Sphingidae. E. G. Munroe (personal communication) has indicated generic placements in the Pyralidae, J. A. Powell in the Tortricidae, and R. J. Collins (personal communication) has checked bibliographic references throughout. In Washington, sections of the manuscript were reviewed as follows:

D. R. Davis (USNM)—Tortricidae (Olethreutinae), Tineidae; W. D. Duckworth (USNM)—Pyralidae (Phycitinae), Yponomeutidae; W. D. Field (USNM)—Pieridae, Nymphalidae, Danaidae, Lycaenidae, Hesperidae, Springidae, Arctiidae; R. W. Hodges (USDA)—Pyralidae (Pyraustinae, Crambinae), Pterophoridae, Tortricidae (Tortricinae), Gelechiidae, Blastobasidae; E. L. Todd (USDA)—Noctuidae, Geometridae.

Suborder RHOPALOCERA

Family Pieridae

Genus **Phoebis**

sennae Linnaeus, 1766, Syst. Nat., Ed. 12, p. 764 (*Papilio Danaus*) (form *sennae* Edwards *fide* Williams, 1911).	Isabela, San Cristóbal, Floreana, Santa Cruz, Santiago, Fernandina, Eden, Daphne, Baltra, Pinta

Family Nymphalidae

Genus **Agraulis**

vanillae galapagensis Holland, 1889, Proc. U. S. National Mus., vol. 12, p. 194 (as var.).	Isabela, Floreana, San Cristóbal, Santa Cruz, Santiago, Fernandina, Pinta, Baltra, Eden

Genus **Vanessa**

virginiensis Drury, 1773, Ill. Exot. Ent., 2, pl. 13, fig. 2 (*Papilio*).	Isabela
carye Hübner, 1945, Samml. exot. Schmet., vol. 1, pl. 41 (*Vanessa*).	San Cristóbal

Family Danaïdae

Genus **Danaus**

plexippus Linnaeus, 1758, Syst. Nat. Ed. 10, p. 471 (*Papilio Danaus*).	San Cristóbal

Family Lycaenidae

Genus **Leptotes**

parrhasioides Wallengren, 1860, Wien. Ent. Monat., vol. 4, p. 37 (*Lycaena*).	Floreana, San Cristóbal, Isabela, Fernandina, Santiago, Española, Pinzón, Santa Cruz, Eden, Baltra

Family Hesperiidae

Genus **Urbanus**

dorantes galapagensis Williams, 1911, Proc. Calif. Acad. Sci., ser. 4, vol. 1, p. 303.	San Cristóbal, Isabela, Española, Pinzón, Floreana, Santiago, Santa Cruz, Genovesa, Eden, Baltra

Genus **Erynnis**

funeralis Scudder and Burgess, 1870, Proc. Boston Soc. Nat. Hist., vol. 13, p. 293 (*Nisoniades*). *persius* Van Duzee, 1933 (not Scudder, 1864), Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 145 (*Thanaos*). (Van Duzee suggests an error in labeling).	San Cristóbal

Genus **Heteropia**

sp. near **imalena** Butler, 1874, Lep. Exot., p. 109, pl. 40, fig. 1 (*Telegonus*). (Van Duzee, 1933, suggests error in labeling).	Isabela

Suborder HETEROCERA

Family Sphingidae

Genus **Agrius**

cingulatus Fabricius, 1775, Syst. Ent., p. 545 (*Sphinx*).	San Cristóbal, Isabela, Santa Cruz, Baltra, Floreana

Genus **Protoparce**

sexta leucoptera Rothschild and Jordan, 1903, Nov. Zool. Suppl., vol. 9, p. 79.	San Cristóbal, Isabela, Santa Cruz
rustica calapagensis Holland, 1889, Proc. U. S. Nat. Mus., vol. 12, p. 195.	Floreana, San Cristóbal, Española, Isabela, Baltra, Santa Cruz, Genovesa
nigrita Rothschild and Jordan, 1903, Nov. Zool. Suppl., vol. 9, p. 86 (*rustica* ab.).	
postscripta Clark, 1926, Proc. New England Zool. Club, vol. 9, p. 70 (*rustica* subsp.).	

Genus **Erinnyis**

alope dispersa Kernbach, 1962, Opusc. Zool., vol. 63, p. 9.	Santa Cruz
ello encantada Kernbach, 1962, Opusc. Zool., vol. 63, p. 10.	Santa Cruz, Floreana, San Cristóbal, Isabela
obscura conformis Rothschild and Jordan, 1903, Nov. Zool. Suppl., vol. 9, p. 369.	Isabela, Baltra, Santa Cruz, Floreana

Genus **Epistor**

lugubris delanoi Kernbach, 1962, Opusc. Zool., vol. 63, p. 11.	Santa Cruz, Isabela, Floreana

Genus **Pholus**

fasciatus tupaci Kernbach, 1962, Opusc. Zool., vol. 63, p. 12.	Santa Cruz
labruscae yupanquii Kernbach, 1962, Opusc. Zool., vol. 63, p. 13.	Santa Cruz, Floreana

Genus **Xylophanes**

norfolki Kernbach, 1962, Opusc. Zool., vol. 63, p. 14.	Santa Cruz
tersa Linnaeus, 1771, Mant. Plant., vol. 2, p. 538 (*Sphinx*).	San Cristóbal

Genus **Celerio**

lineata florilega Kernbach, 1962, Opusc. Zool., vol. 63, p. 16.	Santa Cruz, Floreana, San Cristóbal, Isabela, Baltra

Family ARCTIIDAE

Genus **Utetheisa**

galapagensis Wallengren, 1860, Wien. Ent. Monat., vol. 4, p. 161 (*Euchalia*).	Isabela, Santa Cruz, Santiago, Floreana, Baltra
ornatrix Linnaeus, 1758, Syst. Nat., Ed. 10, vol. 1, p. 511 (*Phalaena noctua*).	Isabela, Baltra

Family Noctuidae

Subfamily Agrotinae

Genus **Agrotis**

ipsilon Hufnagel, 1766, Berl. Mag., vol. 3, p. 416 (*Phalaena*).	Isabela, Floreana
galapagosensis Kohler, 1961, An. Soc. Cient. Argentina, vol. 172, p. 71–72 (subgen. *Scotia*).	Floreana

Genus **Feltia**

subterranea Fabricius, 1794, Ent. Syst., vol. 3, no. 2, p. 70 (*Noctua*).	Santiago, Isabela

Genus **Peridroma**

conwayi Richards, 1941, Hancock Pac. Exp., vol. 5, p. 235.	Floreana
saucia Hübner, 1803–1808, Samml. Eur. Schmett. Noct. f. 378 (*Noctua*).	Floreana

Genus **Heliothis**

cystiphora Wallengren, 1860, Wien. Ent. Monat., vol. 4, p. 172 (*Anthoecia*). *inflata* Wallengren, 1860, Wien. Ent. Monat., vol. 4, p. 172 (*Anthoecia*). *onca* Wallengren, 1860, Wien. Ent. Monat., vol. 4, p. 172 (*Anthoecia*).	Santa Cruz, Santiago, Isabela, San Cristóbal, Baltra
virescens Fabricius, 1781, Spec. Ins., vol. 2, p. 216 (*Noctua*).	San Cristóbal, Isabela, Genovesa

Genus **Euxoa**

williamsi Schaus, 1923, Zoologica, vol. 5, p. 32.	Santa Cruz, Santiago, Isabela, Baltra

Genus **Lycophotia**

oceanica Schaus, 1923, Zoologica, vol. 5, p. 32.	Baltra

Subfamily Hadeninae

Genus **Pseudaletia**

cooperi Schaus, 1923, Zoologica, vol. 5, p. 33 (*Cirphis*).	Santa Cruz

Subfamily Amphipyrinae

Genus **Magusa**

orbifera Walker, 1857, Cat. Lep. Brit. Mus., vol. 11, p. 761 (*Xylina*).	Isabela

Genus Platysenta

apameoides Guenée, 1852, Sp. Gen., Noct., vol. 1, p. 229 (*Perigea*).	Santiago
ebba Schaus, 1923, Zoologica, vol. 5, p. 36 (*Perigea*) n. comb.	Santiago, Santa Cruz, Baltra
ruthae Schaus, 1923, Zoologica, vol. 5, p. 35 (*Perigea*).	Santa Cruz, Isabela

Genus Harrisonia

williamsi Schaus, 1923, Zoologica, vol. 5, p. 36.	Baltra, Santa Cruz

Genus Prodenia

dolichos Fabricius, 1794, Ent. Syst., vol. 3, p. 95 (*Noctua*).	Floreana
eridania form **linea** Fabricius, 1794, Ent. Syst., vol. 3, p. 106 (*Noctua*).	Floreana

Genus Spodoptera

frugiperda J. E. Smith, 1797, Lep. Ins. Georgia, vol. 2, p. 191, pl. 96 (*Phalaena*).	Santa Cruz
roseae Schaus, 1923, Zoologica, vol. 5, p. 33 (*Trachea*), n. comb.	Santiago, Isabela, Baltra, Santa Cruz

Genus Catabena

sp.? Schaus, 1923, Zooolgica, vol. 5, p. 25.	Genovesa

Genus Amyna

insularum Schaus, 1923, Zoologica, vol. 5, p. 37.	Isabela, Santa Cruz, Santiago, Floreana, San Cristóbal, Baltra

Subfamily ACONTIINAE

Genus Heliocontia

margana Fabricius, 1794, Ent. Syst., vol. 3, no. 2, p. 257 (*Pyralis*).	Santa Cruz, Baltra

Genus Spragueia

creton Schaus, 1923, Zoologica, vol. 5, p. 38.	Genovesa, Baltra
plumbeata Schaus, 1923, Zoologica, vol. 5, p. 38.	Santa Cruz

Subfamily PLUSIINAE (= PHYTOMETRINAE)

Genus Pseudoplusia

includens Walker, 1857, Cat. Lep. Brit. Mus., vol. 12, p. 914 (*Plusia*).	Santa Cruz, Floreana, Sanitago, San Cristóbal, Baltra

Genus Autoplusia

egena galapagensis Schaus, 1923, Zoologica, vol. 5, p. 41 (as form) (*Syngrapha*).	Santiago

Subfamily Euteliinae

Genus **Paectes**

indefatigabilis Schaus, 1923, Zoologica, vol. 5, p. 38.	Santa Cruz, Baltra
isabel Schaus, 1923, Zoologica, vol. 5, p. 39.	Santa Cruz

Subfamily Sarrothripinae

Genus **Characoma**

nilotica Rogenhofer, 1882, Verh. Zool. Bot. Ges. Wien., vol. 31, p. 26 (*Sarrothripa*).	San Cristóbal

Subfamily Catocalinae (*sensu* Richards = Noctuinae Schaus)

Genus **Melipotis**

harrisoni Schaus, 1923, Zoologica, vol. 5, p. 42.	Santa Cruz, Isabela, Baltra, Santiago
indomita Walker, 1857, Cat. Lep. Brit. Mus., vol. 13, p. 1161 (*Bolina*).	Santa Cruz, Baltra, Isabela, Floreana
nigrescens Williams, 1911, Proc. Calif. Acad. Sci., ser. 4, vol. 1, p. ?	

Genus **Anticarsia**

gemmatalis Hübner, 1818, Zutr. Exot. Schmett., vol. 1, p. 26, figs. 153, 154.	Santa Cruz, San Cristóbal, Baltra

Genus **Gonodonta**

biarmata galapagensis Todd, 1959, Tech. Bull. 1201, U. S. Department of Agriculture, p. 20.	Floreana, San Cristóbal, Santa Cruz

Genus **Epidromia**

zephyritis Schaus, 1923, Zoologica, vol. 5, p. 43.	Floreana, Santa Cruz

Genus **Psorya** (? *Smyra*—see Richards, 1941)

hadesia Schaus, 1923, Zoologica, vol. 5, p. 44.	Baltra, Floreana

Genus **Zale**

sp. (**viridans** group) Richards, 1941, Hancock Pac. Exp., vol. 5, p. 243.	Floreana

Genus **Ascalapha**

odorata Linnaeus, 1758, Syst. Nat., ed. 10, p. 505 (*Phalaena Bombyx*).	Floreana

Genus **Anomis**

professorum Schaus, 1923, Zoologica, vol. 5, p. 42.	Isabela, Baltra, Santa Cruz, San Cristóbal

Genus **Mocis**

incurvalis Schaus, 1923, Zoologica, vol. 5, p. 41.	Floreana, Santa Cruz, Baltra
latipes Guenée, 1852, Sp. Gen., Noct., vol. 3, p. 314 (*Remigia*).	Santa Cruz, Baltra

Genus **Rivula**	
dubiosa Schaus, 1923, Zoologica, vol. 5, p. 44.	Santa Cruz
Family Geometridae	
Genus **Camptogramma**	
stellata Guenée, 1857, Uranides et Phalenites, vol. 2, p. 443 (*Scotosia*).	Santa Cruz, Baltra
Genus **Cosymbia**	
impudens Warren, 1904, Nov. Zool., vol. 11, p. 487 (*Perixera*).	Santa Cruz, Santiago, Isabela, Gardner
Genus **Sericosema**	
lignata Warren, 1905, Nov. Zool., vol. 12, p. 362.	San Cristóbal
Family Pyralidae	
Subfamily Pyraustinae	
Genus **Hymenia**	
recurvalis Fabricius, 1775, Syst. Ent., 644 (*Phalaena*).	Baltra
Genus **Pilocrocis**	
ramentalis Lederer, 1863, Wien. Ent. Monat., vol. 7, p. 430.	Santiago, Baltra
Genus **Herpetogramma**	
chathamalis Schaus, 1923, Zoologica, vol. 5, p. 45 (*Pilocrocis*) (n. comb.).	San Cristóbal, Santa Cruz, Baltra
Genus **Asciodes**	
gordialis Guenée, 1854, Delt. et Pyral., p. 374.	Santa Cruz, Isabela, San Cristóbal, Baltra
Genus **Pleuroptya**	
silicalis Guenée, 1854, Delt. et Pyral., p. 349 (*Botys*) (n. comb.).	Santa Cruz, Santiago, Isabela, San Cristóbal, Baltra
Genus **Polygrammodes**	
elevata Fabricius, 1793, Ent. Syst. III, 2, no. 325, p. 216 (*Phalaena*).	Santiago
Genus **Pyrausta**	
eneanalis Schaus, 1923, Zoologica, vol. 5, p. 45.	Santa Cruz, Baltra, Genovesa
Genus **Piletocera**	
bufalis Guenée, 1854, Delt. et Pyral., p. 245 (*Stenia*).	Santa Cruz
Genus **Beebea**	
guglielmi Schaus, 1923, Zoologica, vol. 5, p. 46.	San Cristóbal

Subfamily Crambinae

Genus **Euchrombius**

ocelleus Haworth, 1811, Lep. Brit., p. 486 (*Palparia*).	Santa Cruz, Baltra

Subfamily Phycitinae

Genus **Etiella**

zinckenella (Treit.) 1832, Schmett. Eur., vol. 9, no. 1, p. 201.	Santa Cruz, Baltra

Genus **Fundella**

agapella Schaus, 1923, Zoologica, vol. 5, p. 47.	Isabela

Genus **Fulrada**

carpasella Schaus, 1923, Zoologica, vol. 5, p. 47 (*Piesmopoda*).	Santa Cruz

Genus **Tota**

galdinella Schaus, 1923, Zoologica, vol. 5, p. 46 (*Elasmopalpus*).	Santa Cruz, Baltra, Santiago

Genus **Nicetiodes**

apianella Schaus, 1923, Zoologica, vol. 5, p. 48.	Santa Cruz, Baltra, Genovesa

Family Pterophoridae

Genus **Trichoptilus**

derelictus Meyrick, 1926, Trans. Ent. Soc. Lond., vol. 74, p. 276.	Floreana

Genus **Pterophorus**

nephogenes Meyrick, 1926, Trans. Ent. Soc. London, vol. 74, p. 276.	Floreana, Isabela
sp. Schaus, 1923, Zoologica, vol. 5, p. 30.	Daphne Major, Santa Cruz

Family Tortricidae

Subfamily Tortricinae

Genus **Platynota**

colobota Meyrick, 1926, Trans. Ent. Soc. Lond., vol. 74, p. 276.	Isabela

Subfamily Olethreutinae

Genus **Strepsicrates**

smithiana Walsingham, 1892, Proc. Zool. Soc. London, p. 506.	Baltra
spp. Schaus, 1923, Zoologica, vol. 5, p. 31 (3 species).	Baltra, Santiago

Genus **Crocidosema**

plebiana Zeller, 1847, Isis, p. 721.	Baltra, Isabela,

synneurota Meyrick, 1926, Trans. Ent. Soc. Lond., vol. 74, p. 276.	Santa Cruz

Family Gelechiidae

Genus **Aristotelia**

howardi Walsingham, 1909, Biol. Centr. Am. Ins. Lep.-Heter., IV, p. 23.	Baltra
naxia Meyrick, 1926, Trans. Ent. Soc. London, vol. 74, p. 277.	Floreana

Genus **Stegasta**

bosqueella Chambers, 1875, Canad. Ent., vol. 7, p. 92 (*Oecophora*).	Santa Cruz

Genus **Gelechia**

gnathodoxa Meyrick, 1926, Trans. Ent. Soc. London, vol. 74, p. 277.	Santiago
protozona Meyrick, 1926, Trans. Ent. Soc. London, vol. 74, p. 277.	Isabela

Family Blastobasidae

Genus **Blastobasis**

crotospila Meyrick, 1926, Trans. Ent. Soc. London, vol. 74, p. 278.	Santiago

Family Yponomeutidae

Genus **Atteva**

hysginiella Wallengren, 1861, Freg. Eugenies Resa, vol. 2, p. 386.	Isabela, Santa Cruz, Santiago, San Cristóbal, Baltra, Daphne Major
sylpharis Butler, 1877, Proc. Zool. Soc. Lond., 1877, p. 87.	
monerythra Meyrick, 1926, Trans. Ent. Soc. London, vol. 74, p. 278.	Floreana

Family Tineidae

Genus **Xylesthia**

pruniramiella Clemens, 1859, Proc. Acad. Nat. Sci. Philadelphia, vol. 11, p. 259.	Santiago

Order DIPTERA

Comprehensive reports on Galápagos Diptera may be found in Coquillett (1901), Johnson (1924), and Curran (1932, 1934). Authority for the synonymy of *Pseudolfersia diomedae* Coquillett with *Olfersia aenescens* Thomson, is Maa (1963), and for that of *Ceratopogon galapagensis* Coquillett with *Forcipomyia fuliginosa* Meigen, Wirth (1956). This section has been read by R. H. Foote, C. W. Sabrosky, G. C. Steyskal, Alan Stone, and W. W. Wirth.

Family Chironomidae

Genus **Chironomus**

sp., Johnson, 1924, Zoologica, vol. 5, p. 86.	Baltra
sp., Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 149.	San Cristóbal

Genus **Tanypus**

sp., Johnson, 1924, Zoologica, vol. 5, p. 86.	Baltra

Genus **Thalassomya**

longipes Johnson, 1924, Zoologica, vol. 5, p. 86 (*Galapagomyia*).	Santa Cruz, Floreana

Genus **Clunio**

schmitti Stone & Wirth, 1947, Proc. Ent. Soc. Washington, vol. 49, p. 217.	Fernandina

Family Tipulidae

Genus **Erioptera**

(Subgenus **Trimiera**)

pilipes Fabricius, 1787, Mantissa Insectorum, vol. 2, p. 324 (*Tipula*).	San Cristóbal

Genus **Limonia**

(Subgenus **Dicranomyia**)

galapagoensis Alexander, 1962, Opuscula Zoologica, vol. 61, p. 1.	Santa Cruz, San Cristóbal

(Subgenus **Geranomyia**)

stigmatica Philippi, 1865, Verhandl. Kais. Kon. Zool.-bot. Ges. Wien, vol. 15, p. 598 (*Plettusa*).	Isabela
tibialis Loew, 1851, Linn. Ent., vol. 5, p. 397 (*Aporosa*).	Santa Cruz, San Cristóbal, Floreana

Family Culicidae

Genus **Aedes**

taeniorhynchus Wiedemann, 1821, Diptera Exot., p. 43 (*Culex*).	Genovesa, Isabela, Santiago, Rábida, Santa Cruz, Baltra, San Cristóbal, Floreana

Family Ceratopogonidae

Genus **Forcipomyia**

fuliginosa Meigen, 1818, Syst. Beschr. Eur. Zweifl. Ins., vol. 1, p. 86 (*Ceratopogon*).	Isabela, Baltra, Santa Cruz, Gardner
galapagensis Coquillett, 1901, Proc. Washington Acad. Sci., vol. 3, p. 372 (*Ceratopogon*).	

Family Sciaridae

Genus **Sciara**

sp., Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 149.	Baltra

Family Stratiomyidae

Genus **Pelagomyia**

dubia Curran, 1932, Nyt Mag. Naturvidensk., vol. 71, p. 348.	Isabela, Santiago, Santa Cruz, Baltra, San Cristóbal, Floreana
albitalus Coquillett (not Williston), 1901, Proc. Washington Acad. Sci., vol. 3, p. 373.	

Genus **Nemotelus**

acutirostris Loew, 1863, Berliner Ent. Zeitschr., vol. 7, p. 8.	Isabela
albiventris Thomson, 1869, Freg. Eugenies Resa, Zool., vol. 1, p. 462.	Isabela

Family Tabanidae

Genus **Tabanus**

vittiger Thomson, 1869, Freg. Eugenies Resa, Zool., vol. 1, p. 451.	Isabela, Santa Cruz, San Cristóbal, Floreana

Family Bombyliidae

Genus **Villa**

brachialis Thomson, 1869, Freg. Eugenies Resa, Zool., vol. 1, p. 484 (*Anthrax*).	Isabela
curvirostris Thomson, 1869, Freg. Eugenies Resa, Zool., vol. 1, p. 483 (*Anthrax*).	Galápagos Islands
primitiva Walker, 1849, List Diptera Brit. Mus., vol. 2, p. 257 (*Anthrax*).	Santa Cruz, Santa Fé, Floreana
lateralis Thomson, 1869, Freg. Eugenies Resa, Zool., vol. 1, p. 482 (*Anthrax*).	
nudiuscula Coquillett (not Thomson), 1901, Proc. Washington Acad. Sci., vol. 3, p. 373 (*Anthrax*).	

Genus **Lepidanthrax**

tincta Thomson, 1869, Freg. Eugenies Resa, Zool., vol. 1, p. 483 (*Anthrax*).	Santa Cruz, Bartholomew

Family Asilidae

Genus **Ommatius**

marginellus Fabricius, 1781, Spec. Ins., vol. 2, p. 464 (*Asilus*).	Santiago, Santa Cruz

Family Empididae

Genus **Drapetis**

zonalis Curran, 1932, Nyt Mag. Naturvidensk., vol. 71, p. 351.	Santa Cruz, Floreana

Family Dolichopodidae

Genus **Condylostylus**

dentaticauda Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 66.	Santiago
tibialis Thomson, 1869, Freg. Eugenies Resa, Zool., vol. 1, p. 507 (*Auchineura*).	Fernandina, Isabela

Genus **Chrysotus**

brevicornis Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 68.	Santa Cruz
brevispina Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 68.	Isabela, Santa Cruz, San Cristóbal
latifacies Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 69.	Santa Cruz

Genus **Asyndetus**

interruptus Loew, 1861, Ent. Monatschr., vol. 5, p. 37.	Pinta
versicolor Johnson, 1924, Zoologica, vol. 5, p. 88.	Baltra

Genus **Aphrosylus**

setosus Curran, 1932, Nyt Mag. Naturvidensk., vol. 71, p. 352.	Floreana

Genus **Paracleius**

? **pusillus** Macquart, 1844, Diptera Exot., suppl. 1, p. 121 (*Dolichopus*).	Fernandina, Isabela

Genus **Vanduzeeia**

cheesmani Parent, 1934, Mem. Soc. Sci. Nat. & Math. Cherbourg, vol. 41, p. 258.	Santiago

Family Phoridae

Genus **Dohrniphora**

cornuta Bigot, 1856, Sagra's Hist. Fis. Nat. Cuba, vol. 7, p. 348.	Baltra, Floreana
venusta Coquillett, 1895, Canadian Ent., vol. 27, p. 107.	
crockeri Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 70.	
willowsi Van Duzee, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 70.	Baltra

Genus **Megaselia**

scalaris Loew, 1866, Berliner Ent. Zeitschr., vol. 10, p. 53 (*Phora*).	Genovesa

Family SYRPHIDAE

Genus **Allograpta**

splendens Thomson, 1869, Freg. Eugenies Resa, Zool., vol. 1, p. 501 (*Syrphus*).	Santiago, San Cristóbal, Floreana

Genus **Baccha**

clavata Fabricius, 1794, Ent. Syst., vol. 4, p. 298 (*Syrphus*).	Isabela, Santiago, San Cristóbal, Floreana
facialis Thomson, 1869, Freg. Eugenies Resa, Zool., vol. 1, p. 504.	

Genus **Mesograpta**

crockeri Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 154.	Isabela, Santiago, San Cristóbal, Floreana
duplicata Coquillett (not Wiedemann), 1901, Proc. Washington Acad. Sci., vol. 3, p. 374.	

Genus **Xanthandrus**

sp., Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 155.	Pinta
albomaculatus Smith, 1877, Proc. Zool. Soc. London, 1877, p. 84 (*Syrphus*).	Floreana

Family OTITIDAE

Genus **Acrosticta**

scrobiculata Loew, 1867, Berliner Ent. Zeitschr., vol. 11, p. 293.	Floreana

Genus **Euxesta**

galapagensis Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 156.	Española
nitidiventris Loew, 1873, Mon. No. Amer. Diptera, vol. 2, p. 157.	Isabela, Santa Cruz, Floreana
notata Wiedemann, 1830, Ausser. Zweifl. Insekten, vol. 2, p. 462 (*Ortalis*).	Floreana

Genus **Pareuxesta**

hyalinata Coquillett, 1901, Proc. Washington Acad. Sci., vol. 3, p. 377.	Isabela
latifasciata Coquillett, 1901, Proc. Washington Acad. Sci., vol. 3, p. 376.	Genovesa, Isabela
intermedia Coquillett, 1901, Proc. Washington Acad. Sci., vol. 3, p. 377.	

obscura Coquillett, 1901, Proc. Washington Acad. Sci., vol. 3, p. 377.	Daphne Major, Isabela

Family Tephritidae

Genus **Paroxyna**

crockeri Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 157, fig. 1.	Isabela, Santiago, Rábida, Santa Cruz, Baltra, Floreana

Genus **Euaresta**

aesia Walker, 1849, List Diptera Brit. Mus., vol. 4, p. 1006 (*Trypeta*).	Galápagos Islands

Family Sphaeroceridae

Genus **Leptocera**

discalis Malloch, 1912, Smithsonian Misc. Coll., vol. 59, p. 433.	Floreana

Genus **Sphaerocera**

galapagensis Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 158.	San Cristóbal

Family Drosophilidae

Genus **Drosophila**

immigrans Sturtevant, 1921, Carnegie Inst. Washington, Publ. 301, p. 83.	Santiago, Floreana
nebulosa Sturtevant, 1916, Ann. Ent. Soc. Amer., vol. 9, p. 327.	San Cristóbal
simulans Sturtevant, 1919, Psyche, vol. 26, p. 153.	San Cristóbal, Baltra
willistoni Sturtevant, 1916, Ann. Ent. Soc. Amer., vol. 9, p. 327.	Baltra
sp., Wheeler, 1961, Ann. Ent. Soc. Amer., vol. 54, p. 750.	Santa Cruz

Genus **Gitona**

braziliensis Costa Lima, 1950, Arthropoda, vol. 1, p. 251.	Santa Cruz

Family Ephydridae

Genus **Dimecoenia**

gilvipes Coquillett, 1901, Proc. Washington Acad. Sci., vol. 3, p. 377 (*Ephydra*).	Isabela

Genus **Scatella**

galapagensis Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 161.	San Cristóbal

Family CANACEIDAE

Genus **Canace**

maritima Wirth, 1951, Occ. Pap. Bernice P. Bishop Mus., vol. 20, p. 263.	Bartholomew
snodgrassii Coquillett, 1901, Proc. Washington Acad. Sci., vol. 3, p. 378.	Fernandina, Isabela

Genus **Nocticanace**

galapagensis Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 160 (*Procanace*).	Isabela, Santa Cruz, Wenman, Tower, Abingdon, Hood

Family CHLOROPIDAE

Genus **Hippelates**

galapagensis Curran, 1932, Nyt Mag. Naturvidensk., vol. 71, p. 356.	Floreana
pusio Loew, 1872, Berliner Ent. Zeitschr., vol. 16, p. 279.	Isabela

Genus **Cadrema**

pallida Loew, 1865, Berliner Ent. Zeitschr., vol. 9, p. 184 (*Hippelates*).	Baltra

Genus **Oscinella**

galapagensis Curran, 1932, Nyt Mag. Naturvidensk., vol. 71, p. 357.	Floreana

Family MILICHIIDAE

Genus **Desmometopa**

m-nigrum Zetterstedt, 1848, Diptera Scand., vol. 7, p. 2743 (*Agromyza*).	Baltra

Family TETHINIDAE

Genus **Trixoscelis**

costalis Coquillett, 1901, Proc. Washington Acad. Sci., vol. 3, p. 378 (*Rhicnoessa*).	Isabela, Floreana, Española

Genus **Tethina**

insulans Curran, 1932, Nyt Mag. Naturvidensk., vol. 71, p. 359.	Floreana

Family ODINIIDAE

Genus **Odinia**

williamsi Johnson, 1924, Zoologica, vol. 5, p. 90.	Pinta, Rábida, Santa Cruz, Baltra, Santa Fé, Floreana

Family Agromyzidae

Genus **Cerodontha**

dorsalis Loew, 1863, Berliner Ent. Zeitschr., vol. 7, p. 54 (*Odontocera*).	Santa Cruz, Floreana

Family Muscidae

Genus **Xenocoenosia**

devia Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 164.	Santiago, San Cristóbal

Genus **Fannia**

canicularis Linnaeus, 1761, Fauna Suecica, p. 1871 (*Musca*).	Isabela
sp., Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 164 (? *pusio* Wiedemann).	San Cristóbal

Genus **Ophyra**

aenescens Wiedemann, 1830, Ausser. Zweifl. Insekten, vol. 2, p. 435 (*Anthomyia*).	Fernandina, Isabela, Baltra, Floreana
setia Walker, 1849, List Diptera Brit. Mus., vol. 4, p. 956 (*Anthomyia*).	

Genus **Synthesiomyia**

nudiseta Wulp, 1833, Tijf. v. Ent., vol. 26, p. 42 (*Cyrtoneura*).	Isabela, Floreana
brasiliana Brauer & Bergenstamm, 1893, Denkschr. Math. Nat. Kais. Akad. Wiss. Wien, vol. 60, p. 96.	

Genus **Lispe**

sp., Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 165.	Floreana

Genus **Musca**

domestica Linnaeus, 1758, Systema Naturae, ed. 10, p. 596.	Baltra, Floreana

Genus **Stomoxys**

calcitrans Linnaeus, 1758, Systema Naturae, ed. 10, p. 604.	Baltra, San Cristóbal, Floreana

Genus **Morellia**

ochricornis Wiedemann, 1830, Aussereur. Zweifl. Insekten, vol. 2, p. 408.	Floreana

Family Calliphoridae

Genus **Viridinsula**

pionia Walker, 1849, List Diptera Brit. Mus., vol. 4, p. 880 (*Musca*).	Santa Cruz, Floreana

deceptor Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 166.	Isabela, Seymour, Floreana, Española
pionia Curran (not Walker), 1932, Nyt Mag. Naturvidensk., vol. 71, p. 361.	

Genus **Cochliomyia**

macellaria Fabricius, 1775, Systema Ent., p. 776.	Isabela, Santa Cruz, Floreana
phanda Walker, 1849, List Diptera Brit. Mus., vol. 4, p. 869 (*Musca*).	
quadrisignata Thomson, 1869, Freg. Eugenies Resa, Zool., vol. 1, p. 554 (*Lucilia*).	

Family SARCOPHAGIDAE

Genus **Opsophytopsis**

inoa Walker, 1849, List Diptera Brit. Mus., vol. 4, p. 832 (*Sarcophaga*).	Darwin, Fernandina, Isabela, Santiago, Santa Cruz, San Cristóbal, Floreana, Española
insularis Townsend, 1917, Insecutor Inscitae Mens., vol. 5, p. 163.	

Genus **Sarcophagula**

occidua Fabricius, 1794, Ent. Syst., p. 315 (*Musca*).	Santiago, San Cristóbal, Floreana

Genus **Prosthetocirca**

cana Townsend, 1917, Proc. Biol. Soc. Washington, vol. 30, p. 196.	Santa Cruz, Española

Genus **Sarcophaga**

isla Curran, 1934, Proc. Calif. Acad. Sci., 4th ser., vol. 21, p. 169, fig. 3.	Española, Gardner
plinthopyga Wiedemann, 1830, Aussereur. Zweiflug. Insekten, vol. 2, p. 360.	Floreana
quadriforceps Curran, 1932, Nyt Mag. Naturvidensk., vol. 71, p. 363.	
reversa Aldrich, 1916, Sarcophaga and Allies, p. 127.	Baltra
taitensis Schiner, 1868, Novara Reise, Diptera, p. 314.	Isabela, Pinzón, San Cristóbal, Floreana
obtusifrons Thomson, 1869, Freg. Eugenies Resa, Zool., vol. 1, p. 536.	
violenta Walker, 1849, List Diptera Brit. Mus., vol. 4, p. 826.	Isabela, Santa Cruz, Baltra, Santa Fé
galapagensis Townsend, 1917, Proc. Biol. Soc. Washington, vol. 30, p. 195.	
williamsi Curran, 1934, Proc. Calif. Acad. Sci., 4th ser., vol. 21, p. 170, fig. 4.	Floreana

Family Tachinidae

Genus **Galapagosia**

minuta Curran, 1934, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 172.	Santa Cruz

Family Hippoboscidae

Genus **Olfersia**

aenescens Thomson, 1869, Freg. Eugenies Resa, Zool., vol. 1, p. 610.	Isabela, Santa Cruz, Española
diomedae Coquillett, 1901, Proc. Washington Acad. Sci., vol. 3, p. 379 (*Pseudolfersia*).	
fossulata Macquart, 1843, Mem. Soc. Sci. Lille, 1842, p. 434.	Wolf, Daphne Major
spinifera Leach, 1817, on genera and species Eprobosc. Ins., p. 11, pl. 26 (1–3); 1818, Mem. Wernerian Nat. Hist. Soc., vol. 2, p. 557, pl. 24, figs. 1–3.	Genovesa, Floreana

Genus **Lynchia**

nigra Perty, 1833, Delectus Anim. Artic. Brasil, vol. 3, p. 190, pl. 37, fig. 15 (*Hippobosca*).	Santa Cruz
intertropica Walker, 1849, List Diptera Brit. Mus., vol. 4, p. 1144 (*Ornithomyia*).	
americanus, Johnson (not Leach), 1924, Zoologica, vol. 5, p. 91 (*Ornithoponus*).	
albipennis Say, 1823, Jour. Acad. Nat. Sci. Philadelphia, vol. 3, p. 101 (*Olfersia*).	Genovesa, Fernandina, Santiago, Santa Cruz, Seymour
intertropicus, Johnson (not Walker), 1924, Zoologica, vol. 5, p. 91 (*Ornithoponus*).	

Genus **Microlynchia**

galapagoensis Bequaert, 1955, Entom. Americana, vol. 35, p. 384.	Santa Cruz, Española
pusilla Speiser, 1902, Zeitschr. Syst. Hym. Dipt., vol. 2, p. 157 (*Lynchia*).	Española

Order HYMENOPTERA

The leading references on Hymenoptera other than ants are by Rohwer (1924) and Williams (1926). Formicidae were treated by Wheeler (1919 and 1924) and by Stitz (1932). Dr. William L. Brown kindly reviewed the present manuscript and made valuable corrections and proposed new synonymy.

Family Chalcididae

Genus **Chalcis**

sp., Rohwer, 1924, Zoologica, vol. 5, p. 175.	Baltra

Family Bethylidae

Genus **Scleroderma**

galapagense Brues, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 309.	Santiago

Family Thynnidae

Genus **Agriomyia**

vagans Smith, 1877, Proc. Zool. Soc. London, 1877, p. 83.	Floreana

Family Mutillidae

Genus **Photopsis**

galapagensis Williams, 1926, Proc. Calif. Acad. Sci., ser. 4, vol. 18, p. 350.	Baltra

Family Formicidae

Genus **Cylindromyrmex**

striatus tibialis Stitz, 1932, Nyt Mag. f. Naturvidensk., vol. 71, p. 367.	Floreana
williamsi Wheeler, 1924, Zoologica, vol. 10, p. 101, fig. 19b, c. *striatus* Wheeler (not Mayr, 1870), 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 266.	Santa Cruz, Baltra

Genus **Hypoponera**

beebei Wheeler, 1924, Zoologica, vol. 10, p. 107, fig. 21.	Genovesa

Genus **Odontomachus**

bauri Emery, 1891, Ann. Soc. Ent. France, vol. 60, p. 591. *haematoda* Stitz (not Linnaeus), 1932, Nyt Mag. Naturvidensk., vol. 71, p. 369.	San Cristóbal, Floreana

Genus **Pheidole**

sp., Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 271.	Isabela
williamsi seymourensis Wheeler, 1924, Zoologica, vol. 5, p. 108.	Baltra, Daphne
williamsi williamsi Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 267.	Santa Cruz

Genus **Monomorium**

floricola Jerdon, 1851, Madras J. Litt. Sci., vol. 17, p. 107 (*Atta*).	Genovesa

**floreanum* Stitz, 1932, Nyt Mag. Naturvidensk., vol. 71, p. 368, figs. 1, 2.	Floreana
pharaonis Linnaeus, 1758, Systema Naturae, ed. 10, vol. 1, p. 580 (*Formica*).	Pinta, Santa Cruz

Genus **Solenopsis**

geminata galapageia Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 272.	Floreana
globularia pacifica Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 272.	Genovesa, Isabela, Daphne, Santa Cruz
globularia rubida Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 273.	Española
saevissima F. Smith, 1855, Trans. Ent. Soc. London, 1855, p. 166, pl. 13, fig. 18 (*Myrmica*).	Santa Cruz

Genus **Tetramorium**

guineense Fabricius, 1793, Ent. Syst., vol. 2, p. 357 (*Formica*).	Genovesa, Isabela, Santa Cruz, San Cristóbal
simillimum F. Smith, 1851, List Hymenoptera Brit. Mus., vol. 6, p. 118 (*Myrmica*).	Santiago, Floreana

Genus **Crematogaster**

brevispinosa chathamensis Wheeler, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 58 (subgenus *Orthocrema*).	San Cristóbal

Genus **Conomyrma**

pyramica albemarlensis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 275.	Isabela, Rábida, Eden, Santa Cruz, Baltra

Genus **Tapinoma**

melanocephalum Fabricius, 1793, Ent. Syst., vol. 2, p. 353 (*Formica*).	Genovesa, Santa Cruz, San Cristóbal, Española

Genus **Paratrechina**

fulva nesiotis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 277 (*Prenolepis*).	Isabela, Santiago, Santa Cruz, Española
longicornis Latreille, 1802, Hist. Nat. Fourmis, p. 113 (*Formica*).	Santa Cruz, San Cristóbal, Floreana, Española, Gardner
vividula edenensis Wheeler, 1924, Zoologica, vol. 5, p. 111 (*Prenolepis v. guatemalensis* variety).	Eden

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* New synonymy, *fide* W. L. Brown, 1964.

vividula itinerans Forel, 1901, Mitt. naturh. Mus. Hamburg, vol. 18, p. 81.	Santa Cruz, San Cristóbal

Genus **Camponotus**

Subgenus **Pseudocolobopsis**

macilentus albemarlensis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 284.	Isabela
macilentus altinota Stitz, 1932, Nyt Mag. Naturvidensk., vol. 71, p. 370, fig. 3.	Floreana
macilentus barringtonensis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 282.	Santa Fé
macilentus bindloensis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 286.	Marchena
macilentus castellanus Wheeler, 1924, Zoologica, vol. 10, p. 116, fig. 25.	Genovesa
macilentus duncanensis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 283.	Pinzón, Floreana
macilentus hoodensis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 285.	Española
macilentus jacobensis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 280.	Santiago
macilentus macilentus F. Smith, 1877, Proc. Zool. Soc. London, 1877, p. 83.	Floreana
macilentus narboroensis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 286.	Fernandina
macilentus pervicus Wheeler, 1924, Zoologica, vol. 10, p. 115.	Santa Cruz
macilentus sapphirinus Wheeler, 1924, Zoologica, vol. 10, p. 114, fig. 24.	Santa Cruz, Baltra
macilentus vulcanalis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 284.	Isabela
macilentus wollebaeki Stitz, 1932, Nyt Mag. Naturvidensk., vol. 71, p. 371, fig. 4.	Floreana

Subgenus **Myrmocladoecus**

planus fernandinensis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 296.	Fernandina
planus fidelis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 295.	Santa Fé
planus hephaestus Wheeler, 1933, Proc. Calif. Acad. Sci., ser. 4, vol. 21, p. 59.	Isabela
planus indefessus Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 294.	Santa Cruz

planus isabelensis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 293.	Isabela
planus peregrinus Emery, 1893, Ann. Soc. Ent. France, vol. 63, p. 91.	San Cristóbal, Floreana
planus pinzonensis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 297.	Pinzón
planus planus F. Smith, 1877, Proc. Zool. Soc. London, 1877, p. 83.	Floreana
planus sansalvadorensis Wheeler, 1924, Zoologica, vol. 10, p. 119, fig. 27.	Santiago
planus santacruzensis Wheeler, 1919, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 294.	Santa Cruz, Baltra

Family VESPIDAE

Genus **Odynerus**

galapagensis Williams, 1926, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 353 (subgenus *Pachyodynerus*).	San Cristóbal

Family POMPILIDAE

Genus **Aporinellus**

galapagensis Rohwer, 1924, Zoologica, vol. 5, p. 174.	Baltra

Family SPHECIDAE

Genus **Nitela**

darwini Turner, 1916, Ann. Mag. Nat. Hist., ser. 8, vol. 18, p. 345.	Floreana

Genus **Tachysphex**

galapagensis Rohwer, 1924, Zoologica, vol. 5, p. 173.	Isabela, Baltra

Family APIDAE

Genus **Xylocopa**

darwini Cockerell, 1926, Ann. Mag. Nat. Hist., ser. 9, vol. 17, p. 659.	Isabela, Santiago, Pinzón, Santa Cruz, Baltra, San Cristóbal, Floreana, Gardner
mordax Smith (not Smith, 1874), 1877, Proc. Zool. Soc. London, 1877, p. 83.	
brasilianorum Maidl (not Linnaeus, 1767), 1912, Ann. K. K. Naturhist. Hofmus., vol. 26, p. 312.	
transitoria Brues (not Perez, 1901), 1924, Zoologica, vol. 5, p. 125.	
colona Rohwer (not Lepeletier, 1841), 1924, Zoologica, vol. 5, p. 173.	

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Banks, N.

1901. Papers from the Hopkins Stanford Galapagos Expedition, 1898–1899. V. Entomological Results (5): Thysanura and Termitidae. Proceedings of the Washington Academy of Science, vol. 3, pp. 541–546. [Thysanura: *Lepisma galapagoensis,* n. sp. (p. 541, figs. 47–50), (Hood Island); *L. insularis*, n. sp. (p. 543, figs. 51–52), (Narborough and Albemarle islands); Termitidae: *Calotermes galapagoensis,* n. sp. (p. 544, figs. 55–56), (Wenman Island); *Calotermes pacificus,* n. sp. (p. 545, fig. 57), (Albemarle and Narborough islands).]

1924. Neuroptera from the Williams Galapagos Expedition. Zoologica, vol. 5, pp. 117–180. [4 species in 3 families (Myrmeleonidae, Chrysopidae, Hemerobiidae): *Myrmeleon perpilosus*, n. sp. (Indefatigable Island); *Chrysopa nigripilosa*, n. sp. (South Seymour Island); *Chrysopa galapagoensis,* n. sp. (South Seymour Island); *Megalomus darwini*, n. sp. (Indefatigable Island).]

Banning, G. H., and J. S. Barth

1933. Hancock expedition of 1933 to the Galapagos Islands. Bulletin of the Zoological Society of San Diego, vol. 10, pp. 1–30. [Popular account of the expedition.]

Barber, H.G.

1925. Hemiptera–Heteroptera from the Williams Galapagos Expedition. Zoologica, vol. 5, pp. 241–254. [8 new species in 6 families; total of 16 species listed—*Harmostes disjunctus*, n. sp. (Indefatigable Island); *Heraeus pacificus*, n. sp. (James Island); *Creontiades fuscosus*, n. sp. (Indefatigable and James islands); *Orthaea insularis,* n. sp. (James, S. Seymour, Albemarle, and Indefatigable islands); *Psallus insularis*, n. sp. (James Island); *Repipta annulipes*, n. sp. (Indefatigable Island); *Corythaica renormata*, n. sp. (Daphne Major Island); *Halobates robustus*, n. sp. (Indefatigable Island).]

1934. The Norwegian Zoological Expedition to the Galapagos Islands 1925, conducted by Alf Wollebaek. XI. Hemiptera–Heteroptera. Nyt Magazin for Naturvidenskaberne, vol. 74, pp. 281–289. [Reprinted as Meddelelser fra det Zoologiske Museum, Oslo, nr. 42, pp. 281–289 (1934).] [40 species recorded including *Aknisus galapagensis*, n. sp., (Chatham Island) (Neididae).]

Barlow, Nora (editor)

1934. Charles Darwin's Diary of the Voyage of HMS "Beagle." Cambridge University Press, xxx + 442 pp. Map.

1946. Charles Darwin and the Voyage of the Beagle, unpublished letters and notebooks, 279 pp. The Philosophical Library, New York.

Beebe, Wm.

1923. Williams Galapagos Expedition. Zoologica, vol. 5, pp. 1–20, 10 figs. 1 map.

1923. Notes on Galapagos Lepidoptera. Zoologica, vol. 5, pp. 51–59.

1924. Galapagos, World's End. C. P. Putnam's Sons, New York and London, xxi + 433 pp., illus.

1925. Logging the Arcturus. Bulletin of the New York Zoological Society, vol. 28, pp. 103–116.

Beebe, Wm., and Ruth Rose

1925. The second half of the Arcturus Adventure. Bulletin of the New York Zoological Society, vol. 28, pp. 119–129, 4 col. plates.

Bequaert, J. C.

1933. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 11. The Hippoboscidae of the Galápagos Archipelago (Notes on the Hippoboscidae. 8), with an Appendix on the Tabanidae. Proceedings of the California Academy of Sciences, ser. 4, vol. 21, pp. 131–138. [3 genera: *Olfersia,* three species; *Lynchia,* two species; and *Microlynchia,* one species; no new species.]

1955. The Hippoboscidae or louse-flies (Diptera) of mammals and birds. Part II. Taxonomy, evolution and revision of American genera and species. Entomologica Americana, vol. 35, pp. 233–416, 38 figs. [*Microlynchia galapagoensis,* n. sp., (Indefatigable and Hood islands). (p. 384, figs.).]

Blair, K. G.

1928. Coleoptera (Heteromera, Teredilia, Malacodermata and Bruchidae) from the Galápagos Islands, collected on the St. George Expedition, 1924. The Annals and Magazine of Natural History, ser. 10, vol. 1, pp. 671–680.

1933. Further Coleoptera from the Galápagos Archipelago. The Annals and Magazine of Natural History, ser. 10, vol. 11, pp. 471–487. [New records and/or new species in Carabidae, Hydrophilidae, Histeridae, Coccinellidae, Languridae, Dermestidae, Scarabaeidae, Bostrychidae, Lycidae, Cantharidae, Cleridae, Elateridae, Tenebrionidae, Cistelidae, Oedemeridae, Cerambycidae, Chrysomelidae, Curculionidae, and Scolytidae.]

Boheman, C. H.

1858–1859. Coleoptera. Species novas descripsit. *in:* Kongliga Svenska Fregatten Eugenies resa omkring Jorden . . . Zoologi I, Insecta, pp. 1–218, 2 pls. [7 new species from Galápagos: *Feronia insularis, Copris lugubris, Heterocrepedius puberulus, Tessaroma morio, Phaleria manicata,* and *Eburia amabilis.*]

Borgmeier, T.

1960. Gefluegelte und ungefluegelte Phoriden aus der neotropischen Region, nebst Beschreibung von sieben neuen Gattungen (Diptera, Phorida). Studia Entomologica (new series), vol. 3, pp. 257–374, figs. [*Dohrniphora cornuta* (Bigot) (p. 277).]

Bowman, R. I.

1961. Morphological Differentiation and Adaptation in the Galápagos Finches. University of California Publications in Zoology, vol. 58, pp. iv + 302, 22 pls., 74 text figs. [Food habits of birds.]

Brauer, F., and Y. E. von Bergenstamm

1892. Die Zweiflugler des Kaiserlichen Museums zu Wien. v. Vorarbeiten zu einer Monographie der *Muscaria schizometopa* (Exclusive Anthomyidae). Pars II.

Denkschriften der Kaiserlichen Akademie der Wissenschaften, vol. 58, pp. 305–446, Wien.

Breuning, S.

1927. Monographie der Gattung *Calosoma* Web. (Carab.) Koleopterologische Rundschau, vol. 13, pp. 129–232. [*Calosoma galapageum* Hope (pp. 200–201); synonymy, distribution (Galápagos Islands and adjacent coast of South America).]

Brinck, P.

1951. Anoplura from the Galápagos Islands. Nyt Magazin Naturvidenskaberne, vol. 88, pp. 246. [*Polyplax spinulosa* recorded from *Epimys rattus alexandrinus* on Floreana Island.]

Brues, C. T.

1919. A new species of the Hymenopterous genus *Scleroderma* from the Galápagos Islands. Proceedings of the California Academy of Sciences, ser. 4, vol. 2, pp. 309–310.

1924. Triungulin larvae from the Williams Galápagos Expedition. Zoologica, vol. 5, pp. 125–136, figs. 28–32. [Larvae of a meloid beetle (presumably *Cissites maculata* (Swederer) from carpenter bee (*Xylocopa*) captured on South Seymour Island.]

Burns, J. M.

1964. Evolution in skipper butterflies of the genus *Erynnis*. University of California Publications in Entomology, vol. 37, pp. 1–214, 1 pl. [p. 177, corrects Van Duzee's 1933 record of *Thanaos persius* to *Erynnis funeralis* Scudder and Burgess.]

Butler, A. G.

1877. Account of the Zoological Collection made during the visit of H.M.S. "Peterel" to the Galapagos Islands. X. Lepidoptera, Orthoptera, Hemiptera. Proceedings of the Zoological Society of London, 1877, pp. 86–91.

Calvert, P. P.

1901–1908. Insecta. Neuroptera. Odonata. Biologia Centrali-Americana, pp. xxx + 17–419, 9 pls., 1 map. [*Anomalagrion hastatum* (p. 130); *Tramea darwini* (p. 303); *Pantala flavescens* (p. 307); *Pantala hymenea* (p. 309); *Cannacria batesii* (= *Cannacria fumipennis*) (p. 326).]

1947. The Odonate collections of the California Academy of Sciences from Baja California and Tepic, Mexico, of 1889–1894. Proceedings of the California Academy of Sciences, ser. 4, vol. 23, pp. 603–609.

1947. Odonata of Voyages under the auspices of the New York Zoological Society. Entomological News, vol. 58, pp. 227–230. [Records *Pantala flavescens* (Fabricius) (Indefatigable and South Seymour islands); *Tramea cophysa darwini* Kirby (Hood and Albemarle islands).]

1952. New taxonomic entities in Neotropical Aeshnas (Odonata: Aeshnidae). Entomological News, vol. 63, pp. 253–264. [*Neureclipa galapagoensis* (p. 258).]

1956. The Neotropical species of the "subgenus *Aeschna*" *sensu* Selysii 1883 (Odonata). Memoirs of the American Entomological Society, vol. 15, pp. 1–251, 47 pls., 19 tables, maps I–IV. [*Aeshna* (*Neureclipa*) *galapagoensis*, p. 137, pl. 17.]

Campos, R. Francisco

1932. Estudio sobre una pequeña coleccion de Insectos de Puna Vieja y Archipielago de Galápagos. Revista del Colegio Nacional Vicente Rocafuerte. Ciño XIV, Núm. 46–47, pp. 9–14. [Lists 53 species from Puna Vieja and the Galápagos. The following are the Galápagos species: *Sphingonotus fusco-irroratus* Stål (Puna and Chatham islands); *Calosoma howardi* Linell (Chatham Island);

Tropisternus lateralis Fabricius (Chatham Island); *Dermestes carnivorus* Fabricius (Chatham Island); *Pseuderyctes galapagoensis* Linell (Chatham Island); *Stomion galapagoense* Waterhouse (Chatham Island); *Gnathocerus cornutus* Fabricius (Chatham Island); *Acanthoderes galapagoensis* Linell (Chatham Island); *Phlegethontius rustica* var. *galapagensis* Holland (Santa Cruz Island); *Celerio lineata* Fabricius (Chatham Island).]

Candeze, E. C. A.

1859. Monographie des Elaterides. 2. Mémoires de la Société Royale des Sciences de Liège, vol. 14, pp. 1–543, pls. 1–7. [*Physorhinus galapagoensis* (p. 394).]

Carriker, M. A., Jr.

1957. Notes on some of the Vernon L. Kellogg types of Mallophaga. Microentomology, vol. 22, pp. 95–110. [Corrects generic assignments of two Galápagos species.]

Carvalho, J. C. M.

1957–1960. A Catalogue of the Miridae of the World. Arquivos do Museu Nacional, Rio de Janeiro, Brazil. vol. 44, 158 pp. (part 1); vol. 45, 216 pp. (part 2); vol. 47, 161 pp. (part 3); vol. 48, 384 pp. (part 4); vol. 51, 194 pp. (part 5). [Lists Galápagos species with new generic assignment for *Capsus nigritulus* Walker.]

Carvalho, J. C. M., and E. Wagner

1957. A world revision of the genus *Trigontylus* Fieber. Arquivos do Museu Nacional, Brazil, vol. 43, pp. 121–155. [*Miris lineatus* Butler treated on p. 135; recorded from Seymour Island.]

Caudell, A. N.

1932. Insects of the order Orthoptera of the Pinchot Expedition of 1929. Proceedings of the United States National Museum, vol. 80, pp. 1–7. [8 species listed from the Galápagos Islands.]

Champion, G. C.

1918. Notes on various South American Coleoptera collected by Charles Darwin during the voyage of the "Beagle," with descriptions of new genera and species. The Entomologist's Monthly Magazine, vol. 54, pp. 43–55.

1924. The insects of the Galapagos Islands. The Entomologist's Monthly Magazine, vol. 60, pp. 259–260. [Review of entomology in Beebe (1924) and the paper by Butler (1877b); generic placements by W. E. China.]

Cheesman, L. E.

1929. Hymenoptera collected by the "St. George" Expedition in Central America and the W. Indies. Transactions of the Entomological Society of London, vol. 77, pp. 141–154. [*Xylocopa darwini*: ♂, ♀; (Albemarle, Charles, Indefatigable, and James islands) (pp. 143–144, figs. 2a, b).]

Clark, B. P.

1926. A revision of the Protoparce of the Galápagos Islands. Proceedings of the New England Zoology Club, vol. 9, pp. 67–71. [Recognizes: *Protoparce calapagensis* Holland; *Protoparce nigrita* Rothschild and Jordan; *Protoparce rustica postscripta* n. subsp. (Charles Island) (p. 70); and *Protoparce leucoptera* Rothschild and Jordan.]

Clarke, J. F. Gates

1928. Catalogue of the Type specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. London, British Museum, vol. III, 600 pp. [*Plateprota colobota*, p. 179. *Crocidosema plebeiana*, p. 319.]

Clay, Theresa

1958. Revisions of Mallophaga genera. *Degeeriella* from the Falconiformes. Bulletin of the British Museum (Natural History), vol. 7, no. 4, pp. 123–207, 9 pls. [Synonymy of *Degeeriella regalis*, p. 186.]

Cockerell, T. D. A.

1926. Descriptions and records of bees.—CXI. The Annals and Magazine of Natural History, ser. 9, vol. 17, pp. 657–665. [*Xylocopa darwini*, n. sp., ♀, (Chatham Island) (pp. 659–660).]

1935. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. no. 28. The carpenter bees of the Galápagos Islands. Proceedings of the California Academy of Sciences, ser. 4, vol. 21, pp. 379–382. [Discussion of *Xylocopa darwini*; history, variation.]

Collenette, C. L.

1925. Sea-Girt Jungles. The experiences of a naturalist with the "St. George" Expedition. London. Hutchinson & Co., pp. xiv + 275, map, plates.

Condé, B.

1960. Présence des Diploures Campodéidés sur les Iles Galapagos. Bulletin du Museum d'Histoire Naturelle, Paris, ser. 2, vol. 32, pp. 172–176, 1 fig. [*Lepidocampa juradoi seclusa*, n. subsp. (p. 172), (Santa Cruz Island).]

Coquillett, D. W.

1901. Papers from the Hopkins Stanford Galapagos Expedition, 1898–1899. II. Entomological results (2): Diptera. Proceedings of the Washington Academy of Science, vol. 3, pp. 371–379. [Records of 35 species; *Ceratopogon galapagensis*, n. sp. (p. 372), (Albemarle Island); *Pareuxesta* (n. gen.) *latifasciata*, n. sp. (p. 376), (Tower Island); *Pareuxesta obscura*, n. sp. (p. 377), (Albemarle Island); *Pareuxesta hyalinata*, n. sp. (p. 377), (Albemarle Island); *Ephydra gilvipes*, n. sp. (p. 377), (Albemarle Island); *Canace snodgrassii*, n. sp. (p. 378), (Albemarle and Narborough islands); *Rhicnoessa costalis*, n. sp. (p. 378), (Albemarle Island); *Pseudolfersia diomedeae*, n. sp. (p. 379), (Albemarle Island).]

Curio, E.

1964. Über das Nächtigen von *Nocticanace galapagensis* Curran (Diptera, Canaceidae). Zeitschrift für Tierpsychologie. Band 21, Heft 7, pp. 794–797.

Curran, C. H.

1932. [The Norwegian Zoological Expedition to the Galápagos Islands 1925, conducted by Alf Wollebaek. IV.] Diptera (excl. of Tipulidae and Culicidae). Nyt Magazin Naturvidenskaberne, vol. 71, pp. 347–366, 1 fig. [Reprinted as Medelelser fra det Zoologiske Museum, Oslo, nr. 30, pp. 347–366, 1 fig. (1932).] [Summary list of previously known species with many new records; keys to: species of *Villa* (p. 350), genera of Dolichopodidae (p. 352), species of *Hippelates* (p. 356); descriptions of 7 new species.]

1933. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. no. 12. Diptera. Proceedings of the California Academy of Sciences, ser. 4, vol. 21, pp. 147–172, 4 figs. [Many records and the following new species: *Pipunculus galapagensis* (Albemarle, Gardner, Charles, and James islands); *Mesogramma crockeri* (Charles, Chatham, Albemarle, and Indefatigable islands); *Euxesta galapagensis* (Hood Island); *Paroxyna crockeri* (Albemarle, Charles, James, S. Seymour, Jervis, Duncan, and Indefatigable islands); *Sphaerocera galapagensis* (Chatham Island); *Procanace galapagensis* (Albemarle Island); *Scatella galapagensis* (Chatham Island); *Xenocoenosia devia* (Chatham and James islands); *Viridinsula deceptor* (N. Seymour, Albemarle, Hood, and Charles islands); *Sarcophaga isla* (Gardner and Hood islands); *Sarcophaga williamsi* (Charles Island); *Galapagosia minuta* (Indefatigable Island).]

Currie, R. P.

1901. Papers from the Hopkins Stanford Galapagos Expedition, 1898–1899. Entomological Results (3): Odonata. Proceedings of the Washington Academy of Science, vol. 3, pp. 381–389. [7 species recorded: *Aeschna galapagoensis*, n. sp. (p. 382, fig. 29, 30), (Chatham Island); *Cannacria fumipennis* (p. 387, figs. 31–34), (Albemarle Island).]

Dallas, W. S.

1851–1852. List of the Specimens of Hemipterous Insects in the collection of the British Museum, London, Part I, pp. 1–368, 11 pls.; Part II, pp. 369–592, 4 pls. [*Anasa obscura*, *Stenocephalus insularis*, *Nysius ? marginalis*, new species, all collected by C. Darwin.]

Darwin, C.

1839. Journal and remarks. *In*: Fitzroy, Narrative of the surveying voyages of His Majesty's Ships *Adventure* and *Beagle*, between the years 1826 and 1836, describing their examination of the southern shores of South America and the *Beagle's* circumnavigation of the globe. vol. 3, pp. xiv + 615. H. Colburn, London.

Distant, W. L.

1900. Undescribed genera and species belonging to the Rhynchotal family Pentatomidae. Transactions of the Entomological Society of London, 1900, pp. 163–174.

1904. Rhynchotal Notes—XXI. The Annals and Magazine of Natural History, ser. 7, vol. 13, pp. 194–206. [Revision of Walker types and description of new genus *Dagbertus*, pp. 203–204.]

1909. VIII—Rhynchotal Notes—XLVIII. The Annals and Magazine of Natural History, ser. 8, vol. 4, pp. 73–87. [*Galapagosana*, n. gen., p. 73, for *Issus rostrifer* Butler.]

d'Orchymont, A.

1937. Sphaeridiini broméliadicoles neuveaux (Coleoptera: Hydrophilidae, Sphaeridiinae). The Annals and Magazine of Natural History, ser. 10, vol. 20, pp. 127–140, 2 figs. [*Galapagodacnum*, n. gen., for *Coelostoma darwini* Blair (p. 134).]

Dos Passos, C. F.

1964. A synonymic list of the Nearctic Rhopalocera. Lepidopterists' Society, Memoirs, vol. 1, pp. 1–145.

Drake, C. J.

1954. Synonymic data and description of a new saldid (Hemiptera). Occasional Papers, Museum of Zoology, University of Michigan, no. 553, 5 pp. [*Salda rubromaculata* Heidemann, a synonym of *Salda sphacelata* Uhler.]

Edwards, R. L.

1961. Studies of the Philopteridae (Mallophaga) from birds of the order Procellariformes. 1. The genus *Halipeurus* Thompson. Journal of Parasitology, vol. 47, pp. 125–157. [*Lipeurus limitatus* treated as synonym of *Halipeurus diversus* (Kellogg); *Halipeurus pelagicus* recorded from Galapagos, with synonymy.]

Emery, C.

1891. Voyage de M. Ch. Allnaud dans le territoire d'Assinie. Formicides. Annales de la Société Entomologique de France, 1891, pp. 553–574. [*Champsomyrmex bauri*, n. sp. (p. 561), Galápagos Islands.]

1893. Notice sur quelques Fourmis des îles Galápagos. Annales de la Société Entomologique de France, vol. 62, pp. 89–92. [5 species recorded, two described as new.]

Esben-Petersen, P.

1920. Revision of some of the type specimens of Myrmeleonidae, described by Navas and placed in the Vienna Museum. Annales de la Société Entomologique de Belgique, vol. 60, pp. 190–196. [*Dimares formosa* Banks (= *Dimares nummatus* Navas) (p. 191).]

1934. The Norwegian Zoological Expedition to the Galápagos Islands 1925, conducted by Alf Wollebaek. XII. Neuropterous insects from Galápagos Islands. Nyt Magazin Naturvidenskaberne, vol. 74, pp. 291–294. [Reprinted as Meddelelser fra det Zoologiske Museum, Oslo, nr. 43, pp. 291–294 (1934).] [*Chrysopa wollebaeki*, n. sp. (p. 291, figs. 1, 2, (Floreana Island); myrmelionid larva (p. 293, fig. 3), (Floreana Island).]

EVANS, W. H.

1952. A catalogue of the American Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part II (groups B, C, D). Pyrginae. Section 1. British Museum, London. v + 178 pp., 16 pls. [*Urbanus dorantes galapagensis* (Williams), new combination (p. 93).]

EWING, H. E.

1924. Bird-infesting Mallophaga collected by the Williams Galapagos Expedition. Zoologica, vol. 5, pp. 81–84, fig. 12. [Records for 8 species, including *Esthiopterum nannopteri*, n. sp. (p. 82, fig. 12), from *Nannoptera harrisi*, and *Esthiopterum potens* var. *minor*, new (p. 84), from *Sula nebouxii*.]

FENNAH, R. G.

1954. The higher classification of the family Issidae (Homoptera: Fulgoroidea) with descriptions of new species. Transactions of the Royal Entomological Society of London, vol. 105, pp. 455–474. [Key to genera of Acanoloniinae including *Galapagosana* Distant and *Euthiscia* Van Duzee, p. 472.]

FERRIS, G. F.

1916. Notes on Anoplura and Mallophaga, from mammals, with descriptions of four new species and a new variety of Anoplura. Psyche, vol. 23, pp. 97–120. [*Hoplopleura quadridentata* Ferris, not Neumann, from the Galápagos Islands.]

1921. Contributions toward a monograph of the sucking lice. Part II. Stanford University Publication, University series, Biological Sciences, ser. 2, vol. 2, pp. 59–133, figs. 33–89. [*Hoplopleura nesoryzomydis,* n. sp., (Galápagos Islands) (p. 90), based upon specimens previously reported as *Hoplopleura quadridentata* by Ferris (1916).]

1923. Contributions toward a monograph of the sucking lice. Part IV. Stanford University Publication, University series, Biological Sciences, ser. 2, vol. 4, pp. 183–270, figs. 119–172. [*Polyplax spinulosa* recorded from the Galapagos Islands (p. 188).]

1941. Atlas of Scale Insects of North America—S III-362. [*Aspidiotus smilacis* Kuwana, not Comstock, a misidentification for *Melanaspis obtusa* Ferris, n. sp.]

1951. The Sucking Lice. Memoirs of the Pacific Coast Entomological Society, vol. 1, pp. ix + 320. [Galápagos species *Hoplopleura nesoryzomydis,* p. 138; *Hoplopleura quadridentata* (Neumann) a valid species, p. 142; *Polyplax spinulosa* (Burmeister), p. 211.]

FLUKE, C. L.

1942. Revision of the Neotropical Syrphini related to *Syrphus* (Diptera, Syrphidae). American Museum Novitates, no. 1201, pp. 1–24, figs. [*Allograpta splendens* (Thomson) (p. 17, fig. 40).]

1956. Catalogue of the family Syrphidae in the Neotropical Region (Diptera). Revista Brasileira de Entomologia, vol. 6, pp. 193–268. [*Allograpta splendens* (Thomson) (p. 210); *Baccha clavata* (Fabricius) (p. 240).]

Folsom, J. W.

1924. Apterygota of the Williams Galápagos Expedition. Zoologica, vol. 5, pp. 67–76, pls. 3–5. [Three species recorded: *Heterolepisma intermedia*, n. sp. (pp. 67–70, figs. 1–12) (Indefatigable and South Seymour islands); *Acrotelsa galapagoensis* (Banks), (pp. 71–73, figs. 13–20) (Indefatigable, South Seymour, Daphne Major, and James islands); *Lepidocyrtus intermixus*, n. sp., (pp. 75–76, figs. 27–29) South Seymour Island.]

Froeschner, R. C.

1960. Cydnidae of the Western Hemisphere. Proceedings of the United States National Museum, vol. 111, pp. 337–680. [Redescription and generic placement of *Geotomus murinus* Van Duzee in *Dallasiellus*, p. 616.]

Garth, J. S.

1933. IV. Insects. *In*: Banning, G. H., Hancock Expedition of 1933 to the Galapagos Islands. Bulletin of the Zoological Society of San Diego, no. 10, May 1933, pp. 18–20. [Charles Island butterflies—*Leptotes marina*, *Catopsilis eubule*, *Dion vanillae*, *Danaus menippe* (Monarch), and *Eudamus galapagensis*; *Xylocopa* (Charles Island) (nesting in "the agava"), *Amantis* (Barrington Island), *Halobates* (north of Albemarle Island), flat flies on birds.]

Gifford, E. W.

1919. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906. XIII. Field notes on the Land Birds of the Galápagos Islands and of Cocos Island, Costa Rica. Proceedings of the California Academy of Sciences, ser. 4, vol. 2, pt. II, no. 13, pp. 189–258. [Insects as food of the birds.]

Hebard, M.

1920. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906. XVII. Dermaptera and Orthoptera. Proceedings of the California Academy of Sciences, ser. 4, vol. 2, pp. 311–346, pl. 18, t. figs. 1–11. [Reports 1 species of Dermaptera (adventive); 9 species of blattids, all but one, *Anisopygia snodgrassii* (McNeill), adventive; 1 endemic mantid, *Galapagia solitaria* Scudder; 8 species of acridids, 3 dividing into geographic races, 1 also recorded from Puna Island, Ecuador; 4 species of tettigoniids, 3 endemic; 4 species of gryllids, 3 endemic.] [*Halmenus eschatus*, n. sp. (Wenman Island).]

1934. The Norwegian Zoological Expedition to the Galápagos Islands 1925, conducted by Alf Wollebaek. X. Orthoptera of the Galápagos Islands. Nyt Magazin Naturvidenskaberne, vol. 74, pp. 279–280. [Reprinted as Meddelelser fra det Zoologiske Museum, Oslo, nr. 41, pp. 279–280 (1934).] [Records of 11 species from Floreana and/or Chatham Island; 17 species and 4 races regarded as native; of cockroaches, 8 are adventive, one native.]

Heidemann, O.

1901. Papers from the Hopkins Stanford Galápagos Expedition, 1898–1899. I. Entomological Results (1): Hemiptera. Proceedings of the Washington Academy of Science, vol. 3, pp. 364–370. [Records for 21 species of Heteroptera and Homoptera; *Ghilianella galapagensis*, n. sp. (p. 367), (Hood and Albemarle islands); *Salda rubromaculata*, n. sp. (p. 368) (Albemarle Island).]

Herring, J. L.

1961. The genus Halobates (Hemiptera: Gerridae). Pacific Insects, vol. 3, no. 2, pp. 223–305. [*Halobates micans*, Galápagos, p. 227; *Halobates sobrinus*, Galápagos, p. 229; *Halobates robustus* (Santa Cruz and Isabela islands), p. 229 and 282–283.]

Hinton, H. E.

1936. New species of *Ataenius* allied to *Ataenius cribrithorax* Bates (Coleoptera, Scarabaeidae). The Annals and Magazine of Natural History, ser. 10, vol. 17, pp. 413–428. [*Ataenius arrowi*, n. sp. (p. 414), Galápagos Islands.]

Holland, W. J.

1889. Lepidoptera. *In*: Howard, L. O., Scientific results of explorations by the U. S. Fish Commission Steamer Albatross. no. V—Annotated catalogue of the insects collected in 1887–'88. Proceedings of the United States National Museum, vol. 12, pp. 194–196.

Hope, F. W.

1838. Descriptions of some species of Carabidae, collected by Charles Darwin, Esq., in his late voyage. Transactions of the Entomological Society of London, vol. 2, pp. 128–131. [*Calosoma galapageium*, n. sp., Galápagos Islands.]

Hopkins, G. H. E.

1951. xxxvi.—Stray notes on Mallophaga.—xi. The Annals and Magazine of Natural History, ser. 12, vol. 4, pp. 375–377. [Lectotypes designated for Brülia species of Kellogg and Kuwana.]

Hopkins, G. H. E., and T. Clay

1952. A check list of the genera and species of Mallophaga. British Museum (Natural History), London, 362 pp.

Horn, W.

1915. Coleoptera, Adephaga, Fam. Carabidae, Subfam. Cicindelinae. Genera Insectorum, fasc. 82c, pp. 209–486, pls. 16–23. [*Cicindela galapagoensis*, n. sp. (p. 52, *et seq.*).]

1920. Cicindelinen-Studien aus dem schwedischen Reichsmuseum nebst einigen Bemerkungen neuer Arten, etc. Archives für Zoologi, vol. 13, no. 11, pp. 1–21. [*Cicindela galapagoensis* Horn (p. 17).]

Howard, L. O.

1890. Scientific results of explorations by Steamer Albatross, No. 5. Annotated catalogue of the insects collected in 1887–'88. Proceedings of the United States National Museum, vol. 12, pp. 185–216 (1889).

Hurd, P. D., Jr.

1955. Observations on the nesting habits of some New World carpenter bees with remarks on their importance in the problem of species formation. Annals of the Entomolgical Society of America, vol. 51, pp. 365–375, 5 figs. [Reference to the Galápagos carpenter bee, *Xylocopa darwini* Cockerell, as host of parasitic beetle *Cissites maculata* (Swederus) (p. 372).]

1958. The carpenter bees of the eastern Pacific oceanic islands. Journal of the Kansas Entomological Society, vol. 31, pp. 249–255. [*Xylocopa darwini*, summary of literature.]

Hutchinson, G. E.

1931. On the occurrence of *Trichocorixa* Kirkaldy (Corixidae, Hemiptera-Heteroptera) in salt water and its zoogeographic significance. The American Naturalist, vol. 65, pp. 573–574. [Cites a personal note from Dr. H. B. Hungerford that *Trichocorixa* had been received from the Galápagos Islands.]

John, H.

1959. Neue Spezies der Gattungen *Notiophygus* Gory und *Fallia* Sharp (Ins., Col., Discolomidae = Notiophygidae). Senckenbergiana Biologie, vol. 40, pp. 289–296, 2 pls., 2 figs. [*Fallia galapagana*, n. sp. (p. 295, fig. 2) (Santa Cruz Island); *Fallia colorata*, n. sp. (p. 295, pl. 35, figs. 2a–2e), (Galápagos Islands).]

Johnson, C. W.

1924. Diptera of the Williams Galápagos Expedition. Zoologica, vol. 5, pp. 85–92, figs. 13–14. [28 species recorded, 13 for first time; new species: *Galapagomya* *longipes* (Indefatigable Island); *Asyndetus versicolor* (S. Seymour Island); *Odinia williamsi* (S. Seymour Island).]

Kéler, S. von

1957. Die Mallophaga von Sturmvögeln und Ruderfüssern. I. *Harrisoniella* Bedford und *Perineus* Thompson (Mallophaga) (2. Fortsetzung). Beiträge zur Entomologie, vol. 7, pp. 493–527, 30 figs. [*Perineus oblongus*, n. sp. (p. 523, figs. 27–28) (on *Diomedea irrorata*) (Galápagos Islands).]

Kellogg, V. L.

1901. Insects and spiders of the Galápagos Islands. Psyche, vol. 9, pp. 173–175.

1903. Two new genera of Mallophaga. Biological Bulletin, vol. 5, pp. 85–91.

1906. A second collection of Mallophaga from birds of the Galápagos and Revillagigedo islands and neighboring waters. Transactions of the American Entomological Society, vol. 32, pp. 315–324. [Records of 41 spp. from Galápagos Islands, including *Nirmus ridgewayi*, n. sp. (p. 317) (Indefatigable Island), and *Menopon beckii*, n. sp. (p. 322) (Daphne Island).]

Kellogg, V. L., and S. I. Kuwana

1902. Papers from the Hopkins Stanford Galápagos Expedition, 1898–1899. Entomological Results (8): Mallophaga from birds. Proceedings of the Washington Academy of Science, vol. 4, pp. 457–499, pls. 28–31. [43 species reported, many described as new.]

Kernbach, K.

1962. Die Schwärmer einiger Galapagos-Inseln (Lep. Sphingidae). Opuscula Zoologica, vol. 63, pp. 1–19, abb. 1–12. [12 species recorded, 1 described as new; 6 named as new subspecies of mainland forms.]

Kirby, Harold, Jr.

1939. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. no. 39. Two new flagellates from termites in the genera *Coronympha* Kirby, and *Metacaronympha* Kirby, new genus. Proceedings of the California Academy of Sciences, ser. 4, vol. 22, pp. 207–220, 4 pls.

Kirby, W. F.

1889. A revision of the subfamily Libellulinae, with descriptions of new genera and species. Transactions of the Zoological Society of London, vol. 12, pp. 249–348, pls. 51–57. [*Tramea darwini*, n. sp. (p. 315, pl. 51, fig. 1).]

1890. A synonymic catalogue of Neuroptera Odonata or dragonflies with an appendix of fossil species. London. pp. 1–202.

Köhler, P.

1961. Noctuidarum miscellanea III. Anales de la Sociedad Cientifica Argentina, Buenos Aires, vol. 172, pp. 69–94, 25 figs. [*Agrotis* (*Scotia*) *galapagosensis*, n. sp.]

Kuschel, G.

1963. Composition and relationship of the terrestrial faunas of Easter, Juan Fernandez, Desventuradas, and Galapagos islands. Occasional Papers of the California Academy of Sciences, no. 44, pp. 79–95, 1 fig., 11 tab. [Includes climatological data for San Cristóbal and Seymour islands and comparison of Coleoptera of Galápagos and Juan Fernandez by families.]

Kuwana, S. J.

1902. Coccidae from the Galapagos Islands. Journal of the New York Entomological Society, vol. 10, pp. 28–33, 2 pls. [Removed from herbarium specimens collected by the Snodgrass–Heller Expedition; includes: *Orthezia galapagoensis*, n. sp. (p. 28); *Lecanium hesperidum* var. *pacificum*, n. var. (p. 30).]

Lack, David

1945. The Galápagos Finches (Geospizinae), a study in variation. Occasional Papers of the California Academy of Sciences, no. 21, 152 pp., 4 pls. [Insects as food.]

Lesne, P.

1910. Notes sur les Coléoptères Térédiles. 4. Les Bostrychides des Îles Galápagos. Bulletin du Muséum National d'Histoire Naturelle, vol. 16, pp. 183–186. [*Schistoceros cornutus galapaganus*, n. subsp. (p. 184).]

Light, S. F.

1935. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. no. 20. The termites. Proceedings of the California Academy of Sciences, ser. 4, vol. 21, pp. 233–258, pls. 9–10, 10 t. figs. [5 species recorded: *Kalotermes immigrans* Snyder (Chatham, Indefatigable, James, Albemarle, Jarvis, Narborough, South Seymour, and Tower islands); *Kalotermes pacificus* Banks (Albemarle and James islands); *Kalotermes darwini*, n. sp. (Albemarle, Charles, and James islands); *Kalotermes fatulus*, new name (Albemarle and James islands); *Heterotermes orthognathus* Light (Indefatigable Island).]

Linell, M. L.

1898. On the coleopterous insects of the Galápagos Islands. Proceedings of the United States National Museum, vol. 21, no. 1143, pp. 249–268.

Linnavuori, R.

1959. Revision of the Neotropical Deltocephalinae and some related subfamilies (Homoptera). Annales Zoologici Societatis Zoologicae Botanicae Fennicae "Vanamo," vol. 20, 370 pp., 144 figs. Finnland. [Generic placement of *Deltocephalus*, *Scaphytopius*, *Amplicephalus*, *Exetranus*, and synonymy under *Balclutha* (= *Eugnathodus*).]

Linsley, E. G.

1965. Pollinating insects of the Galápagos Islands. *In*: Bowman, R. I. (Ed.), Proceedings of the symposia of the Galápagos International Scientific Project. University of California Press, Berkeley–Los Angeles (in press).

Linsley, E. G., C. M. Rick, and S. G. Stephens

1965. Observations on the floral relationships of the Galápagos carpenter bee. Pan-Pacific Entomologist (in press).

MacSwain, J. W.

1961. Primary larvae of *Cissites* associated with New World carpenter bees. The Pan-Pacific Entomologist, vol. 37, pp. 191–194.

Maa, T. C.

1963. Genera and species of Hippoboscidae (Diptera): types, synonymy, habitats and natural groupings. Pacific Insects Monograph 6, pp. 1–186. [*Olfersia diomedeae* (p. 29).]

Maidl, F.

1912. Die Xylocopen (Holzbienen) des Wiener Hofmuseums. Ein Beitrag zu einer Monographie dieser Gattung. Annalen des Kaiserlichen-Königlichen Naturhistorischen Hofmuseums, vol. 26, pp. 249–330, tag. 3–4. [*Xylocopa* recorded from the Galápagos Islands (p. 312) (as *Xylocopa brasilianorum*).]

Martin, R.

1908. Collections zoologiques Edm. de Selys Longchamps. Fasc. 18, Aeschnines. [*Aeschna galapagoensis* (p. 50, fig. 47).]

Marx, F.

1890. ?Arachnida. *In*: Howard, Scientific results of explorations by Steamer Albatross, no. 5. Annotated catalogue of the insects collected in 1887–88. Proceedings of the United States National Museum, vol. 12, pp. 207–211.

McLachlan, R.

1877. Account of the zoological collection made during the visit of H.M.S. *Peterel* to the Galapagos Islands. Neuroptera. Proceedings of the Zoological Society of London, 1877, pp. 84–86. [*Pantala hymenaea* (Say) and *Tramea* sp. from Galápagos expedition of H.M.S. *Peterel.*]

McNeill, J.

1901. Papers from the Hopkins Stanford Galápagos Expedition, 1898–1899. Entomological Results (4): Orthoptera. Proceedings of the Washington Academy of Science, vol. 3, pp. 487–506. [Distribution of 26 known species summarized and occurrence by islands analyzed: *Temnopteryx snodgrassii*, n. sp. (p. 493) (Albemarle Island); *Liparoscelis cooksoni* Butler (p. 497, fig. 38); *Liparoscelis cooksoni ensifera*, n. subsp. (p. 498, fig. 39) (Hood Island); *Liparoscelis paludicola*, n. sp. (p. 499, fig. 40) (Albemarle Island); *Liparoscelis pallidus*, n. sp. (p. 500, fig. 41) (Barrington Island); *Xiphidium exitiosum*, n. sp. (p. 501, fig. 42); *Nemobius speculi*, n. sp. (p. 503, figs. 43–44) (Albemarle Island); *Cycloptilum lepismoide*, n. sp. (p. 505) (Albemarle, Narborough, and Abington islands).]

Meise, W.

1933. The Norwegian Zoological Expedition to the Galápagos Islands 1925, conducted by Alf Wollebaek. VIII. Scorpiones. Nyt Magazin Naturvidenskaberne, vol. 74, pp. 25–43, figs. [Reprinted as Meddelelser fra det Zoologiske Museum, Oslo, nr. 39, pp. 25–43, figs. (1933).] [*Rhopalurus testaceus exsul*, n. subsp. (p. 26), Floreana Island.]

Melichar, L.

1906. Monographie der Issiden (Homoptera). Abendlungen der Kaiserlichen-Königlichen Zoologisch-Botanische Gesellschaft Wien, vol. 3, no. 4, pp. 1–327, 75 figs. [*Issus varius* Walker transferred to *Thionia.*]

Metcalf, Z. P.

1943. General Catalogue of the Hemiptera. Fasc. IV, part 3, pp. 552. [Catalogues *Ilburnia simulans* (Walker) p. 317; *Delphacodes substitua* (Walker), p. 518, and *Delphacodes vicaria* (Walker), p. 522.]

1954. General Catalogue of the Homoptera. Fasc. IV, pt. 14, pp. vii + 54. [Genus *Philatis* catalogued, pp. 43–45.]

1958. General Catalogue of Homoptera. Fasc. IV, part 15, pp. vii + 561. [*Galapagosana* catalogued on pp. 289–290.]

Meyrick, E.

1926. On Microlepidoptera from the Galápagos Islands and Rapa. Transactions of the Entomological Society of London, vol. 74, pp. 269–278. [11 species listed; one probably introduced, 10 represent endemic species in American genera.]

Morrison, H.

1924. The Coccidae of the Williams Galapagos Expedition. Zoologica, vol. 5, pp. 143–152, figs. 33–37. [6 identified species recorded, all endemic; new species: *Margarodes similis* (South Seymour and Indefatigable islands); *Eriococcus papillosus* (Indefatigable Island); *Phenacoccus parvus* (Tower Island); *Pseudococcus galapagoensis* (Eden and Indefatigable islands); *Pseudococcus insularis* (South Seymour Island).]

Muir, F.

1919. Notes on the Delphacidae in the British Museum Collection. The Canadian Entomologist, vol. 51, pp. 6–8. [Places Walker's *Delphax simulans* in *Ilburnia.*]

1919. On the Genus *Ilburnia* White (Homoptera, Delphacidae). Proceedings of the Hawaiian Entomological Society, vol. 4, pp. 48–50. [Notes on *Ilburnia simulans* (Walker).]

MUTCHLER, A. J.

1925. Coleoptera of the Williams Galápagos Expedition, Zoologica, vol. 5, pp. 219–240.

1938. Coleoptera of the Galápagos Islands. American Museum Novitates, no. 981, pp. 1–19.

NAVAS, R. P. LONGIN

1912. Myrméléonides (Ins. Néur.) nouveaux oú peu connus. Annales de la Société Scientifique de Bruxelles, vol. 36, pp. 203–248. [*Dimares nummatus,* n. sp. (p. 229, fig. 16). (S. Elena Island, Galápagos).]

NEEDHAM, J. G.

1902. New dragon-fly nymphs in the United States National Museum. Proceedings of the United States National Museum, vol. 27, pp. 685–720, 7 pls. [*Aeschna galapagoensis* Currie (nymph) (p. 695, pl. 40, fig. 3).]

OSBORN, H.

1889. Mallophaga. *In*: Howard, L. O., Scientific results of explorations by the U. S. Fish Commission Steamer Albatross. No. V—Annotated catalogue of the insects collected in 1887–'88. Proceedings of the United States National Museum, vol. 12, pp. 188–189.

1924. Homoptera of the Williams Galapagos Expedition. Zoologica, vol. 5, pp. 77–79. [Four species recorded: *Jassus galapagoensis,* n. sp. (pp. 77–78) (Indefatigable and James islands); *Philatis productus* Stål (p. 78) (Tower Island); *Philatis cinerea,* n. sp. (pp. 78–79) (Tower Island); and *Philatis major,* n. sp. (Indefatigable Island).]

PALCT, J.

1956. Biologie der primär flügellosen Insekten. Jena. [*Stylifer galapagoensis* (Banks), n. comb. (p. 27).]

1959. Über die Lepismatidae (Ins. Thysanura) von den Galapagos-Inseln. Senckenbergiana Biologie, vol. 40, pp. 171–172. [*Heterolepisma insulare* (Banks), *Stylifera galapagoensis* (Banks), synonymy, distribution.]

PAPP, C. S.

1954. New record for *Calosoma galapageium* Hope (Coleoptera: Carabidae). Bulletin of the Southern California Academy of Sciences, vol. 53, pp. 169–174, pls. 45–46. [Original descriptions of the 4 nominal Galápagos species of *Calosoma* reproduced; *Calosoma galapageium* recorded from Chatham Island.]

PARENT, O.

1934. Diptères Dolichopodides exotiques. Mémoires de la Société Nationale des Sciences Naturelles et Mathématiques de Cherbourge, vol. 41, pp. 257–312, 13 pls. [*Vanduzeeia cheesmani,* n. sp. (p. 258) (Galápagos Islands).]

PETROVITZ, R.

1961. Neue und verkannte Aphodiinae aus allen Erdteilen (Col. Scarab.) II. Entomologische Arbeiten, vol. 12, pp. 344–356, 5 figs. [*Ataenius aequatorialis,* n. sp. (p. 355) (Santa Cruz Island); *Ataenius dampieri,* n. sp. (p. 356) (Floreana Island).]

RICHARDS, A. G., JR.

1941. The noctuid moths of the Galapagos from the collections of the Allan Hancock Foundation. Report of the Allan Hancock Pacific Expedition, vol. 5, pp. 233–251, 4 pls.

RICHARDSON, H.

1901. Papers from the Hopkins Stanford Galapagos Expedition, 1898–1899. VI. The Isopods. Proceedings of the Washington Academy of Science, vol. 3, pp. 365–368.

Rick, C. M.

1963. Biosystematic studies on Galápagos tomatoes. Occasional Papers of the California Academy of Sciences, no. 44, pp. 59–77. [Includes records of flower visits of *Xylocopa darwini* Cockerell (p. 63).]

1965. Some plant–animal relationships on the Galápagos Islands.

Ris, F.

1913. Libelulinen. Collections zoologiques du Baron Edm. de Selys Longchamps, Fasc. 15, pp. 837–964, pl. 7; 16, pp. 965–1042, pl. 8.

Roeschke, H.

1900. Carabologische Notizen V. Entomologische Nachrichten, vol. 26, pp. 57–63. [*Calosoma galapageium* Hope: notes on the type (♂) in the British Museum.]

Rohwer, S. A.

1924. Hymenoptera collected by the Williams Galápagos Expedition. Zoologica, vol. 5, pp. 173–175. [Four species recorded, including *Tachysphex galapagensis*, n. sp. (Albemarle Island), and *Aporinellus galapagensis*, n. sp. (South Seymour Island).]

Rothschild, W., and K. Jordan

1903. A revision of the lepidopterous family Sphingidae. Novitates Zoologicae, ix supplement, pp. cxxxv + 972, 67 pls.

Ruckes, H.

1957. Three new species of *Thyanta* Stål (Heteroptera: Pentatomidae). The Pan-Pacific Entomologist, vol. 33, pp. 175–180, 8 figs. [*Thyanta setigera*, n. sp.]

Schaus, W.

1923. Galapagos Heterocera, with descriptions of new species. Zoologica, vol. 5, pp. 23–48.

Scudder, G. G. E.

1957. The systematic position of *Dicranocephalus* Hahn, 1826, and its allies. Proceedings of the Royal Entomological Society of London, ser. A, vol. 32, pp. 147–158. [Discusses anomalous distribution in Galápagos—the only locality in the Western Hemisphere.]

Scudder, S. H.

1893. Reports on the dredging operations off the west coast of Central America to the Galápagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U. S. Fish Commission Steamer "Albatross" during 1891, Lieut. Commander Z. L. Tanner, U.S.N., Commanding. VII. The Orthoptera of the Galapagos Islands. Bulletin of the Museum of Comparative Zoology, vol. 25, pp. 1–25, pls. I–III.

Signoret, V.

1859. Monographie du genre *Corizus*. Annales de la Société Entomologique de France, ser. 3, vol. 28, pp. 75–105. [*Corizus lugens*, p. 92, n. sp. also described in Stål 1859, Kongliga Svenska Fregatten Eugenies Resa Omkring Jorden, ... Zoologi 1, Insecta, p. 240.]

Slevin, J. R.

1931. Log of the Schooner "Academy," on a voyage of scientific research to the Galapagos Islands, 1905–1906. Occasional Papers of the California Academy of Sciences, no. 17, 162 pp., 16 pls., 1 map.

Smith, F.

1877. Hymenoptera and Diptera. *In*: Gunther, Account of the zoological collection made during the visit of H.M.S. "Peterel" to the Galápagos Islands, VIII. Proceedings of the Zoological Society of London, 1877, pp. 82–84.

Snodgrass, R. E.

1902. Papers from the Hopkins Stanford Galapagos Expedition, 1898–1899. VIII. Entomological Results (7): *Schistocerca*, *Sphingonotus*, and *Halmenus*. Proceedings of the Washington Academy of Science, vol. 4, pp. 411–454, pls. XXVI–XXVII.

Stach, J.

1932. The Norwegian Zoological Expedition to the Galápagos Islands 1925, conducted by Alf Wollebaek. III. Die Apterygoten aus den Galápagos-Inseln. Nyt Magazin Naturvidenskaberne, vol. 71, pp. 331–346, pls. 1–4. [Reprinted as Meddelelser fra det Zoologiske Museum, Oslo, nr. 29, pp. 331–346, pls. 1–4 (1932).] [Records of 3 species of Thysanura: *Lepisma insularis* (Fernandina and Isabela islands), *Heterolepisma intermedia* (Santa Cruz, South Seymour, and Floreana islands), *Acrotelsa galapagoensis* (Española, Santa Cruz, Daphne Major, South Seymour, San Salvador, and Floreana islands); 2 species of Collembola: *Anurida maritima* (Floreana Island), *Lepidocyrtus intermixtus* (South Seymour Island).]

Stål, C.

1859. Hemiptera. Species novas descripsit. Kongliga Svenska Fregatten Eugenies Resa Omkring Jorden, under befäl af C. A. Virgin, åren 1851–3. Zoologi 1, Insecta, pp. 219–298, 2 pls. [*Arma sordida*, *Rhaphigaster viridans*, *Rhopalus lugens*, *Cymus galapagensis*, *Mycterodus productus*, n. spp.]

1860. Orthoptera species novas descripsit. *In*: Kongliga Svenska Fregatten Eugenies Resa Omkring Jorden . . . Zoologi 1, Insecta, pp. 299–350, 1 pl. [*Acridium melanocerum*, *Oedipoda fusco-irrorata*, n. spp.]

Stephan, J.

1937. Schmetterlingsleben auf den Galapagos-Inseln. Entomologische Rundschau, vol. 54, pp. 165–168.

Stitz, H.

1932. [The Norwegian Zoological Expedition to the Galapagos Islands 1925, conducted by Alf Wollebaek. V.] Formicidae. Nyt Magazin Naturvidenskaberne, vol. 71, pp. 367–372, 4 figs. [Reprinted as Meddelelser fra det Zoologiske Museum, Oslo, nr. 31, pp. 367–372, 4 figs. (1932).] [Records for 10 species, including *Cylindromyrmex striatus tibidis*, n. var. (p. 367) (Floreana Island); *Monomorium floreanum*, n. sp. (p. 368) (Floreana Island); *Camponotus macilentus altinota*, n. var. (p. 370) (Floreana Island); *Camponotus macilentus wollebaeki*, n. var. (p. 371) (Floreana Island).]

Stone, A., and W. W. Wirth

1947. On the marine midges of the genus *Clunio* Haliday (Diptera, Tendipedidae). Proceedings of the Entomological Society of Washington, vol. 49, pp. 201–224, 3 pls. [*Clunio schmitti*, n. sp. (p. 217) (Narborough Island).]

Thomson, C. G.

1869. Diptera species novas descripsit. *In*: Kongliga Svenska Fregatten Eugenies Resa Omkring Jorden . . . Zoologi 1, Insecta, pp. 443–614, 1 pl., 1868. [*Tabanus vittiger*, *Chrysochlora fasciata*, *Anthrax lateralis*, *Anthrax curvirostia*, *Anthrax tincta*, *Anthrax brachialis*, *Syrphus splendens*, *Baccha facialis*, *Anchineura tibialis*, *Myobia dasycnemis*, *Lucilia quadrisignata*, and *Sarcophaga obtusifrons*, all new species.]

Timmerman, G.

1952. The species of the genus *Quadraceps* (Mallophaga) from the Larinae, with some remarks on the systematics and the phylogeny of the gulls. Part 1. The Annals and Magazine of Natural History, ser. 12, vol. 5, pp. 209–222, 1 pl., 6 figs. [*Quadraceps ernstmayri*, n. sp. (on *Creagrus furcatus*).]

1954. CI.—Studien über Mallophagen aus den Sammlungen des Britischen Museums (Natural History), London. The Annals and Magazine of Natural History, ser. 12, vol. 7, pp. 829–841, 1 pl., 3 figs.

1962. Neue zangenläuse (Mallophaga, Philopteridae) von procellariiformen und charadriiformen wirten. Zeitschrift für Parisitenkunde, vol. 21, pp. 426–436, 5 figs. [*Docophoroides irroratae*, n. sp., p. 435, Galápagos Islands.]

1963. Ein interressanter neuer Kletterfederling vom Galapagos-Albatros. Bonner Zoologische Beiträge, vol. 14, pp. 157–164, 3 figs. [*Docophoroides levequei*, n. sp.]

Todd, E. L.

1959. The fruit-piercing moths of the genus *Gonodonta* Hübner (Lepidoptera, Noctuidae). Technical Bulletin of the United States Department of Agriculture. no. 1201, pp. 1–52, 12 pls. [*Gonodonta biarmata galapagensis* n. subsp. (p. 20, figs.) (Santa Cruz, San Cristóbal, Floreana islands).]

Tokunaga, Masaaki

1964. Insects of Micronesia. Diptera. Chironomidae. Bernice P. Bishop Museum. Insects of Micronesia, vol. 12, no. 5, pp. 485–628. [*Galapagomyia* Johnson. A synonym of *Thalassomyia* Schiner (p. 539).]

Townsend, C. H.

1930. The Astor Expedition to the Galapagos Islands. Bulletin of the New York Zoological Society, vol. 33, pp. 135–172, 2 col. pl.

Townsend, C. H. T.

1917. Genera of the dipterous tribe Sarcophagini. Proceedings of the Biological Society of Washington, vol. 30, pp. 189–198. [*Prosthetocirca cana*, n. sp. (Narborough and Albemarle islands); *Gigantotheca galapagensis*, n. sp. (Albemarle Island); *Sarothromyiops cinctus*, n. sp. (Culpepper Island).]

1917. New Genera of Amobiinae (Diptera). Insecutor Inscitae Menstruus, vol. 5, pp. 157–165. [*Opsophytopsis* (n. gen.) *insularis*, n. sp. (p. 163), (Isabela Island).]

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1937. No. 33. Hemiptera of the Templeton Crocker Expedition to Polynesia in 1934–1935. Proceedings of the California Academy of Sciences, ser. 4, vol. 22, pp. 111–126. [Records of 13 previously described species and *Europiella mella*;

Euthiscia crockeri; *Agallia mera*; *Platymetopius retusus*; and *Jassus infestus*; all new species and all from Santa Cruz Island.]

Van Duzee, M. C.

1933. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. no. 7. Dolichopodidae and Phoridae. Proceedings of the California Academy of Sciences, ser. 4, vol. 21, pp. 65–74, 1 pl. [Key to species of *Chrysotus*; new species: *Condylostylus dentaticauda* (James Island); *Chrysotus brevicornis* (Indefatigable Island); *Chrysotus brevispina* (Indefatigable, Albemarle islands); *Chrysotus latifacies* (Indefatigable Island); *Dohrniphora willowsi* (South Seymour Island); *Dohrniphora crockeri* (South Seymour Island).]

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1870. Catalogue of the specimens of Dermaptera Saltatoria in the collection of the British Museum, vol. 4, pp. 605–809. [*Acridium literosum*, n. sp. (p. 620) (Galápagos Islands).]

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Ward, R. A.

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WATERHOUSE, G. R.

1845. Descriptions of coleopterous insects collected by Charles Darwin, Esq., in the Galapagos Islands. Annals of Natural History, vol. 16, pp. 19–41. [20 new species.]

WHEELER, M. R.

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1924. The Formicidae of the Harrison Williams Galapagos Expedition. Zoologica, vol. 5, pp. 101–122, figs. 19–27, 1 tab. [Records of 18 forms, 2 species and 1 variety described as new; *Monomorium floricola*, a tropicopolitan species, reported for the first time; also, a termite, *Calotermes pacificus*, recorded from South Seymour Island.]

1933. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. no. 6. Formicidae of the Templeton Crocker Expedition. Proceedings of the California Academy of Sciences, ser. 4, vol. 21, pp. 57–64. [Notes and new species as follows: *Crematogaster brevispinosa chathamensis* (Chatham Island); *Camponotus planus* var. *hephaestus* (Albemarle Island).]

WILLIAMS, F. X.

1907. [Report of the expedition of the California Academy of Sciences to the Galapagos Islands.] Entomological News, vol. 18, pp. 260–261. [Insects taken include at least 5 species each of butterflies and sphinx moths, numerous noctuids, Microlepidoptera, and Orthoptera, few Diptera and Hemiptera, more than 150 species of Coleoptera.]

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1926. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906. The bees and aculeate wasps of the Galápagos Islands. Proceedings of the California Academy of Sciences, ser. 4, vol. 2, pp. 347–357. [Several records and the following new species: *Photopsis galapagensis* (South Seymour Island); *Odynerus* (*Padrodynerus*) *galapagensis* (Chatham Island); new species.]

WILLIAMS, R. C.

1926. Studies in the Neotropical Hesperoidea. Paper I. Transactions of the American Entomological Society, vol. 52, pp. 61–87, 3 pls., 28 figs. [*Eudamus galapagensis* Williams (p. 64, pl. 2, fig. 4).]

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WIRTH, W. W.

1951. A revision of the dipterous family Canaceidae. Occasional Papers of the Bernice

P. Bishop Museum, vol. 20, pp. 245–275, 4 figs. [*Canace snodgrassii* Coquillet (= *macateei* Malloch) (p. 260) (Narborough and Albemarle islands); *Canace maritima*, n. sp. (p. 263) (Bartholomew Island).]

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1896. Die Ausbeute des "Pisani" an Halobates während der Erdumseglung 1882–1885. Wiener Entomologische Zeitung, vol. 5, pp. 177–182, pp. 231–234. [*Halobates splendens*—Pacific Ocean near the Galápagos Islands; *Halobates wüllerstorffi*, somewhat east of Galápagos Islands, a feather with *Halobates* eggs, off southwest coast of the Galápagos Islands.]

WOLF, T.

1892. Geografía y Geología del Ecuador. Leipzig, F. A. Brockhaus. pp. xii + 671, 12 pls., 47 figs., 2 maps. [Galápagos, part V, pp. 469–493; Insects, very brief, p. 485.]

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 8, pp. 197–236; 28 figs.; 5 tables January 31, 1966

CERAMBYCIDAE OF THE GALÁPAGOS ISLANDS*

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Introduction

According to Kuschel (1963), no Cerambycidae have been found in the Juan Fernandez Islands, nor in Desventuradas. Thus the only Cerambycidae currently known from eastern Pacific oceanic islands are from the Galápagos, Cocos, and the Revilla Gigedos. They are treated in the present series of three companion papers.

Charles Darwin, as the record shows (Darwin, 1839; Champion, 1918), was a keen coleopterist, yet during his visit to the Galápagos Islands in September and October, 1835, he found no Cerambycidae (G. R. Waterhouse, 1845; C. Waterhouse, 1877). The first member of this family reported from the archipelago was described by Boheman (1859) from the collections made by the Swedish frigate *Eugenie* in May, 1852, but the "species" named (*Eburia amabilis*) has not since been reported from the Galápagos and, in fact, may not have come from the islands. H.M.S. *Peterel,* which visited the archipelago in June, 1875, likewise found no Cerambycidae, and it was not until the *Albatross* Expedition of April, 1888, that two longicorn species ("*Stenodontes molarius*" and *Eburia lanigera*) were reported (Linell, 1899) the presence of which in the Galápagos has been confirmed subsequently. Dr. G. Baur, who visited the islands from June to September, 1891, captured three species (Linell, 1899), and F. X. Williams, with the California Academy of Sciences Expedition of 1905–1906, ten (Williams, 1907; Van Dyke, 1953). No expedition until the present one has equalled the record of F. X. Williams. The Beebe Expedition of 1923 found one species (Mutchler, 1925); the 1924 St. George Expedition, four (Blair, 1933); G. Bateson's collections of 1925, also contain four (Blair, 1933); and those of Von Hagen in 1935–1936, four (Mutchler, 1938). Of these "species," eleven are here recognized as definitely occurring in the Galápagos

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* Contribution No. 28 from the Charles Darwin Foundation for the Galápagos Islands.

Islands, to which may be added the two "new" ones described below, for a total of 13. Types of new species are deposited in the collections of the California Academy of Sciences, San Francisco.

Geographical Affinities of the Galápagos Flora

The flora of the Galápagos Islands has been discussed and analyzed on numerous occasions, most comprehensively by Stewart (1911) and Svenson (1935, 1946), and will no doubt be further considered in reports prepared by botanists of the Galápagos International Project. The published accounts are not in agreement as to the origin of the Galápagos flora, and obviously we are in no position to make an independent judgment on this matter. Nevertheless, we believe that it can be said that when the widespread or pan-tropical weedy species and strand plants are disposed of, the literature can be interpreted as indicating that the flora has a great deal in common with that of the west coast of South America, particularly but not exclusively the drier zones; it can also be interpreted as having relationship, especially among the older endemic elements, with the flora of the Caribbean, Central America, and Mexico. Such an explanation, at least as it affects the woody plants, would be consistent with our finding with regard to the Cerambycidae, which as larvae are wood-boring beetles.

Cerambycidae were associated with a number of plant hosts in the Galápagos, but evidence of borings by unidentified members of this family as well as by buprestids, bostrycids, weevils, etc., were seen in many more (table 1).

Endemism and Faunal Affinities of Galápagos Cerambycidae

Mutchler (1925) states that ". . . six conspicuous species of Cerambycidae appear to be of recent introduction, as they were not reported by the earlier writers and these beetles would almost surely have been found, had they been there. They were probably taken over in wood which formed a part of boat's cargo or of the boats themselves." The six species referred to by Mutchler represent all of those reported up to the time his paper was published: *Stenodontes molarius*, *Achryson galapagoensis*, *Eburia lanigera*, *E. bauri* (= *proletaria*), *E. amabilis*, and *Acanthoderes galapagoensis*. (When his statement was made, five of these six species were known only from the Galápagos Islands, although two have been reported subsequently from South America.) However, it should be pointed out that Darwin's visit to the Galápagos in 1835 occurred during the dry season and he obtained relatively few insects altogether, including only 29 species of Coleoptera—less than one-fifth of those found by F. X. Williams of the California Academy of Sciences Expedition of 1905–1906 which spent a year in the archipelago. Thus, the absence of Cerambycidae among his material can hardly be considered significant. The same may be said of the collections brought back by the British H.M.S. *Peterel*, which visited

Table 1. *Principal observed woody-plant hosts of seed- and wood-boring beetles—Santa Cruz Island (January–February, 1964).*

Littoral Zone	*Arid Zone*	*Transition Zone*	*Moist Forest Zone*
Cryptocarpus pyriformis	*Acacia macrantha*	*Piscidia erythrina*	*Ochroma lagopus*
Hippomane mancinella	*Parkinsonia aculeata*	*Prosopis dulcis*	*Persea gratissima*
Hibiscus tiliaceus	*Piscidia erythrina*	*Castela galapageia*	*Scalesia pedunculata*
Laguncularia racemosa	*Prosopis dulcis*	*Bursera graveolens*	*Pisonia floribunda*
Avicennia officinalis	*Castela galapageia*	*Croton scouleri*	*Psidium galapageum*
Maytenus obovata	*Bursera graveolens*	*Opuntia echios*	
Rhizophora mangle	*Croton scouleri*	*Jasminocereus howelli*	
Scaevola plumieri	*Opuntia echios*	*Cordea lutea*	
	Jasminocereus howelli	*Maytenus obovata*	
	Cordea lutea	*Psidium galapageum*	
	Scalesia helleri		
	Scalesia affinis		
	Maytenus obovata		

the Islands in 1875. In fact, the New York Zoological Society Expedition of April, 1923, under the direction of William Beebe, upon which Mutchler reported, found only one specimen of cerambycid, although members of the group brought back seven new species of beetles, all in genera not previously reported from the Islands! On the other hand, members of the 1852 expedition aboard the Swedish frigate, *Eugenie,* collected one of the six species referred to by Mutchler; those of the 1887–1888 expedition on the U. S. fisheries steamer *Albatross,* five. The absence of Cerambycidae from the collections of the early expeditions (presumably meaning those prior to the voyage of the *Albatross*) is hardly a convincing argument for their introduction by man. Further, if one excludes the published but doubtfully authentic records of *Eburia amabilis* and *Taeniotes hayi* (see below) and some elements of the obviously endemic *Estola insularis* and *Nesozineus galapagoensis* complexes, only three of the presently known species were not found by Williams during the 1904–1905 expedition of the California Academy of Sciences. Two of these, *Compsa apicalis* and *Desmiphora maculosa* occur on more than one island, which argues somewhat against their subsequent introduction, although there has been extensive commerce between the islands and the mainland in the intervening 50 years. A possible candidate for a recently introduced species is *Eburia proletaria* which has thus far been found on only three islands. Another is

Nesoeme kuscheli (described below), a single example of which was captured at light at the Darwin Station on the first evening we occupied quarters newly constructed from wood imported from Ecuador. Although hundreds of Cerambycidae were attracted to these same lights during the next six weeks, no further examples of this species were taken. However, *N. kuscheli* is not presently known from elsewhere and may ultimately prove to be endemic. Its affinities appear to us to be with forms in Mexico and the West Indies.

While Mutchler's arguments for introduction of the Cerambycidae by man are unconvincing, nevertheless, it is quite possible that early Galápagos visitors and settlers did accidentally introduce some of the species currently living there. Several are known to occur elsewhere, including *Stenodontes molarius* (*sensu lato*) (Baja California, Mexico, Central and South America), *Strongylaspis kraepelini* (*sensu lato*) (Guayaquil, Ecuador), *Achryson galapagoensis* (*sensu lato*) (western South America from Colombia to Chile), *Eburia proletaria* (western South America from Colombia to Chile), and *Compsa apicalis* (Colombia). Some of these species must have reached the Galápagos without the aid of man, since they show some differentiation from mainland populations (mostly at what we interpret as a subspecific level). The most likely candidate for a man-introduced species in this list appears to be *Eburia proletaria,* if, as stated by Blair (1933) and Van Dyke (1953), Galápagos specimens agree with those from South America.

Although the species which appear to be relatively recent adventives (whether they arrived with or without the aid of man) must have come from South America (*Stenodontes molarius* excepted), the principal affinities of the species presumed to be endemic are with Mexico and/or Central America and/or the West Indies. These include *Parandra galapagoensis, Nesoeme kuscheli, Eburia lanigera, Estoloides galapagoensis, Estola insularis,* and *Nesozineus galapagoensis*. Further, several of these break up into allopatric or host-restricted populations of closely related species or subspecies. Thus, although our taxonomic analyses are far from complete, it appears that a distinctive population of the *Estola insularis* complex is attached to *Scalesia affinis* on each of the major islands. On Santa Cruz, the population on *Scalesia helleri* may be different from that on *Scalesia affinis,* agreeing with that associated with *S. helleri* on nearby Santa Fé Island, but our samples are too small to judge. On the other hand, where we have significantly large collections, the separate insular populations on the upland *Scalesia pedunculata* appear to be similar, if not identical, with those of the adjacent lowland *Scalesia affinis.*

Insular allopatry to a lesser extent is also recognizable in populations of *Nesozineus* associated with *Croton,* but apparently not in *Estoloides* associated with *Bursera* and *Scalesia.* The more recently adventive Cerambycidae show less host specificity in general and less variation between populations on the different islands.

Table 2. *Known occurrence of Cerambycidae on the principal islands of the Galápagos archipelago.*

	North-Western islands		*North-Central islands*			*Central islands*									*Southern islands*		
	Darwin	Wolf	Pinta	Marchena	Genovesa	Fernandina	Isabela	Santiago	Rábida	Pinzón	Santa Cruz	Baltra	Santa Fé	San Cristóbal	Floreana	Española	Gardner
Parandra galapagoensis							x	x			x						
Stenodontes molarius							x	x		x	x			x	x		
Strongylaspis kraepelini								x			x						
Nesoeme kuscheli											x						
Achryson galapagoensis											x	x		x	x		
Eburia lanigera			x		x	x	x	x	x	x	x		x	x	x	x	x
Eburia proletaria							x	x						x			
Compsa apicalis								x			x						
Desmiphora maculosa						x		x			x						
Estoloides galapagoensis							x	x			x		x				
Estola insularis						x	x	x		x	x		x		x		
Acanthoderes galapagoensis							x	x			x			x			
Nesozineus galapagoensis						x	x	x	x		x			x			

General Abundance

On the larger islands during the rainy season, Cerambycidae are numerous in individuals by mainland standards, although species are relatively few. Under what is assumed to have been unusually favorable circumstances, we encountered during a 6-week period, 11 species; during a similar period in the Chiricahua Mountains we found 132 species; in Ecuador an identical effort might have yielded several hundred species. All of the known Galápagos Cerambycidae are nocturnal, and only a few such as *Desmiphora maculosa* and *Nesozineus galapagoensis* were observed also to fly in the daytime, and their diurnal activity was largely limited to the late afternoon or to overcast days.

Being nocturnal, Galápagos Cerambycidae are readily attracted to light. For example, between 7:30 P.M. and 9:30 P.M. on January 20, 1964, 139 individuals were captured at four white lights in the residential area of the Darwin Research Station on Santa Cruz Island as follows:

Nesozineus galapagoensis: 28 ♂♂, 34 ♀♀
Eburia lanigera: 15 ♂♂, 28 ♀♀
Achryson galapagoensis: 8 ♂♂, 12 ♀♀
Estoloides galapagoensis: 4 ♂♂, 6 ♀♀
Desmiphora maculosa: 1 ♂, 3 ♀♀
Acanthoderes galapagoensis: 1 ♂
Stenodontes molarius galapagoensis: 1 ♀

NATURAL ENEMIES

PREDATORS OF ADULTS. As mentioned previously, adult Galápagos Cerambycidae confine their activity largely to the night. During the hours of darkness their principal predators are insects and other arthopods, and probably only the smaller species are subject to attack. On one occasion, at about 10 P.M., G. Kuschel saw an adult clerid (*Pelonium longfieldae*) attack, overcome, dismember, and devour an adult *Nesozineus*, leaving only the elytra. Carcasses of this species were twice found in spider webs and fragments of a representative of *Estoloides galapagoensis* were once found under loose bark of *Bursera graveolens* adjacent to a scorpion which was presumed to have eaten it. On another occasion, several dead adults of *Stenodontes molarius* with the soft parts removed by fire ants were found on the ground beneath a standing dead *Bursera* tree. Live individuals of *Stenodontes* were found under the bark but there seemed no obvious method for determining whether the fire ants had attacked the beetles while they were on the tree or whether the beetles had died from some other cause.

No vertebrate predators were seen to capture adult beetles at night, although geckos were abundant about the lights and were seen to capture other insects. Diurnal vertebrate predators were seen to capture cerambycids occasionally, but generally they avoided them. Mockingbirds (*Nesomimus parvulus parvulus*) and lava lizards (*Tropodurus albemarlensis*) quickly learned to prey in the morning on insects which had been attracted to protected light installations the night before. The mockingbirds first captured the sphinx moths (most commonly *Phlegathontius rusticus galapagensis*), then the larger noctuids, and finally smaller moths and soft-bodied beetles (avoiding, however, oedemerids of the genera *Oxacis* and *Alloxacis*). On the first morning, a bird was seen to capture and eat a medium-sized *Achryson galapagoensis* and later pick up and drop a large female specimen of *Eburia lanigera*. This last species was by far the most numerous cerambycid about the lights but it was consistently avoided by both mockingbirds and lava lizards, possibly because of the sharp spines on the thorax, elytral apices and femora, or perhaps because of some noxious quality not evident to us.

Predators and parasites of larvae. At various times larvae of the ostomatid *Temnochila galapagoensis* were found preying on immature stages of Cerambycidae. G. Kuschel found the pupa of *Eburia lanigera* being attacked in its cell in the wood of *Croton scouleri* and E. G. Linsley found a larva being devoured in a sapwood gallery of *Bursera graveolens*. Williams (1926) records larvae of the bethylid *Scleroderma galapagoensis* Brues feeding as external parasites of larvae now known to have been *Parandra galapagoensis* in the wood of tree *Scalesia* (*S. pedunculata typica*) at an elevation of 2,000 feet on James (Santiago) Island, December 27, 1906.

Genera and Species

Parandra galapagoensis Van Dyke

(Figure 9.)

Parandra galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 127.

Parandra (?) sp., Williams, 1926, Proc. Calif. Acad. Sci., ser. 4, vol. 2, p. 350 (host, parasite).

Moderate sized, elongate, surface glabrous, shining, color pale brownish to dark rufous. Male mandibles large, arcuate, notched at apex, inner margin with short tooth before middle and several small teeth at middle; antennae not extending to base of pronotum; submentum without a transverse furrow. Prothorax wider than long, hind angles not produced; disk flattened, almost impunctate. Elytra almost twice as long as broad, sides parallel; disk almost impunctate. Length (exclusive of mandibles), 14–25 mm.

General distribution. Presumably endemic to the Galápagos Islands.

Galápagos distribution. Isabela, Santa Cruz, and Santiago islands.

Seasonal occurrence of adults. Unknown (unemerged adults found in pupal cells in September, December, January).

Host plant. *Scalesia pedunculata* Hooker.

Van Dyke (1953) compared this species with the Mexican *P. brachyderes* Lameere. It differs in the smoother upper surface, curved, toothed mandibles, and almost impunctate undersurface.

Of the 63 specimens available for study, all but eight are from Santiago Island. Three represent the Santa Cruz population and the remaining five that of Isabela.

Comparison of these samples gives no indication of subspecific differentiation. No adults were taken during the 1964 expedition but larvae were found on Santa Cruz Island in *Scalesia*.

Material examined. Santiago: 39 ♂♂, 16 ♀♀, December, 1905, January, 1906, all chopped from rotten logs (F. X. Williams); Santa Cruz: 3 ♂♂, December, 1905, January 11, 1906 (Williams); Isabela: 5 ♀♀, San Tomas, 1,200 ft., September, 1906 (Williams).

According to Williams (1926) larvae of the bethylid parasite, *Scleroderma galapagoensis* Brues, were found as external larval parasites on James Island, in December. The small wingless adults were also taken in the beetle borings.

Stenodontes molarius (Bates).

Mallodon molarium Bates, 1879, Biologia Centrali-Americana, Coleoptera, vol. 5, p. 9, pl. 1, figs. 1, 2.

Stenodontes (*Mallodon*) *molarius*, Lameere, 1902, Mem. Soc. Ent. Belgique, vol. 9, p. 74.

This robust species occurs from Mexico into South America. It may be distinguished from other species of *Stenodontes* (*Mallodon*) by the single-toothed genal process, the possession of a small terminal tooth at the base of the mandibular carina, the two internal teeth near the apex of the male mandibles, and the slightly curved antennal scape.

The species is presently known from the islands of Santa Cruz, Isabela, Santiago, San Cristóbal, Pinzón, and Floreana. At least three Galápagos subspecies may be recognized.

Stenodontes molarius galapagoensis Mutchler.

(Figures 3–8.)

Stenodontes (*Mallodon*) *galapagoensis* Mutchler, 1938, Amer. Mus. Nov., no. 981, p. 11, fig. 6.

Stenodontes (*Mallodon*) *molarius*, Mutchler, 1938, Amer. Mus. Nov., no. 981, p. 11 (records).

Stenodontes molarius, Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 129 (records).

This subspecies differs from the mainland populations by the more coarsely, confluently punctate head, the distinctly, sparsely punctate scutellum, the presence of small, scattered punctures over the elytra, and the less densely pubescent mandibles of the male. Length of males: 30–61 mm.; mandibles: 4–13 mm. Ratio of body length to mandible length in 43 specimens from 4 : 1 to 8 : 1 with a median ratio of 4.8 : 1.

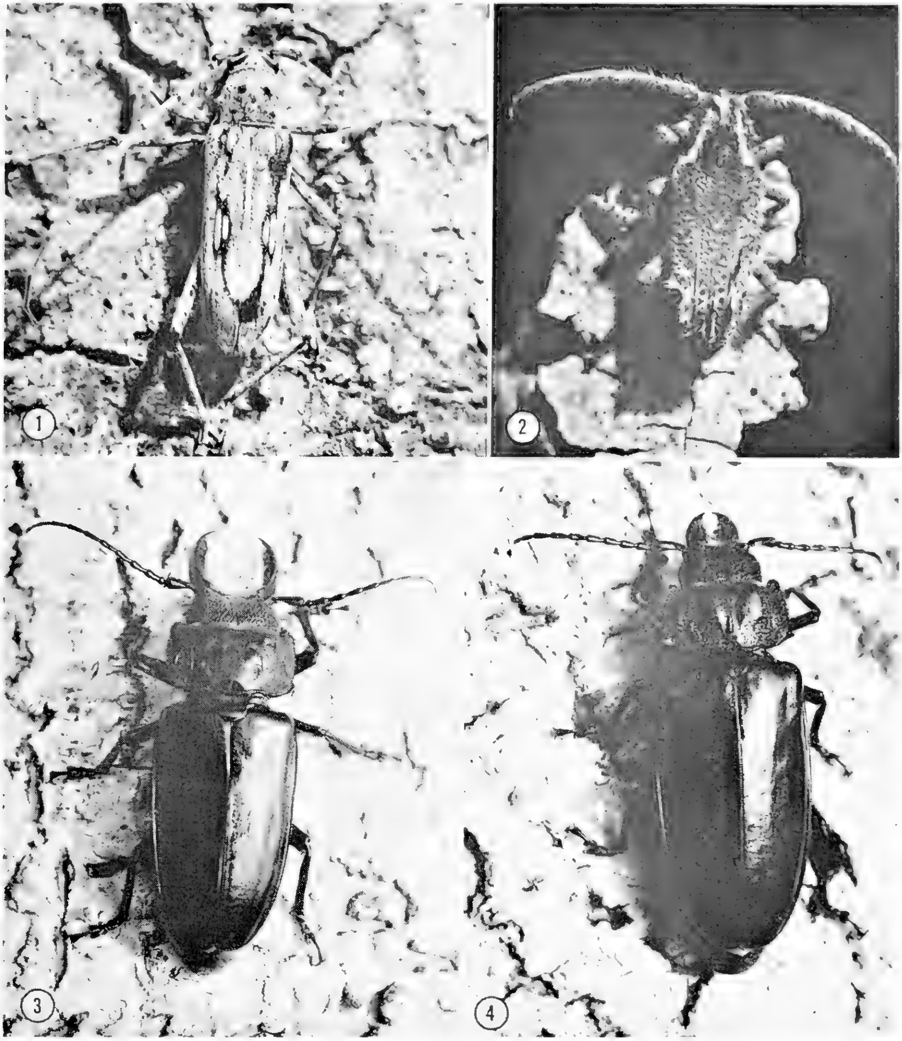
The uniformly black color, usually elongate, slightly arcuate male mandibles, and more densely punctate scutellum and elytra will separate *S. m. galapagoensis* from other subspecies in the archipelago.

Galápagos distribution. Santa Cruz Island.

Flight period. January to July.

Host plants. *Piscidia crythrina, Hippomane macinella, Cieba pentandra, Scalesia pedunculata svensoni, Bursera graveolens, Ochroma lagopus.*

Material examined. Santa Cruz: Darwin Research Station: 1 ♀, January 21, 1964, at white light (R. L. Usinger); 1 ♂, 1♀, February 3, 1964 (R. O. Schuster); 1♀, February 6, at white light (G. Kuschel); 1 ♀, February 7,



Figures 1–4. Adults *in situ* (D. Q. Cavagnaro): figure 1, *Eburia lanigera* Linell, ♂; figure 2, *Desmiphora maculosa* Linsley and Chemsak, ♂; figure 3, *Stenodontes molarius galapagoensis* Mutchler, ♂; figure 4, same, ♀.

flying in late afternoon on heavily overcast day (E. G. Linsley); 1 ♂, 3 ♀♀, February 8 (Kuschel); 1 ♂, February 20 (Schuster); 1 ♂, 1♀, February 21, at white light (Linsley); Littoral Zone: 1 ♂, February 6, at white light (Linsley); Transition Zone, 160 meters above Academy Bay: 3 ♂♂, 2 ♀♀, February 4, under bark of *Piscidia erythrina* (Linsley); 4 ♂♂, 7♀♀, May 1 (D. Q. Cavagnaro); Moist Forest Zone, 240 meters above Academy Bay: 3 ♂♂, 2 ♀♀, January 28–February 1 (Kuschel); Horneman Ranch: 3 ♂♂, 1 ♀, February 15 (Cavagnaro); 3 ♀♀, March 2 (Cavagnaro); 2 ♂♂, 3 ♀♀, March 10 (Cavagnaro); 1 ♂, March 19 (Cavagnaro); 1 ♂, March 25 (Cavagnaro); 1 ♂, April 11 (Cavagnaro); 1 ♂, 2 ♀♀, May 5 (Cavagnaro); 2 ♂♂, 1 ♀, May 7 (Cavagnaro); 3 ♂♂, 1 ♀, May 16 (Cavagnaro); 2 ♂♂, 3 ♀♀, June 1 (Cavagnaro); Upper NE. Slope 2,400 ft.: 2 ♂♂, April 10 (Cavagnaro); Table Mountain, 1,400 ft.: 4♂♂, 1 ♀, April 15 (Cavagnaro); 5 miles N. Academy Bay: 1 ♂, 1 ♀, February 8 (I. Wiggins); Santa Cruz Island: 2 ♂♂, 5 ♀♀, January 11, 1906 (F. X. Williams); 1 ♂, 2 ♀♀, July 1906 (Williams); 1 ♂, January 29, 1935 (W. von Hagen) (holotype).

Specimens examined in the collection of the Darwin Research Station: Darwin Research Station: 1 ♂, September 20, 1963 (D. Snow); 1 ♀, October 19, 1963 (D. Snow); 1 ♀, October 23, 1963 (D. Snow); 1 ♂, February 22, 1961 (R. Levêque); 2 ♂♂, March 13, 1961 (R. Levêque). Bella Vista Trail: 1 ♂, October 9, 1963, on trunks of balsa (D. Snow).

Stenodontes molarius vandykei Linsley and Chemsak, new subspecies.

Mallodon molarium, Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 259 (records).

Stenodontes molarius, Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., vol. 22, p. 129 (records).

Similar in form to *S. m. galapagoensis* but averaging smaller in size. Elytra usually dark brownish, paler than pronotum and head. Mandibles of males smaller with allometric development not pronounced. Head usually less coarsely, confluently punctate. Elytra and scutellum more sparsely punctate. Length of males: 34–53 mm.; mandibles: 3–8 mm. Ratio of body length to mandible length in eight specimens ranging from 6.6 : 1 to 11.3 : 1 with a median ratio of 8.4 : 1.

Holotype ♂ from Villamil, Albemarle Island (Isabela), March 22, 1906 (F. X. Williams); 5 ♂ paratypes with same data and 2 ♂♂, Albemarle, March 4, 1899.

We dedicate this subspecies to E. C. Van Dyke who first recorded the characteristics of this island population in his 1953 treatise on Galápagos Coleoptera.

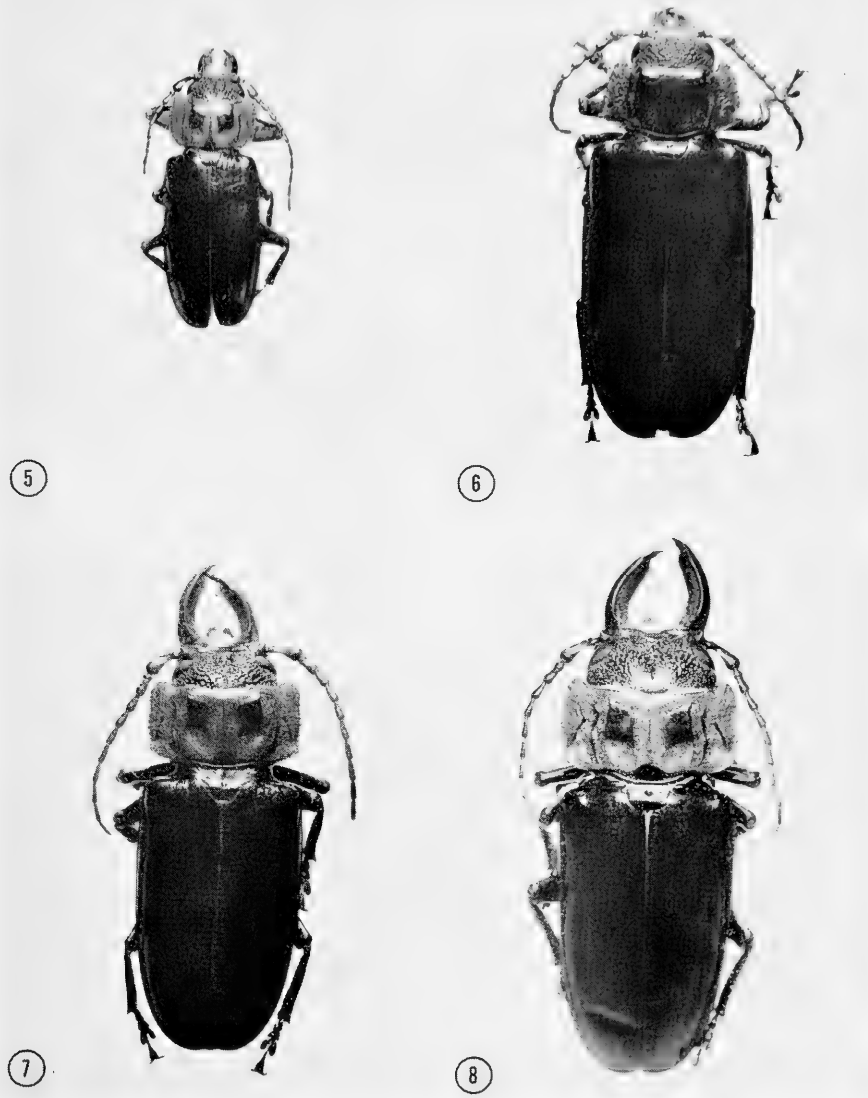
Stenodontes molarius glabratus Linsley and Chemsak, new subspecies.

Mallodon sp.? Howard, 1889, Proc. U. S. Nat. Mus., vol. 12, p. 191 (records).

Mallodon molarium, Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 259 (records).

Stenodontes moliarius, Mutchler, 1924, Zoologica, vol. 5, p. 238 (record).

Form, size, and coloration of *S. m. galapagoensis* but with a tendency to paler elytra. Mandibles of males with a lesser degree of allometric development than in *S. m. galapagoensis* but more than in *S. m. vandykei.* Head usually coarsely, confluently punctate. Elytra and scutellum almost impunctate. Length



Figures 5–8. Size variation of *Stenodontes molarius galapagoensis* Mutchler, with all figures about natural size. Figures 5, 7, and 8, ♂♂; figure 6, ♀.

of males: 31–57 mm.; mandibles: 4–12 mm. Ratio of body length to mandible length in seven specimens ranging from 4.8 : 1 to 7.7 : 1 with a median ratio of 5.8 : 1. Length of female: 43 mm.; mandibles, 4 mm.

HOLOTYPE ♂, allotype ♀ from Chatham Island (San Cristóbal), July, 1906, and January, 1906 (F. X. Williams); 5 ♂ paratypes, July, 1906, and January, 1906, from Chatham Island (Williams); one ♂ paratype, Baquerizo Morene, San Cristóbal Island, February 22, 1964 (R. L. Usinger).

Stenodontes molarius subspecies.

Material from other islands where this species is known to occur is either unavailable to us or too scanty to permit interpretations of relationships with the preceding populations. Available material consists of two specimens, one of each sex, from Santiago Island, NW. Slope, 300 M., May 30, 1964 (D. Q. Cavagnaro). These resemble examples from the Santa Cruz subspecies in coloration and punctation.

Other records include Duncan (Pinzón) Island (Howard, 1889) and Charles (Floreana) Island, Linell, 1898.

Strongylaspis kraepelini Lameere.

Strongylaspis (*Strongylaspis*) *Kräpelini* LAMEERE, 1903, Mem. Soc. Ent. Belgique, vol. 11, p. 28.

Strangylaspis (*Strongylaspis*) *kraepelini,* LAMEERE, 1919, Genera Insectorum (Wytsman), vol. 72, p. 25, pl. 2, fig. 4.

Size large, robust to small, dark reddish brown to fuscous. Head coarsely punctate; antennae extending slightly beyond middle of elytra in male, shorter in female, scape robust, up to 1½ times longer than third segment, third segment as long as the fourth and one-half of the fifth. Pronotum with disk opaque, asperate punctate except for large well defined Tau-shaped glabrous callus; sides acutely spined at base in female. Scutellum not heart-shaped, without a median groove, inflated dorsally and asperate. Elytra not pubescent, asperate punctate at base, opaque, apices often feebly dentate. Length, 16–33 mm.

TYPE LOCALITY. Guayaquil, Ecuador.

RANGE. Ecuador and Galápagos Islands (Santiago and Santa Cruz).

FLIGHT PERIOD. December to May.

This distinctive species is known presently only from Ecuador and from two of the Galápagos Islands. The island populations are subspecifically distinct from the mainland forms in a number of characteristics.

Strongylaspis kraepelini kraepelini Lameere.

Strongylaspis (*Strongylaspis*) *Kräpelini* LAMEERE, 1903, Mem. Soc. Ent. Belgique, vol. 11, p. 28.

Strongylaspis (*Strongylaspis*) *kraepelini,* LAMEERE, 1919, Genera Insectorum (Wytsman), vol. 72, p. 25, pl. 2, fig. 4.

Size usually large, robust. Antennae with first segment about 1⅓ longer than third. Elytra densely asperate basally, than densely rugosely punctate. Scutellum moderately inflated, rounded behind, rarely impressed apically. Prosternum finely asperate. Length, 22–33 mm.

Type locality. Guayaquil, Ecuador.

Range. Lowlands of Ecuador near Guayas River.

In addition to the type locality, this subspecies is known from Puna Island and Villa Rica.

Strongylaspis kraepelini parvula Linsley and Chemsak, new subspecies.
(Figures 10 and 12.)

Ground color brownish to dark reddish brown. Antennae with first segment about 1½ times longer than third. Elytra finely asperate punctate at base, opaque over basal one-third and down sides in males, punctures over remainder fine, well separated. Scutellum not greatly inflated, usually impressed and slightly emarginate at apex. Prosternum barely asperate, slightly shining. Length, 16–27 mm.

Holotype ♂, allotype ♀ and 3 ♂ paratypes from Moist Forest Zone, 240 meters above Academy Bay, Santa Cruz Island, January 28–February 1, 1964, at white light (G. Kuschel); additional paratypes from Horneman Ranch, 2 ♂♂, February 16, 1964 (D. Q. Cavagnaro); 1 ♂, March 2 (Cavagnaro); 2 ♀♀, March 10 (Cavagnaro); 1 ♂, March 19 (Cavagnaro); 1 ♂, March 25 (Cavagnaro); 1 ♂, 1 ♀, April 5 (Cavagnaro); 2 ♂♂, April 8 (Cavagnaro); 2 ♂♂, April 11 (Cavagnaro); 1 ♀, May 11 (Cavagnaro); 3 ♂♂, May 16 (Cavagnaro); 2 ♂♂, Table Mountain, 1,400 ft., April 15 (Cavagnaro).

The smaller average size, more finely punctate, nonrugose elytra and the proportions of the antennal segments will readily separate this subspecies from the typical form.

A number of larval instars, pupae and teneral adults were found in dead, rotting logs of *Scalesia pedunculata* at the higher elevations on Santa Cruz Island by D. Q. Cavagnaro.

Strongylaspis kraepelini subspecies.

Strongylaspis kraepelini, Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 130, pl. 7, fig. 5.

Three females from James (Santiago) Island collected by F. X. Williams, December, 1905, average considerably larger than those collected on Santa Cruz Island. The larger size and paler coloration may be indicative of a distinct population, but the absence of males from this collection makes subspecific assignment impractical.

Nesoeme Linsley and Chemsak, new genus.

Form elongate, slender. Head moderate sized; eyes moderately deeply emarginate, lower lobe large, upper lobes widely separated above; genae small,

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Figures 9–12. Figure 9, *Parandra galapagoensis* Van Dyke, ♂, × 1⅔; figure 10, *Strongylaspis kraepelini parvula* Linsley and Chemsak, ♂, × 1⅔; figure 11, *Nesoeme kuscheli*, Linsley and Chemsak, ♂, × 4; figure 12, *Strongylaspis kraepelini parvula* Linsley and Chemsak, ♀, × 1⅔.

mandibles small; maxillary palpi elongate, much longer than labial, apical segment obliquely truncate, not dilated; antennae 11-segmented, slender, scape gradually thickening apically, asperate near apex at outside, third segment slightly longer than first. Pronotum longer than broad, sides arcuate, broadest just behind middle, base not abruptly constricted, disk convex, shallowly impressed medially at apical one-half, surface subopague, minutely punctate; prosternal process absent, coxal cavities wide open behind, slightly angulate externally; mesosternal process absent, middle coxae contiguous. Elytra elongate, slightly tapering, sides slightly impressed at basal one-third; surface not costate; apices rounded. Legs with femora moderately clavate, tibiae slender, tarsi elongate. Abdomen normally segmented.

Type species. *Nesoeme kuscheli* Linsley and Chemsak, new species.

This genus may be distinguished from other Methiini by the elongate palpi, moderately deeply emarginate eyes, nonabruptly constricted pronotum, and absence of pro- and mesosternal processes. A single species is presently known.

Nesoeme kuscheli Linsley and Chemsak, new species.

(Figure 11.)

Male. Form narrow, elongate, elytra slightly tapering, sides moderately impressed before middle; color testaceous, pronotum at sides and middle, femora at apex and apex of antennal segments darker; pubescence fine, golden. Head about as wide as greatest width of pronotum; antennal tubercles broadly divergent on vertex, area between tubercles shallowly convex; eyes separated above by twice the diameter of antennal scape, more broadly beneath; front almost vertical, subopaque, minutely asperate punctate, pubescence sparse, short, subdepressed; neck behind eyes abruptly subparallel; antennae slender, extending five segments beyond body, segments darkly annulated apically, pubescence dense, suberect, slightly longer internally; scape slightly shorter than third segment, third shorter than fourth, fourth shorter than fifth, following segments gradually decreasing in length. Pronotum longer than wide, sides gradually rounded, broadest behind middle, base impressed, not abruptly constricted; disk convex, narrowly, shallowly impressed at middle on apical half, basal half with an elongate, narrow, glabrous, nonprominent callus; surface opaque, punctures vague, minute, pubescence short, fine, depressed; prosternum broad, impressed, finely punctate and transversely rugulose, prosternal process absent between coxae; mesosternum small, mesosternal process absent between coxae; metasternum asperate punctate and finely rugose; scutellum small, apically rounded, medially impressed, nonpubescent. Elytra over three times as long as broad, moderately tapering apically; each elytron with a dark vitta extending from base to almost apex, vittae coalescing at suture to enclose two pale elongate areas behind scutellum and two more before middle; punctures fine, sparse, surface opaque; each puncture bearing a short, suberect, recurved hair, hairs longer at apex; apices rounded. Legs with femora moderately clavate, finely pubescent; first segment of hind tarsi longer than following segments together. Abdomen finely, shallowly punctate, moderately pubescent; apex of last sternite rounded, vaguely emarginate at middle. Length, 8 mm.

HOLOTYPE male from Darwin Research Station, Santa Cruz Island, January 23, 1964, at white light (G. Kuschel).

This species is dedicated to G. Kuschel who made intensive, successful efforts to collect Cerambycidae during the Expedition, and who generously made his captures available to us for study.

Achryson galapagoensis Linell.

Achryson galapagoensis LINELL, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 259; VAN DYKE, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 131, pl. 7, fig. 6.

This species may be recognized by its testaceous ground color, the black markings of the pronotum and elytra and especially by the rounded nonelongate shape of the pronotum which is broader than long even in the male.

Individuals vary greatly in size, ranging in length from 10 to 22 mm. Of the material at hand from four islands, a sufficient series is represented from Santa Cruz, Floreana, and San Cristóbal islands to permit recognition of differences between the populations. The island of Baltra is represented by only two examples.

Van Dyke (1953) reports that this species occurs on the South American mainland in Peru, Chile, Colombia, and Ecuador. We have seen examples from Peru.

Achryson galapagoensis galapagoensis Linell.

Achryson galapagoensis LINELL, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 259; VAN DYKE, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 131, pl. 7, fig. 6.

Ground color usually pale testaceous, head and pronotum darker, surface dull, not shining. Pubescence of elytra dense, subdepressed with longer suberect hairs abundantly interspersed. Pronotum of males opaque, small asperites numerous, females with surface slightly shining, punctures coarse, dense, subconfluent around irregular median callus. Elytra rather coarsely, contiguously punctate over basal one-third, larger males with sutural spines at apex. Length, 11–20 mm.

TYPE LOCALITY. Chatham Island (San Cristóbal).

FLIGHT PERIOD. February to July.

MATERIAL EXAMINED. Chatham (San Cristóbal) Island: 4 ♂♂, 1 ♀, February 23, 1905 (F. X. Williams); 1 ♂, 1♀, July, 1906 (Williams); 1 ♂, 2 ♀♀, March 23, 1907 (Williams); 1 ♀, April 15, 1932 (M. Willows, Jr.).

Achryson galapagoensis flavescens Linsley and Chemsak, new subspecies.

Achryson galapagoensis, Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 131.

Ground color brownish testaceous, black markings of pronotum more numerous and larger than typical subspecies, elytra shining with black markings well defined. Elytra with pubescence short, recurved, longer suberect hairs absent; punctures over basal one-third moderately coarse, subcontiguous, apices usually with short tooth at suture. Length, 11–21 mm.

Holotype ♂ from Black Beach, Floreana Island, February 15, 1964, at white light (G. Kuschel); allotype ♀, Black Beach, February 18, 1964, at white light (E. G. Linsley); paratypes as follows: 2 ♀♀, Black Beach, February 14, 1964 (Linsley); 1 ♂, Black Beach, February 15, 1964 (Kuschel); 2 ♀♀, Floreana Island (M. Wittmer); 1 ♂, Charles (Floreana) Island, May 15, 1932 (M. Willows, Jr.). An additional ♀, October, 1963 (A. Leon) is in the collection of the Darwin Research Station.

This subspecies may be recognized by the absence of long suberect hairs on the elytra, its darker coloration, and the moderately coarse, subcontiguous punctures over the basal one-third of the elytra.

Achryson galapagoensis darwini Linsley and Chemsak, new subspecies.

(Figures 15 and 16.)

Ground color testaceous, black elytral markings distinct, pronotal dark bands not extensive, surface shining. Elytra with pubescence recurved, interspersed with longer suberect hairs; punctures over basal one-third small, well separated, apices with only a short sutural tooth even in the largest specimens. Length, 10–22 mm.

Holotype ♂ from Darwin Research Station, Academy Bay, Santa Cruz Island, January 25, 1964 (E. G. Linsley); allotype ♀, same data, February 21, 1964 (Linsley); paratypes (see table 3). Additional material includes 1 ♂, 1 ♀, Littoral Zone, Academy Bay, February 7 (E. G. Linsley, G. Kuschel); 1 ♂, Lower Slope, Santa Cruz Island, April 16, 1964 (D. Q. Cavagnaro).

The finer, less dense punctures, type of elytral pubescence and shining testaceous elytra will distinguish this subspecies from the others occurring on the Galápagos Islands.

Achryson galapagoensis subspecies.

One ♂ and one ♀ from South Seymour Island (Baltra) July, 1906 (F. X. Williams) appear to be distinct from known populations on other islands. The coloration and pubescence are similar to that of the Santa Cruz subspecies but the punctation of the elytra is more like that seen on Floreana. We have not assigned a name to this population because of insufficient material.

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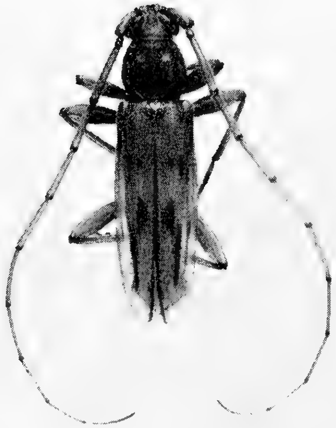

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FIGURES 13–16. Figure 13, *Compsa apicalis* Blair, ♂, × 4; figure 14, same, ♀; figure 15, *Achryson galapagoensis darwini* Linsley and Chemsak, ♂, × 2; figure 16, same, ♀.

Table 3. *Samples of* Achryson galapagoensis darwini *collected at light at Darwin Research Station, Santa Cruz Island, 1964. All material paratypical (E. G. Linsley, G. Kuschel, I. Wiggins, D. Q. Cavagnaro, R. O. Schuster, collectors).*

January	♂	♀	*February*	♂	♀
20	7	13	1	2	7
21	3	3	2	5	3
22	2	–	4	4	4
23	2	2	5	5	4
24	2	3	6	6	5
25	1	1	7	7	16
27	1	3	9	2	1
28	1	3	10	2	4
29[1]	3	3	10–13	2	–
30	1	2	12	2	9
31	5	5	14	1	–
			15	7	2
			21	17	19
			23	1	1
			26	7	7

[1] 1 ♂, 1 ♀ taken in flight trap.

Eburia lanigera Linell.

(Figures 1, 17, and 18.)

Eburia amabilis Howard (*nec* Boheman), Proc. U. S. Nat. Mus., vol. 12, p. 192.

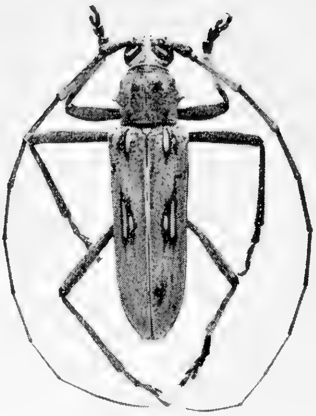
Eburia lanigera Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 259; Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 480 (= *E. stigma* var.); Mutchler, 1938, Amer. Mus. Novitates, no. 981, p. 12, fig. 5; Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 132.

Ground color reddish brown to reddish fuscous; pubescence dense, short, ashy, appressed, entirely covering surface except for eburneous ridges. Pronotum with acute lateral tubercles; disk with two acute glabrous, black tubercles before middle, two flat tubercles present at apex on sides and three small pubescent calluses, one median and two near sides behind middle; punctation shallow, rugose. Elytra usually with four eburneous ridges, two basal, inside pair longer, outer pair frequently absent, outside median pair longer, inside pair about as long as inside basal pair, ridges separated but contiguous with a few short recurved and longer erect hairs; apices moderately bispinose, outer spine slightly longer. Hind and middle femora with short spines, inner pair longer. Length, 10–23 mm.

Type locality: Charles (Floreana) Island.

Galápagos distribution: Pinta, Genovesa, Fernandina, Isabela, Santiago, Rábida, Pinzón, Santa Cruz, Santa Fé, San Cristóbal, Floreana, Española, and Gardner islands.

Flight period. November to May.



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(20)

FIGURES 17–20. Figure 17, *Eburia lanigera* Linell, ♂, × 2; figure 18, same, ♀; figure 19, *Eburia proletaria* Erichson, ♂, × 1⅔; figure 20, same, ♀.

HOST PLANTS. *Croton scouleri, Scalesia affinis, Scalesia pedunculata, Scalesia gummifera, Bursera graveolens.*

This species shows affinities with the West Indian and Central American *Eburia stigma* (Oliver) and Blair (1933) considered it to represent a variety

Table 4. *Samples of* Eburia lanigera *collected at light at Darwin Research Station, Santa Cruz Island, 1964. (D. Q. Cavagnaro, R. O. Schuster, E. G. Linsley, G. Kuschel, I. Wiggins, collectors).*

January	♂	♀	*February*	♂	♀	*February*	♂	♀
20	17	26	1	28	24	11	1	–
21	9	23	2	33	21	12	40	29
22	1	4	3	29	8	13	2	–
24	–	6	4	14	19	14	–	3
25	–	3	5	18	41	15	15	28
26	4	2	6[3]	33	48	18	–	3
27	3	15	7	10	21	19	3	2
28	1	3	8	1	–	20	–	1
29	6	17	9	10	12	21	3	15
30[2]	8	13	10	13	19	22	–	1
31	19	74	10/13	3	3	24	1	5

[2] 1 ♀ *ex Scalesia affinis.*
[3] 1 ♀ *ex Croton scouleri.*

of that species. However, the two are distinct, *E. lanigera* having a darker ground color, shorter elytral and femoral spines, and shorter, contiguous eburneous ridges of the elytra.

This is the most widely distributed species of Cerambycidae among the Galápagos Islands. It occurs on at least 13 of the 15 principal islands of the North-Central, Central, and Southern groups. It also appears to be one of the most structurally uniform from island to island. However, in the material available for study, populations on ten of the islands are represented by a total of only 43 specimens and while good series are included from Santa Cruz and Floreana islands, differentiation does not appear to have proceeded far enough to warrant their recognition as subspecies. The only evident comparative structural difference between the two is in the tendency toward loss of the outer pair of basal eburneous ridges. Among 285 individuals from Santa Cruz, 29 (ten per cent) lack the ridges. Among 83 Floreana specimens, 57 (68 per cent) have this pair of ridges missing. Although these samples are significantly different in this feature, larger series from the other islands are needed before they can be evaluated.

Material examined. Santa Cruz Island, Darwin Research Station: see summary in table 4; Littoral Zone, Academy Bay: 2 ♀♀, February 7, at white light (E. G. Linsley, G. Kuschel); Upper Arid Zone, 100 meters above Academy Bay: 1 ♂, 1 ♀, January 23, *ex Scalesia affinis* (E. G. Linsley, R. L. Usinger); 1 ♂, January 24, *ex Scalesia affinis* (Linsley); Moist Forest Zone, 240 meters above Academy Bay: 3 ♂♂, 1 ♀, January 28–February 1, at white light (Kuschel); 1 ♂, February 23, *ex Scalesia pedunculata* (Linsley); Horneman Ranch: 1 ♀, February 15 (D. Q. Cavagnaro); 2 ♂♂, 5 ♀♀, March 2 (Cavagnaro); 1 ♂, 1 ♀, March 30 (Cavagnaro); 2 ♂♂, April 5 (Cavagnaro); 1 ♂, May 3 (Cavagnaro); Table Mountain, 1,400 ft.: 3 ♀♀, April 14 (Cavagnaro); Lower East Slope: 1 ♂, April 16 (Cavagnaro).

Specimens examined in the collection of the Darwin Research Station: Darwin Research Station: 1 ♂, September 5, 1963, at light (D. Snow); 1 ♂, October 19, 1963, at light (D. Snow). Academy Bay: 1 ♀, December 18, 1963, at light (D. Snow); 1 ♂, March, 1960 (R. Levêque).

Floreana Island, Black Beach: 15 ♂♂, 11 ♀♀, February 14, 1964, at white light and *ex Scalesia affinis* (Linsley); 9 ♂♂, 10 ♀♀, February 15, at white light (Kuschel); 6 ♂♂, 8 ♀♀, February 18, at white light (Linsley); Moist Forest, 300 meters above Black Beach: 5 ♂♂, 10 ♀♀, February 14, at white light (Kuschel); Floreana Island: 4 ♀♀, February 6 (C. B. Koford); 1 ♂, 4 ♀♀ (M. Wittmer).

Pinta Island: 1 ♂, 1 ♀, South Coast, May 25, 1964 (Cavagnaro).

Genovesa Island: 2 ♂♂, 3 ♀♀, Darwin Bay, January 30, 1964, at white light (A. Smith); 1 ♀, March 25, 1961 (R. Levêque, in coll. D.R.S.).

Fernandina Island: 1 ♂, Punta Espinosa, January 29, 1964 (Usinger); 1 ♂ 1 ♀, West Side, 1,100 ft., February 5, 1964 (Cavagnaro).

Isabela Island: 1 ♂, Tagus Cove, January 30, 1964, *ex Scalesia gummifera* (Usinger); 1 ♀, December, 1905 (F. X. Williams); 1 ♀, April 10, 1906 (Williams); 1 ♀, January 28, 1899; 1 ♀, March 11, 1899.

Santiago Island: 1 specimen recorded by Blair (1933).

Rábida Island: 2 ♂♂, 2 ♀♀, December 18, 1905 (Williams).

Pinzón Island: 1 ♀, February 7, 1964 (Cavagnaro); 3 ♂♂, December, 1905 (Williams).

Santa Fé Island: 2 ♀♀, February 5, 1964 (T. Pappenfuss).

San Cristóbal Island: 2 ♂♂, 3 ♀♀, Baquerizo Morene, February 22, 1964 (Usinger); 1 ♂, 3 ♀♀, February, 1906 (Williams).

Española Island: 2 ♂♂, 4 ♀♀, Punta Suarez, February 12, 1964, at white light (Linsley); 1 ♀, November, 1905 (Williams).

Gardner Island: 1 ♂, 1 ♀, January 1906 (Williams).

Blair (1933) also records one specimen from Eden Island.

Eburia proletaria Erichson.

(Figures 19 and 20.)

Eburia proletaria Erichson, 1847, Archiv für Naturgesch., vol. 1, p. 140; Blair, 1935, Ann. Mag. Nat. Hist., ser. 10, vol. 6, p. 481; Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 132.

Eburia bauri Linell, 1898, Proc. U. S. Nat. Mus., vol. 21, no. 1143, p. 260.

Color reddish brown; pale pubescence short, dense, appressed with long erect flying hairs numerous. Antennae with basal segments densely clothed with long erect hairs internally. Pronotum acutely spined at sides, disk with black tubercles on dorsum and at sides behind apex, surface coarsely, rugosely punctate. Elytra with pubescent eburneous ridges, two basal pairs (inside pair longer) and two median pairs, outside pair elongate, inside pair often greatly reduced; base densely asperate punctate; apices moderately bispinose, outer pair more prominent. Femoral spines of moderate length. Length, 20–28 mm.

Type locality. Of *E. proletaria,* Peru; *E. bauri,* Chatham (San Cristóbal) Island, Galápagos Archipelago.

Galápagos distribution. San Cristóbal, Isabela, and Santiago islands.

Although we have not seen representatives of this species from the South American mainland, Van Dyke (1953) records large series in the British Museum from Ecuador, Colombia, Peru, Bolivia, and Chile. The pale ground color and less dense pubescence will readily separate *E. proletaria* from *E. lanigera.*

Material examined. 1 ♀, Santiago Island, December, 1905 (F. X. Williams); 1 ♂, San Cristóbal Island, February 25, 1906 (Williams); 1 ♂, San Cristóbal Island, February, 1906 (Williams); 2 ♂♂, 3 ♀♀, San Cristóbal Island (Baur); 1 ♀, Galápagos Islands, emerged on July 21, 1914, from wood collected by Williams.

We have followed Van Dyke (1953) in treating *E. bauri* as a synonym of *E. proletaria,* since we have not seen the type of the latter nor have we had mainland series available for comparison. Material of both sexes before us from Isabela and Santiago islands agrees well with the female associated by Linell with the male type. However, both males in the type series differ markedly in having smaller eburneous ridges on the elytra with the outer basal pair longer that the inner pair and the outer median pair only as long as the outer basal pair or slightly longer. Further, the apical area of the elytra lacks long suberect hairs, the sutural angle of the elytral apices is rounded, not spinose, and the femoral spines are very short. Presumably these characters are expressions of intraspecific variation, but a remote possibility exists that two species are involved.

As suggested earlier, this species may have been introduced by man, since members of this genus are notoriously long-lived in finished lumber. If so, this would lend credence to the above synonymy. In spite of its large size and presumed susceptibility to attraction to lights, it has been found on only three of the islands—a marked contrast to the situation with *Eburia lanigera.*

Compsa apicalis Blair.

(Figures 13 and 14.)

Compsa apicalis Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 481.

A narrow reddish brown species clothed with very short yellowish appressed pubescence which does not conceal the surface. The elongate cylindrical pronotum possesses a moderately elevated, median glabrous callus. The elytra are sparsely apically asperate punctate with each puncture giving rise to a long suberect seta, more numerous at apex. Each elytron is strongly costate medially and the apices are broadly pale. A short oblique pale fascia is usually present also at the basal one-third of each elytron. Length, 7–12 mm.

TYPE LOCALITY. James Island (Santiago).

GALÁPAGOS DISTRIBUTION. Santiago and Santa Cruz islands.

FLIGHT PERIOD. January and February.

HOST PLANT. *Avicennia officinalis.*

We have not seen specimens from islands other than Santa Cruz. Since Blair's original description is not detailed enough to permit subspecific analysis, we have treated the species as monotypic.

MATERIAL EXAMINED. Santa Cruz Island, Littoral Zone, Academy Bay; 9 ♂♂, 5 ♀♀, February 6, 1964, at white light (E. G. Linsley); 7 ♂♂, 1 ♀, February 7 (Linsley); Darwin Research Station, Academy Bay; 2 ♂♂, 1 ♀, January 26 on dead branches of *Avicennia officinalis* (G. Kuschel); 2 ♂♂, February 21 and 23 on dead branches of *Avicennia officinalis* (Kuschel).

The affinities of *C. apicalis* appear to be with the mainland. Blair (1933) lists two specimens probably of this species from "New Grenada."

Desmiphora maculosa Linsley and Chemsak, new species.

(Figures 2 and 27.)

Desmiphora hirticollis (*non* Olivier, 1795) BLAIR, 1933, Ann. Mag. Nat. Hist., vol. 11, no. 10, p. 482 (Galápagos record).

MALE. Form moderate sized, stout; ground color piceous, pubescence dense, appressed, brownish, mottled, with ashy, long erect hairs numerous, large bicolored erect tufts present at apex of pronotum and at apical one-third of elytra. Head oblique, short; front finely, moderately densely punctate, vertex convex, punctures similar to front; pubescence dense, obscuring surface, brownish with patches of white interspersed, long white erect hairs numerous, a small erect tuft of white and brown hairs present on vertex at middle; antennae extending to apical one-third of elytra, densely clothed with short appressed brown and white pubescence, long erect flying hairs numerous, especially along inside, scape stout, subequal in length to fourth segment, third longer than fourth, fourth longer than fifth, sixth to eleventh gradually decreasing in length. Pronotum broader across lateral tubercles than long, sides diverging to form large, median blunt-tipped, slightly backward directed spine; apex with a large median tuft of brown and white erect hairs, two elevated elongate tubercles present near apex one on each side of hair tuft, tubercles bearing thin tufts; disk with a median, elongate glabrous callus, punctures coarse, well separated, denser toward sides; pubescence dense, brownish with white mottling, two oblique white stripes extending from apical calluses to humeri, additionally an eyelike pale circle present on each side near apex, white erect hairs numerous; prosternum narrow, prosternal process vertical in front, plane between coxae, then abruptly declivous behind, plane area ridged before and behind, apex expanded, coxal cavities closed; mesosternal process vertical in front with a small glabrous callus present medially; sterna densely brown and white pubescent with long erect hairs numerous. Elytra over twice as long as broad, tapering slightly; each elytron with an elevated subsutural costa extending from base almost to apex; basal punctures coarse, contiguous, each puncture asperate at apex, punctures becoming less numerous and nonasperate toward apex; pubescence appressed, brownish, densely mixed with white patches especially behind basal one-third, white hairs forming a faint v-shaped macula at basal one-third, thick long erect tufts of brown and white hairs present outside of costae at apical one-third, thin pale lines of long erect hairs usually extending laterally forward from anterior edge of large tufts, long erect and suberect flying hairs numerous; apices rounded. Legs short, stout; femora brown and white pubescent, black spotted, flying hairs abundant. Abdomen densely clothed with brown and white appressed pubescence, black spotted, flying hairs numerous; fifth sternite elongate, apex rounded, densely setose; apex of fifth tergite rounded. Length, 11–15 mm.

Female. Antennae slightly shorter; fifth abdominal sternite shallow impressed at middle, apex emarginate; apex of fifth tergite emarginate.

Holotype ♂, allotype ♀ from Darwin Research Station, Santa Cruz Island, January 20, 1964, at white light (E. G. Linsley); paratypes as follows: Darwin Research Station; 1 ♂, September 4, 1963 (P. Leon, D. Snow); 1 ♀, September 21, 1963 (D. Snow, P. Leon); 1 ♂, 1 ♀, January 20, 1964, at white light (Linsley); 1 ♀, January 21 (R. O. Schuster); 1 ♀, January 27, at white light (Linsley); 1 ♂, January 31, at white light (Linsley); 1 ♀, February 2, at white light (Linsley); 1 ♀, February 3, at white light (Schuster); 1 ♂, February 9 (Schuster); 1 ♂, 1 ♀, February 21, at white light (Linsley, G. Kuschel); 1 ♂, June 13, 1964 (D. Q. Cavagnaro): Horneman Ranch; 2 ♂♂, May 7, 1964 (Cavagnaro).

Also assignable to this species but not designated as paratypical is one ♂, S. W. Fernandina Island, February 5, 1964, *ex Scalesia cordata* (P. D. Ashlock). Blair (1933) recorded this species (as *D. hirticollis*) from James (Santiago) Island.

The single stripes of the pronotum, differently oriented elytral tufts, and different coloration will separate *D. maculosa* from *Desmiphora hirticollis* (Olivier).

Estoloides galapagoensis (Blair).

(Figures 22 and 24.)

Estola galapagoensis Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 482; Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 134, pl. 7, fig. 4.

Estoloides galapagoensis, Breuning, 1940, Folia Zool. Hydrobiol., vol. 10, p. 75.

FIGURES 21–24. Figure 21, *Acanthoderes galapagoensis vonhageni* Mutchler, ♂, × 3⅓; figure 22, *Estoloides galapagoensis* (Blair), ♂, × 2; figure 23, *Acanthoderes galapagoensis vonhageni*, ♀, × 2⅔; figure 24, *Estoloides galapagoensis*, ♀, × 3⅓.

A relatively large reddish brown to dark brownish species. The body is densely clothed with short recumbent grayish to grayish brown pubescence. The dense pubescence is irregular giving a somewhat mottled appearance. The pronotum has a narrow glabrous median callus and large punctures irregularly scattered over the surface. The elytra are densely, coarsely punctate at the base with the punctures becoming finer and less numerous apically. Each puncture bears a short recurved seta. The antennae are narrowly annulate at the base of each segment and on the male, extend about four segments beyond the body. Length, 10–19 mm.

Type locality. James Island (Santiago).

Range. Santiago, Isabela, Santa Fé, and Santa Cruz Islands.

Flight period. September to April.

Host plants. *Bursera graveolens, Scalesia gummifera, Scalesia affinis.*

Although a large series of specimens is available from Santa Cruz Island, samples from other islands (one from Santa Fé and eight from Isabela) are too small to reveal population differences or trends if they exist.

Blair (1933) considered this species to be allied to the Central American *E. perforata* (Bates) but differing in punctation, appearance, and pubescence.

Material examined. Santa Fé Island; 1 ♂, February 20, 1964, *ex Bursera graveolens* (E. G. Linsley): Isabela Island; 2 ♂♂, 3 ♀♀, Tagus Cove, January 30, 1964, *ex Scalesia gummifera* (R. L. Usinger); 1 ♀, December, 1905 (F. X. Williams); 1 ♂, 1♀, San Tomas, September, 1905 (Williams): Santa Cruz Island; Darwin Research Station (at light); 3 ♂♂, 1 ♀, September 6, 14, 17, 1963 (D. Snow, P. Leon); 4 ♂♂, 6 ♀♀, January 20, 1964 (Linsley); 2 ♂♂, 2 ♀♀, January 21 (R. O. Schuster, G. Kuschel); 1 ♀, January 22 (R. O. Schuster and D. Q. Cavagnaro); 1 ♂, January 22, *ex Scalesia affinis* (P. D. Ashlock); 1 ♂, 3 ♀♀, January 24 (Linsley); 2 ♀♀, January 26 (Schuster, Linsley); 1 ♂, 1 ♀, January 27 (Linsley, Schuster and Cavagnaro); 2 ♂♂, 4 ♀♀, January (Linsley, Schuster); 14 ♂♂, 10 ♀♀, January 30, at light (Schuster) and *ex Scalesia affinis* (Linsley); 2 ♂♂, 3 ♀♀, January 31 (Linsley, Schuster); 5 ♂♂, 4 ♀♀, February 1 (Linsley, Schuster); 6 ♂♂, 3 ♀♀, February 2 (Linsley, Schuster); 6 ♂♂, 3 ♀♀, February 3 (Schuster); 4 ♂♂, 7 ♀♀, February 4 (Linsley, Schuster); 3 ♂♂, 2 ♀♀, February 5 (Schuster); 3 ♂♂, 5 ♀♀, February 6 (Kuschel, Linsley, Schuster); 1 ♂, February 8, flying in late afternoon (Linsley); 2 ♂♂, 1 ♀, February 9 (Schuster and Cavagnaro, Linsley); 2 ♀♀, February 10 (Linsley, Schuster); 1 ♂, 1 ♀, February 10–13 (I. Wiggins); 3 ♂♂, 2 ♀♀, February 12 (Schuster and Cavagnaro); 3 ♂♂, February 15 (Wiggins); 1 ♂, 1 ♀, February 19 (Schuster); 7 ♂♂, 1 ♀, February 21 (Linsley); 1 ♀, February 23 (Kuschel); 3 ♀♀, February 26 (Linsley): Littoral Zone, Academy Bay; 1 ♀, February 7 (Kuschel): Upper Arid Zone, 100 meters above Academy Bay; 4 ♂♂, 2 ♀♀, January 23, *ex Scalesia affinis* (Linsley, Usinger); 4 ♂♂, 9 ♀♀, January 28, *ex Scalesia affinis* (Linsley): Moist Forest Zone, 240 meters above Academy Bay; 3 ♂♂, 2 ♀♀, February 12, *ex Scalesia* (Schuster and Cavagnaro): Lower East Slope; 5 ♂♂, April 16 (Cavagnaro). 1 km. N. Academy Bay: 1 ♂, 2 ♀♀, August 23, 1963 (D. Snow, P. Leon): Bella Vista Trail: 1 ♂, September 4, 1963, in *Scalesia* (D. Snow, P. Leon).

Additionally, Blair (1933) lists four specimens from James (Santiago) Island and one from Indefatigable (Santa Cruz Island).

Extreme larval work was found in dead wood of *Bursera graveolens* on Santa Fé Island on February 21, 1964. The larvae feed under the bark, completely loosening it. The galleries are tightly packed with coarse fibrous frass like that of *Monochamus*. The feeding area includes the main trunk (approximately 5 inches in diameter) and branches down to about 1½ inches in diameter. The larvae eventually bore into the solid heartwood and sapwood. Emergence holes are oval, usually angled.

Acanthoderes galapagoensis Linell.

Acanthoderes galapagoensis LINELL, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 261.

This species is characterized by its brownish to fuscous ground color, ashy to black depressed pubescence, and dark elytral bands. The punctation is moderate and not dense and the short erect hairs of the elytra are not numerous. The antennae are of moderate length and brownish and ashy annulated. Additionally, the elytral apices are emarginate with usually a short spine or tooth at the outside margins. Length, 9–17 mm.

TYPE LOCALITY. Chatham Island (San Cristóbal).

This apparently endemic species is presently known from four of the Galápagos Islands: San Cristóbal, Santa Cruz, Santiago, and Isabela. Judging from the original description and from material at hand, it segregates into distinctive subspecific populations on the various islands.

Linell (1898) commented that this species greatly resembles the Brazilian *A. lateralis* Bates in form, structure, and coloration.

Acanthoderes galapagoensis galapagoensis Linell.

Acanthoderes galapagoensis LINELL, 1898, Proc. U. S. Nat. Mus., vol. 21, p. 261.

Ground color brownish, pubescence ashy gray with lighter and darker brown maculations. Elytra with granules in front of punctures over basal one-half; apices with spine at outside margin. Legs with posterior tarsi long and slender, first segment as long as three following together. Length 14–16 mm.

TYPE LOCALITY. Chatham Island (San Cristóbal).

Although we have not examined specimens from this island, the above characteristics taken from the original description indicate that the San Cristóbal population is distinct from those of other islands.

Acanthoderes galapagoensis vonhageni Mutchler.

(Figures 21 and 23.)

Acanthoderes galapagoensis var. *vonhageni* Mutchler, 1938, Amer. Mus. Nov., no. 981, p. 14.

Ground color brownish to fuscous, pubescence brownish ashy with brown to black maculations. Head with front deeply, distinctly punctate, punctures numerous. Elytra with basal punctures not possessing granules anteriorly, short suberect hairs numerous; apices with at most a short blunt tooth at outside margin. Legs with first segment of posterior tarsi not as long as three following segments together. Length, 9–17 mm.

Type locality. Indefatigable Island (Santa Cruz).

Flight period. January to October.

Host plant. *Scalesia pedunculata.*

Mutchler (1938) thought the material he had from Santa Cruz Island was sufficiently distinct to warrant at least a varietal name. Besides the lack of elytral granules and shorter first segment of the posterior tarsi, this subspecies differs from the typical form by possessing longer suberect elytral hairs, less produced spine at the apical outer margin of the elytra, and slightly different elytral markings.

Material examined. Darwin Research Station; 1 ♀, January 20, 1964, at white light (R. L. Usinger); 1 ♀, January 21, at light (R. O. Schuster); 1 ♂, January 28, at light (Schuster); 1 ♀, January 29, at light (Schuster); 1 ♂, February 1, 1964, at white light (E. G. Linsley); 2 ♂♂, February 4, at light (Schuster); 1 ♀, February 5, at light (Schuster); 1 ♀, February 6, at white light (G. Kuschel); 1 ♀, February 7, at light (Schuster); 1 ♀, February 12, at light (Schuster and D. Cavagnaro); 1 ♀, February 16 (Schuster): Littoral Zone, Academy Bay; 1 ♂, 1 ♀, February 7, at white light (Kuschel, Linsley): Moist Forest Zone, 240 meters above Academy Bay; 7 ♂♂, 5 ♀♀, January 28–February 1, at white light (Kuschel); 1 ♂, 1 ♀, February 1, *ex Scalesia pedunculata* (Kuschel); 1 ♂, 1 ♀, February 13, *ex Scalesia pedunculata* (Linsley); 1 ♀, February 28, *ex Scalesia pedunculata* (Linsley): Horneman Ranch; 3 ♂♂, 2 ♀♀, February 15 (Cavagnaro); 11 ♂♂, 3 ♀♀, March 2, 1964 (Cavagnaro); 3 ♂♂, 2 ♀♀, March 10 (Cavagnaro); 1 ♂, March 11 (Cavagnaro); 2 ♂♂, March 30 (Cavagnaro); 1 ♂, April 2, 1964 (Cavagnaro); 4 ♂♂, 4 ♀♀, April 5 (Cavagnaro); 5 ♂♂, 2 ♀♀, April 8 (Cavagnaro); 8 ♂♂, 2 ♀♀, May 3, 1964 (Cavagnaro); 6 ♂♂, 1 ♀, May 7 (Cavagnaro); 1 ♂, 1 ♀, May 16 (Cavagnaro): Table Mountain, 1,400 feet; 2 ♂♂, 1 ♀, April 14 (Cavagnaro).

Specimens examined in the collection of the Darwin Research Station: Darwin Research Station: 3 ♂♂, 1 ♀, September 14, 1963, at light (D. Snow): Bella Vista Trail: 1 ♂, October 3, 1963, at light (D. Snow).

Acanthoderes galapagoensis williamsi Linsley and Chemsak, new subspecies.

Acanthoderes galapagoensis, Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 136.

Ground color reddish brown, appressed pubescence brownish, suffused with ashy and darker brown, maculations blackish. Head with front containing only a few punctures. Elytra sparsely granulate at base, suberect hairs short; apices bluntly toothed at outer margin. Legs with first segment of posterior tarsi shorter than following segments together. Length, 13–16 mm.

HOLOTYPE ♂, allotype ♀ from James Island (Santiago), January, 1906 (F. X. Williams); paratypes as follows: 2 ♀♀, James Island, January, 1906 (Williams); 2 ♀♀, James Island, March 2, 1906 (Williams).

The paler ground color and pubescence and much less densely punctate front of the head distinguish this subspecies from the Santa Cruz population (*A. g. vonhageni*). The length of the hind tarsi and shorter elytral spines will separate it from the nomino-typical form from San Cristóbal.

Acanthoderes galapagoensis subspecies.

Acanthoderes galapagoensis, VAN DYKE, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 136.

The two specimens available from Albemarle Island (Isabela) suggest that this population may have a more uniform brownish pubescence, reduced black maculae, and longer suberect hairs on the elytra. Also, the front of the head has moderately numerous punctures. However, more material is needed before these indications can be evaluated. 1 ♂, Villamil, S. Albemarle Island, August 20, 1906 (F. X. Williams); 1 ♂, Albemarle, March 4, 1906 (Williams).

Estola insularis Blair.

Estola insularis BLAIR, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 483.

Ground color brownish to fuscous, short depressed pubescence ashy or rufous to fuscous, often suffused with grayish patches to give a maculated appearance; longer suberect hairs pale. Pronotum with acute lateral tubercles behind middle, disk convex, densely punctate. Elytra with coarse punctures arranged in longitudinal rows, apices rounded. Underside coarsely, densely punctate. Antennae annulate. Length, 5–11 mm.

TYPE LOCALITY. Indefatigable (Santa Cruz) Island.

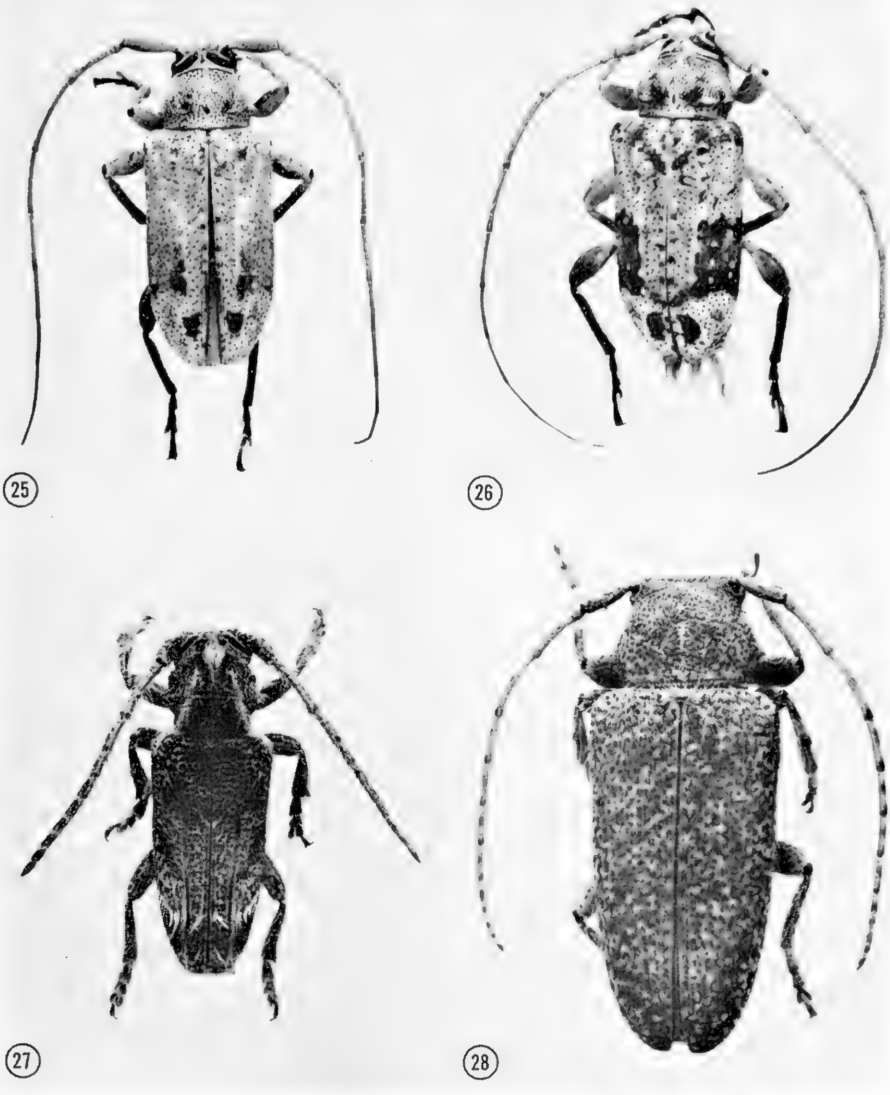
Estola insularis has been found on seven islands: Santa Cruz, Isabela, Santa Fé, Fernandina, Floreana, Pinzón, and Santiago. So far as can be determined, the species is exclusively attached to plants of the endemic genus of tree composites, *Scalesia*. Our series reveals considerable difference among the populations of the various islands.

The affinities of *E. insularis* appear to be with Central America. According to Blair (1933), it most closely resembles *E. misella* Bates.

Estola insularis insularis Blair.

(Figure 28.)

Estola insularis BLAIR, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 483; VAN DYKE, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 135 (record).



Figures 25–28. Figure 25, *Nesozineus galapagoensis variabilis* Linsley and Chemsak, ♀, ×5⅓; figure 26, same, ♂; figure 27, *Desmiphora maculosa* Linsley and Chemsak, ♂, × 3⅓; figure 28, *Estola insularis* Blair, ♀, × 6⅔.

Ground color usually dark reddish brown; recumbent pubescence ashy and brownish, pale hairs forming spots to give mottled appearance; pale subdepressed, recurved hairs fairly long. Disk of pronotum with punctures subcontiguous, lateral tubercles prominent. Length, 5–11 mm.

Type locality. Santa Cruz Island.

Flight period. January to May.

Host plants. *Scalesia affinis, S. pedunculata svensoni, S. helleri.*

This subspecies may be recognized by the condensed patches of grayish pubescence over the elytra which present a mottled appearance. The size range in the series at hand is appreciable.

Material examined. Santa Cruz Island: Darwin Research Station: 6 ♂♂, 2 ♀♀, January 22, 1964, *ex Scalesia affinis* (P. D. Ashlock); 5 ♂♂, 3 ♀♀, January 23, beating *Scalesia affinis* and at white light (G. Kuschel); 4 ♂♂, 1 ♀, January 26, *ex Scalesia affinis* (Kuschel, R. L. Usinger); 3 ♂♂, 2 ♀♀, January 30, *ex Scalesia affinis* (E. G. Linsley); 1 ♀, February 4 (R. O. Schuster). Upper Arid Zone, 100 meters above Academy Bay: 16 ♂♂, 10 ♀♀, January 23, *ex Scalesia affinis* (Ashlock, Linsley, Usinger); 3 ♂♂, 4 ♀♀, January 24, *ex Scalesia affinis* (Linsley); 8 ♂♂, 10 ♀♀, January 28, *ex Scalesia affinis* (Linsley). Moist Forest Zone, 240 meters above Acadamy Bay; 2 ♂♂, 3 ♀♀, January 23, *ex Scalesia pedunculata* (Ashlock); 1 ♂, 1 ♀, January 28–February 1, at white light (Kuschel); 2 ♂♂, 1 ♀, February 12, *ex Scalesia* (Schuster and D. Q. Cavagnaro). Horneman Farm: 1 ♀, March 25 (Cavagnaro); 1 ♂, May 7 (Cavagnaro); 1 ♀, May 11 (Cavagnaro); 1 ♂, 1 ♀, May 16 (Cavagnaro). Table Mountain, 1,400 feet: 2 ♂♂, 1 ♀, April 14 (Cavagnaro). 1 mile E. Tortuga Bay: 2 ♂♂, 2 ♀♀, February 17, *ex Scalesia helleri* (Ashlock).

Specimens examined in the collection of the Darwin Research Station: Darwin Research Station: August 16, 1963, *ex Scalesia* (D. Snow); Bella Vista Trail: August 23, 1963, *ex Scalesia* (D. Snow).

Estola insularis cribrata Blair.

Estola cribrata Blair, 1933, Ann. Mag. Nat. Hist., ser. 10, vol. 11, p. 483.

Ground color dark reddish brown, short recumbent ashy pubescence uniform over surface, not irrorate. Pronotum with lateral spines small; disk with punctures contiguous, often confluent. Length, 7–10 mm.

Type locality. Albemarle (Isabela) Island.

Host plant. *Scalesia gummifera.*

The uniform depressed ashy pubescence and small pronotal spines will separate this subspecies from the typical form.

Material examined. Tagus Cove, Isabela Island: 6 ♂♂, 5 ♀♀, January 30, 1964, *ex Scalesia gummifera* (R. L. Usinger).

Estola insularis duncani Van Dyke.

Estola duncani Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 135.

Ground color pale reddish brown, appressed pubescence reddish brown interspersed with patches of ashy. Pronotum with lateral spines small, disk subconfluently punctate. Length, 10 mm.

Type locality. Duncan (Pinzón) Island.

A single specimen, the female holotype, is the only sample available for study. Judging from this unique individual, the population of Pinzón Island presumably differs from the nomino-typical form in coloration, the punctation of the pronotum, and the smaller pronotal spine. The mottled pubescence distinguishes it from *E. i. cribrata*.

Estola insularis nigrescens Linsley and Chemsak, new subspecies.

Ground color reddish black to black, short recumbent pubescence usually dark brownish with ashy hairs uniformly interspersed often into patches, longer subdepressed hairs with dark tinge. Pronotum with disk convex, confluently punctate, lateral spines small. Elytra with basal punctures coarse, subconfluent. Antennae with black annulations becoming broader toward apex. Length, 7–10 mm.

Holotype ♂, allotype ♀ and 15 paratypes (8 ♂♂, 7 ♀♀) from Black Beach, Floreana Island, February 15, 1964, *ex Scalesia affinis* (E. G. Linsley, R. L. Usinger); additional paratypes as follows: 1 ♀, Black Beach, February 18, 1964, *ex Scalesia affinis* (G. Kuschel); 2 ♂♂, 1 ♀, Moist Forest, 300 meters above Black Beach, February 14, 1964, *ex Scalesia pedunculata* (Kuschel); 2 ♂♂, Moist Forest, February 17, 1964, *ex Scalesia pedunculata* (Usinger).

The very dark ground coloration distinguishes this subspecies from other known Galápagos populations.

Estola insularis subspecies.

For the present, available material will not permit definite subspecific assignments for the following:

Santiago Island: One ♂, January 5, 1906 (F. X. Williams) resembles *E. i. duncani* in coloration but the pubescence is finer and more uniform, without the white patches.

Santa Fé Island: Two ♂♂, February 20, 1964, *ex Scalesia helleri* (E. G. Linsley, R. L. Usinger). These may belong to the nearby Santa Cruz Island population.

Fernandina Island: Three ♂♂, February 5, 1964, *ex Scalesia cordata* (P. D. Ashlock) collected on the southwest part of the island, have a coloration like that expressed in the Isabela population (*E. i. cribrata*). Further, the appressed pubescence is similarly uniform in nature but the long suberect setae are almost twice the length of that found in Isabela sample.

Nesozineus Linsley and Chemsak, new genus.

Form robust, usually small; pubescence short, dense, uniformly recumbent, erect hairs absent. Head small, front convex, rectangular; eyes large, coarsely faceted, deeply emarginate, lower lobe large, transverse, upper lobes separated by about diameter of third antennal segment; palpi short, subequal, apical segments pointed; antennae slender, eleven segmented, third segment longer than scape, fourth longer than third, fifth shorter than fourth but longer than third, remaining segments gradually decreasing in length, erect hairs totally absent. Pronotum transverse, sides behind middle with a small acute tubercle, basal transverse impression broad, beginning immediately behind lateral tubercles, not extending completely over dorsum; disk with three broad calluses, a basal median partially glabrous one and two pubescent ones before middle; prosternum narrow, prosternal process arcuate, about as broad as half the coxal width, expanded behind, coxal cavities closed; mesosternal process broad, concave, each side with a small posterior tubercle, intermediate coxal cavities closed; scutellum broader than long, apically subtruncate. Elytra convex, subparallel to apical one-fourth then tapering to rounded apices; humeri prominent, two large tumid areas present behind scutellum, each elytron with a broad costa-like swelling extending from humeri to apical one-third; erect hairs absent. Legs small, femora moderately clavate; hind tarsi with first segment about half as long as two following segments together. Abdomen normally segmented, fifth sternite longer than fourth.

Type species. *Leptostylus galapagoensis* Van Dyke.

This genus has the facies of *Leptostylus* and shares several characteristics with it. However, the acute lateral tubercles of the prosternum and small tubercles of the mesosternum distinguish *Nesozineus*. Its affinities appear to be with *Ozineus* but the short posterior tarsi readily separate it.

Van Dyke (1953) suggested relationships within *Atrypanius* and *Trypanidius*, but had no female specimens to observe the presence or absence of an elongate ovipositor.

Nesozineus galapagoensis (Van Dyke).

Leptostylus galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 136.

Moderately large to small, ground color usually reddish brown. Surface densely clothed with thick recumbent ashy, yellowish, and darker pubescence interrupted only by coarse or small punctures. Pronotum densely punctate, often with darker spots. Elytra varying from almost concolorous to extensively dark maculate, erect hairs totally absent. Legs with femora often darker. Length, 5–10 mm.

Type locality. Isabela Island.

This species is presently known from six of the islands. Available material consists of a very large series from Santa Cruz, a moderate but distinctive series from Isabela, and single specimens from Santiago, Rábida, San Cristóbal, and Fernandina. This material indicates distinct subspecific differences between the populations on Santa Cruz and Isabela. Although the other island populations are represented by unique specimens, we retain the available name for the Santiago Island group.

Nesozineus galapagoensis galapagoensis (Van Dyke).

Leptostylus galapagoensis Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 136, pl. 7, fig. 1.

Size moderately large; ground color reddish brown, dense appressed pubescence with yellowish tinge, uniform except for shining coarse punctures. Elytra with pubescence usually concolorous except for two small dark sutural patches at apical one-fourth. Punctures of pronotum and elytra coarse, very distinctly interrupting pubescence. Length, 7–10 mm.

Type locality. Villamil, Albemarle (Isabela) Island.

This subspecies is distinctive by its larger average size, reduced elytral maculations, and larger punctures.

Material examined. 15 ♂♂, Villamil, Isabela Island, March 14, 1906 (F. X. Williams).

Nesozineus galapagoensis williamsi (Van Dyke).

Leptostylus williamsi Van Dyke, 1953, Occ. Pap. Calif. Acad. Sci., no. 22, p. 137.

Size small; ground color reddish brown, legs darker; pubescence fine, dense, ashy and dark brown. Elytra maculate with brown patches at base, broadly at middle, and near apex; punctures fine. Length, 6 mm.

Type locality. James (Santiago) Island.

In spite of the fact that this population is represented by a unique specimen (the holotype), this example differs sufficiently from those on Isabela to suggest that it probably represents a separate subspecies.

Material examined. 1 ♂, James Island, March 2, 1906 (F. X. Williams).

Nesozineus galapagoensis variabilis Linsley and Chemsak, new subspecies.

(Figure 25.)

Form small to moderate sized; ground color reddish brown, antennae paler; pubescence ashy, brownish, and black, thick. Head usually yellowish pubescent. Elytra very variable, dark patches either reduced to small subapical spots or extensively dark maculated basally, post medially and subapically; punctures small, well separated, not greatly breaking continuity of appressed pubescence. Pronotum usually with darker spots. Length, 5–10 mm.

Holotype ♂, allotype ♀ from Darwin Research Station, Santa Cruz Island, February 1, 1964, at white light (E. G. Linsley); paratypes (see table 5). Additional material from Santa Cruz Island includes: 1 ♀, April 27 (D. Q. Cavagnaro); 1 ♂, Lower Arid Zone, Academy Bay, January 24, *ex Croton scouleri* (Linsley); 1 ♂, Moist Forest Zone, 240 meters above Academy Bay, January 28–February 1, at white light (G. Kuschel); 2 ♂♂, Horneman Ranch, March 2 and April 8 (Cavagnaro).

Specimens examined in the collection of the Darwin Research Station: Dar-

TABLE 5. *Samples of* Nesozineus galapagoensis variabilis *collected at light at Darwin Research Station, Santa Cruz Island, 1964 (E. G. Linsley, R. L. Usinger, R. O. Schuster, G. Kuschel, D. Q. Cavagnaro, I. Wiggins, collectors). All material paratypical.*

January	♂	♀	*February*	♂	♀
20	35	30	1[3]	5	10
21	23	10	2	5	3
22	12	8	3[4]	10	6
23[1]	10	6	4	12	6
26[2]	4	5	5[5]	4	7
27	5	2	6[6]	18	26
28	8	6	7	12	10
29	6	4	8	–	1
30	3	–	9	12	5
31	4	3	10	4	4
			12	5	3
			14	2	5
			15	–	1
			18	5	10
			20	1	1
			21	5	6
			22	2	1
			23[7]	1	2
			24	3	5
			26	–	1

[1] 2 ♂♂ *ex Laguncularia racemosa.*

[2] 1 ♂ *ex Laguncularia racemosa.*

[3] 1 ♂, 2 ♀♀ *ex Croton scouleri.*

[4] Also flying in late afternoon.

[5] Also *ex Croton scouleri.*

[6] Also flying in late afternoon and as pupae in dead branches of *Croton scouleri.*

[7] Also *ex Hippomane mancinella.*

win Research Station, at light: August 17, 1963 (D. Snow); September 6, 11, 14, 17, 1963 (D. Snow).

Larvae of this subspecies were found by G. Kuschel in dead branches (2–3 cm. in diameter) of *Croton scouleri* which were still attached to living trees. The larvae work beneath the bark for a period, then bore into the sapwood and heartwood. Emergence holes of adults averaged about 3 × 2.5 mm. in diameter.

Adults usually fly in the late afternoon but on overcast days during midday.

Nesozineus galapagoensis subspecies.

Three unique specimens, a ♂ from Fernandina Island (F. Ortiz); a ♀ from Baquerizo Morene, San Cristóbal Island, February 22, 1964 (R. L. Usinger); and a ♀ from Rábida Island, December 18, 1905 (F. X. Williams) cannot be assigned to any of the preceding subspecies. They probably represent distinctive populations but adequate samples will be necessary before a conclusion can be reached.

SPECIES RECORDED FROM THE GALÁPAGOS ISLANDS BUT OF DOUBTFUL OCCURRENCE

Eburia amabilis Boheman.

Eburia amabilis BOHEMAN, 1859, Konliga Svenska Fregatten *Eugenies* resa . . . , Zool., vol. 1, p. 150.

MALE. Integument testaceous, head, antennae, and prothorax orangish; pubescence sparse, minute and appressed and long and erect. Head narrower than pronotum; area between antennal tubercles slightly concave; vertex impunctate, clothed with minute golden appressed pubescence except for a glabrous median line which diverges toward neck; eyes finely densely pubescent internally; antennae extending about four segments beyond body, scape subglabrous, impunctate, slightly flattened above, third segment longer than first, fourth shorter than third, fifth and sixth subequal to fourth, eleventh longer than tenth, appendiculate, basal segments sparsely pubescent, internally clothed with long suberect hairs which diminish in number apically. Pronotum about as long as broad, sides with acute, backward curved spines, base constricted, broadly shallowly impressed; disk with two dark antemedian tubercles; surface opaque, finely pubescent and vaguely, shallowly punctate except for the shining rugose lateral areas extending from apex to lateral tubercles; median line vague, not highly elevated; scutellum small, rounded behind, finely pubescent. Elytra almost three times as long as broad; two pairs of moderate sized, contiguous eburneous ridges present basally, two elongate pairs present at middle, the outside pairs over twice as long as basal ones and the inside pair almost twice as long as the basal pairs, ridges with a few long suberect hairs and dark spots at base of basal pairs and at each end of median pairs; punctures at base moderately coarse, contiguous, becoming very fine at apex; disk sparsely clothed with minute golden pubescence and longer suberect hairs; apices truncate, outer angles with a moderate spine, sutural angles unarmed. Legs with middle and hind femora spined internally, spines subequal in length to elytral ones. Length, 14 mm.

TYPE LOCALITY. "Insulae Gallapagos."

The above description was drawn from the type specimen kindly made available to us by E. Kjellander. There is some doubt as to the actual occurrence of this species on the Galápagos Islands. It has not been collected since the voyage of the *Eugenie* and there is a possibility of error in labeling. Similar discrepancies have been discussed by Van Dyke (1953; p. 94) and Aurivillius (1893).

Taeniotes hayi (Mutchler).

Monochamus hayi MUTCHLER, 1938, Amer. Mus. Novitates, no. 981, p. 13.

Taeniotes hayi, DILLON and DILLON, 1941, Reading Publ. Mus. Art. Gal., Sci. Publ., vol. 1, p. 17 (synonymy).

Monochamus cocoensis MUTCHLER, 1938, Amer. Mus. Novitates, no. 981, p. 13.

A black, shining species with the scutellum and a spot on each side white pubescent and the elytra vaguely white pubescent along the suture, especially at the apex. The antennal scape is robust and the sides of the pronotum prominently spined. The antennae are unusually long in the male.

TYPE LOCALITY. Of *M. hayi*, "Indefatigable Island"; *M. cocoensis*, Cocos Island.

The type specimen of this species, which appears to be relatively common on Cocos Island, may have been mislabeled. In any event, its occurrence in the Galápagos is highly problematical.

ACKNOWLEDGMENTS

This study was made possible through the Galápagos International Project sponsored by the National Science Foundation (Grant 7465–62–512). The analysis of the cerambycid fauna and preparation of the manuscript were accomplished with support from National Science Foundation Grant GB-2326. We wish to thank the following persons and their respective institutions for making material in their care available for study: E. Kjellander, Naturhistoriska Riksmuseum, Stockholm; H. B. Leech, California Academy of Sciences, San Francisco; and J. G. Rozen, American Museum of Natural History, New York. The following people who actively collected cerambycid material during the course of the Galápagos International Project are also gratefully acknowledged: P. D. Ashlock, D. Q. Cavagnaro, G. Kuschel, R. O. Schuster, R. L. Usinger, and I. Wiggins. Dr. Kuschel also made a special effort to obtain host plant data, and Mr. Cavagnaro provided the photographs used in Plate I.

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 9, pp. 237–248; 8 figs. January 31, 1966

CERAMBYCIDAE OF COCOS ISLAND

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Cocos Island is about 300 miles west of Costa Rica, about 350 miles northeast of the Galápagos Islands, and about 940 miles southeast of the Revilla Gigedo Islands. Like the Galápagos and Revilla Gigedos, the island is oceanic, volcanic, and isolated. Unlike them, Cocos Island has an abundant rainfall and a dense, tropical vegetation. However, of the approximately 100 species of plants recorded from the island, only about 10 per cent are regarded as endemic (Stewart, 1912; Svenson, 1935). The remainder mostly show affinity with the mainland. Except for ferns, tropical weeds, and strand plants, the flora has little in common with that of the Galápagos (Svenson, 1935) and less in common with that of the Revilla Gigedos (Johnston, 1931). (For a general summary of the biogeography of Cocos Island, see Hertlein, 1963.)

Eight species of Cerambycidae are now known from Cocos Island, although to our knowledge, only one of these has been previously reported. Apparently the first collection of material in this family was made by F. X. Williams of the California Academy of Sciences Galápagos Expedition of 1905–1906. Williams found two species, *Parandra glabra* and a subsequently named *Taeniotes* (*hayi*) during a brief visit to Cocos in November, 1905. However, until now his specimens have remained unstudied. Collenette (1925), who visited the island in 1924 as a member of the St. George Expedition, refers to the capture of a "longicorn beetle," but we have not seen this specimen and do not know its identity. The first species actually recorded from Cocos was captured by C. L. Hay of the Astor Expedition of 1930, and described by Mutchler (1938). P. Slud, who collected at Wafer Bay in March, 1963, brought back five species (now in the collections of the American Museum of Natural History), records for which appear below. By far the largest collection of Cocos Cerambycidae was made by G. Kuschel and R. O. Schuster on March 8, 1964, when members of the Galápagos International Project, returning to California aboard the "Golden Bear," went ashore at Chatham Bay. This collection consisted of seven species represented by 30 specimens. Types of the new species have been deposited in the collections of the California Academy of Sciences in San Francisco.

Of the eight species presently known from Cocos, two (*Parandra glabra* and *Acanthoderes circumflexus*) range through the West Indies and Mexico into South America. The remainder are not presently known from the mainland, although their affinities are in that direction. This does not necessarily imply that they are endemic since the cerambycid fauna of Central America is still inadequately known. With the possible (but improbable) exception of *Taeniotes hayi* (see below), it can be said with confidence that the known Cocos Cerambycidae have no close affinity with those of the Galápagos or Revilla Gigedos.

Parandra glabra Degeer.

(Figures 1 and 3.)

Attelabus glaber Degeer, 1774, Memoires pour servir a'l'histoire des insects, vol. 4, p. 351, pl. 19, figs. 14–16.

Parandra glabra, Gyllenhal, 1817, in Schönherr, Appendix and synonymia insectorum, vol. 1, no. 3, p. 145; White, 1853, Catalogue of the coleopterous insects . . . British Museum, vol. 7, p. 2; Thomson, 1860, Musée scientifique au recueill d'histoire naturelle, vol. 2, p. 78; Thomson, 1867, Physis, vol. 1, p. 110; Bates, 1879, Biologia Centrali-Americana, Longicornia, vol. 5, p. 2; Lameere, 1902, Ann. Soc. Ent. Belgique, vol. 46, p. 76; Heller, 1904, Stett. Ent. Zeit., vol. 65, p. 383 (larva); Melzer, 1919, Rev. Mus. Paulista, vol. 11, p. 20, pl. 1, figs. 3–4; Andrade, 1928, Bol. Agric., vol. 29, p. 451 (habits); Lima, 1930, Campo, vol. 1, no. 10, p. 29 (habits); Duffy, 1960, Monograph of the immature stages of Neotropical timber beetles, p. 44 (larva, pupa, habits).

Gnathophorus glaber, Kirby, 1837, in Richardson, Fauna Boreali-Americana, p. 166.

Scarites testaceus Fabricius, 1794, Entomologia systematica, vol. 4, p. 437; Fabricius, 1801, Systema eleutheratorum, vol. 1, p. 123.

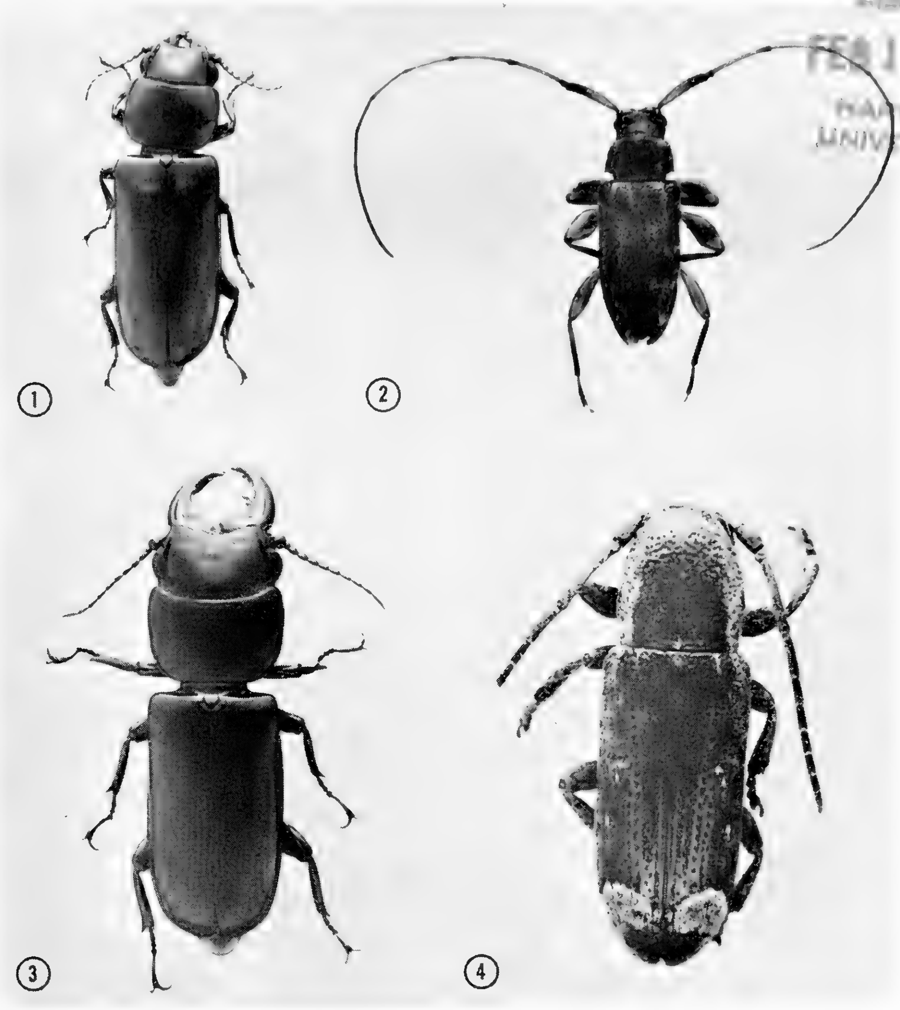
Parandra ferruginea Sturm, 1826, Catalog meiner Insecten-Sammlung, Käfer, p. 78, pl. 4, fig. 33.

Parandra mandibularis Perty, 1830, Delectus animalium articulatorum . . ., p. 84, pl. 17, fig. 1; White, 1853, Catalogue of the coleopterous insects . . . British Museum, vol. 7, p. 2; Thomson, 1860, Musée scientifique au recueill d'histoire naturelle, vol. 2, p. 78; Rojas, 1866, Ann. Soc. Ent. France, ser. 4, vol. 6, p. 237 (habits); Thomson, 1867, Physis, vol. 1, p. 109.

Parandra maxillosa Castelnau, 1840, Histoire naturelle des animaux articules, vol. 2, p. 387; Thomson, 1867, Physis, vol. 1, p. 109.

Parandra lineolata Gory, 1844, in Guérin-Meneville, Iconographie du regne animal de G. Cuvier, p. 207, pl. 42, fig. 7; White, 1853, Catalogue of the coleopterous insects . . . British Museum, vol. 7, p. 2; Thomson, 1860, Musée scientifique ou recueill d'histoire naturelle, vol. 2, p. 78; Thomson, 1867, Physis, vol. 1, p. 108.

Parandra colombica White, 1853, Catalogue of the coleopterous insects . . . British Museum, vol. 7, p. 3; Thomson, 1860, Musée scientifique ou recueill d'histoire naturelle, vol. 2, p. 80; Rojas, 1866, Ann. Soc. Ent. France, ser. 4, vol. 6, p. 237 (habits); Thomson, 1867, Physis, vol. 1, p. 110.



Figures 1–4. Figure 1, *Parandra glabra* Degeer, ♀, × 1⅔; figure 2, *Urgleptes kuscheli* Linsley and Chemsak, ♂, × 10; figure 3, *Parandra glabra*, ♂, × 1⅔; figure 4, *Adetus nesiotes* Linsley and Chemsak, ♂, × 6⅔.

Parandra grandis Thomson, 1860, Musée scientifique ou recueill d'histoire naturelle, vol. 2, p. 79; Thomson 1867, Physis, vol. 1, p. 108.

Parandra barbata Thomson, 1860, Musée scientifique ou recueill d'histoire naturelle, vol. 2, p. 95; Thomson, 1867, Physis, vol. 1, p. 107.

Parandra occipitalis Thomson, 1867, Physis, vol. 1, p. 108.

Parandra obsolescens Casey, 1912, Memoirs on the Coleoptera, vol. 3, p. 217.

This species is large, shining, and usually reddish brown in color. The punctation is obsolete over the entire surface. The mandibles of males are large and bifid at the apices with an indication of a tooth along the dorsal inner margin a little before the middle. The females possess shorter, more angulate mandibles. Length (exclusive of mandibles), 22–30 mm.

TYPE LOCALITY. Of *P. glabra,* Cayenne?; *S. testaceus,* "Senegalia"; *P. ferruginea,* Brasil; *P. mandibularis,* Brasil; *P. maxillosa,* Brasil; *P. lineolata,* Guadaloupe; *P. colombica,* Colombia; *P. grandis,* New Granada; *P. barbata,* New Granada; *P. occipitalis,* New Granada; *P. obsolescens,* "Costa Rica (Chiriqui)."

RANGE. West Indies, Mexico to Paraguay.

FLIGHT PERIOD. September to March (Cocos Island).

HOST PLANTS. *Spondias mombin, Ochroma lagopus, Aspidosperma* sp., *Acacia decurrens, Araucaria brasiliensis, Phoebe* sp.

On Cocos Island, G. Kuschel found this species in the soft wood of balsa (*Ochroma lagopus*) and also on the bark of balsa trees, at night. The other recorded hosts are from elsewhere in its range.

MATERIAL EXAMINED. 3 ♂♂, 4 ♀♀, Chatham Bay, March 8, 1964 (G. Kuschel, R. O. Schuster); 1 ♂, Wafer Bay, March 1, 1963 (P. Slud); 6 ♂♂, 2 ♀♀, Cocos Island, November 3–13, 1905 (F. X. Williams).

Taeniotes hayi (Mutchler).

(Figure 6.)

Monochammus hayi MUTCHLER, 1938, Amer. Mus. Nov., no. 981, p. 13.

Taeniotes hayi, DILLON and DILLON, 1941, Reading Pub. Mus. Art. Gal., Sci. Publ., vol. 1, p. 17 (synonymy).

Monochammus cocoensis MUTCHLER, 1938, Amer. Mus. Nov., no. 981, p. 13.

A black, shining species with the scutellum and a spot on each side white pubescent and the elytra are vaguely, finely, white pubescent along the suture, especially at the apex. The antennae are usually elongate in the males. The antennal scape is robust and the sides of the pronotum are prominently spined. Length, 24–33 mm.

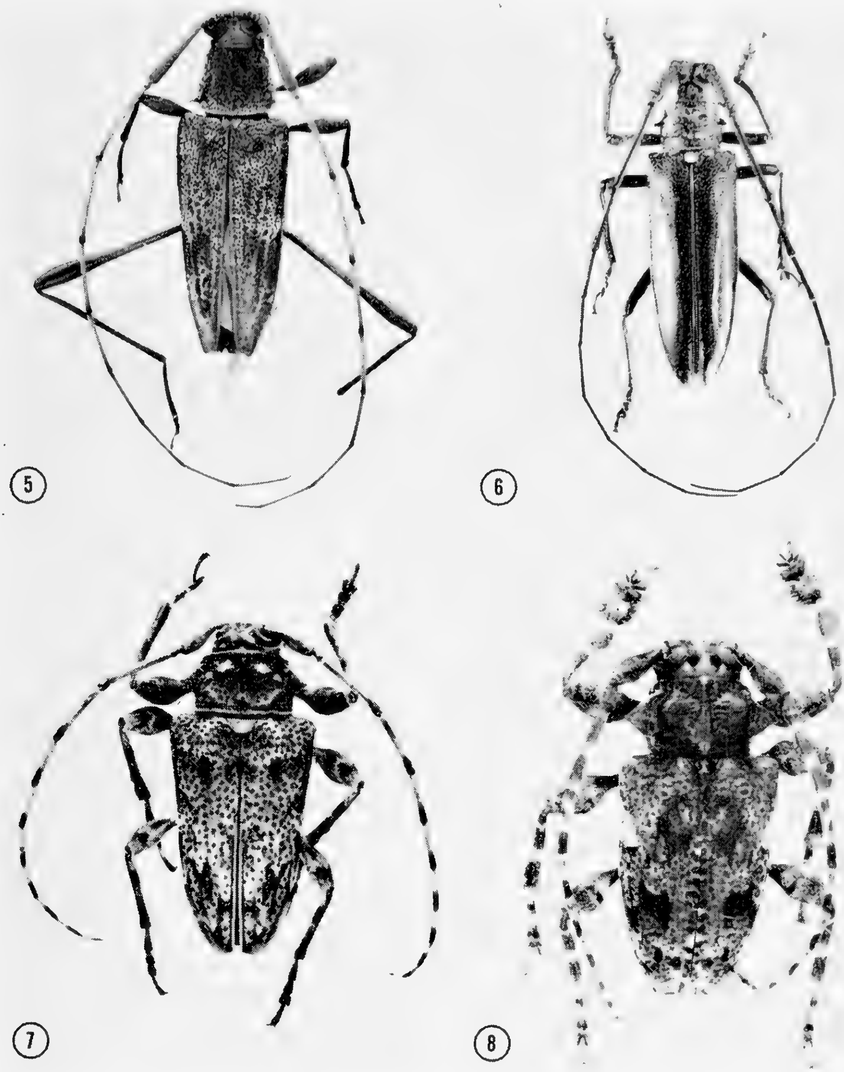
TYPE LOCALITY. Of *M. hayi,* "Indefatigable Island"; *M. cocoensis,* Cocos Island.

RANGE. Cocos Island (Galápagos record not confirmed).

FLIGHT PERIOD. March to September.

HABITS. G. Kuschel captured this species flying during the day in March.

This species was described by Mutchler from three specimens, a female designated as the holotype of *Monochamus hayi,* presumed to have been captured in the Galápagos Islands, and two males designated as holotype and "allotype" of *Monochamus cocoensis,* from Cocos Island. The differences between these two "nominal" species appear to be sexual, primarily involving the width and plication of the prosternum and the length of the antennal segments. Dillon and Dillon (1941) synonymized the two names and we agree that the synonymy



Figures 5–8. Figure 5, *Anisopodus longipes* Linsley and Chemsak, ♂, × 4; figure 6, *Taeniotes hayi* (Mutchler), ♂, × 1⅔; figure 7, *Acanthoderes cocoensis* Linsley and Chemsak, ♂, × 4; figure 8, *Acanthoderes circumflexus* Jacquelin du Val, ♂, × 3⅓.

is probable. Unfortunately they chose the name applied to the putative Galápagos specimen as the senior synonym. We seriously question the occurrence of this species in the Galápagos Islands.

Material examined. 2 ♂♂, Cocos Island (types of *M. cocoensis*); 4 ♂♂, Chatham Bay, March 8, 1964 (G. Kuschel, R. O. Schuster); 1 ♂, Cocos Island, November 3–13, 1905 (F. X. Williams); 1 ♀, Indefatigable Island, Galápagos (?), April, 1930 (C. Hay) (type of *M. hayi*).

Adetus nesiotes Linsley and Chemsak, new species.

(Figure 4.)

MALE. Form moderate sized, cylindrical, subdepressed; ground color dark reddish brown, pubescence grayish ochraceous. Head short, front resting on prosternum; face oblique, broad, vertex curving back from plane area between nonprominent antennal tubercles; punctation coarse, dense; grayish ochraceous pubescence dense along sides and across front, sparser on vertex; eyes small, separated, upper lobes separated above by more than length of antennal scape; antennae extending to about middle of elytra, scape conical, less than half as long as third segment, third segment as long as fourth and fifth combined, fifth shorter than fourth, segments from fifth gradually decreasing in length, segments densely clothed with short, appressed brownish pubescence, all segments except first with numerous erect and suberect hairs beneath. Pronotum about as long as broad, broadly cylindrical, sides broadly rounded; disk very coarsely, contiguously punctate at center behind middle, punctures becoming smaller and more separated apically, basally, and laterally; each side with a densely pubescent band extending from apex to base, median area less densely pubescent, surface not obscured; prosternum fitted for reception of head; prosternal process fairly broad, expanded at apex, coxal cavities closed behind; mesosternal process abruptly declivous in front; metasternum impunctate at middle, coarsely punctate toward sides; scutellum broadly rounded behind, densely pubescent. Elytra more than twice as long as broad, cylindrical; punctures coarse, arranged in longitudinal rows on disk, more irregularly toward sides, decreasing in number toward apex; each elytron with an irregular, ill-defined longitudinal black stripe down middle and a moderately large, arcuate pubescent band near apex, each pubescent band partially enclosing a small black spot near suture; lateral pubescent band of head and pronotum extending back over humeri to about middle of elytra, other pubescence sparser, very short, not obscuring surface; apices rather narrowly rounded. Legs short, densely brown, and pale pubescent. Abdomen densely pubescent, coarsely punctate at sides; apex of last sternite very shallowly emarginate. Length, 11 mm.

HOLOTYPE ♂ from Cocos Island, March 8, 1964 (R. O. Schuster).

Acanthoderes circumflexus Jacquelin du Val.

(Figure 8.)

Acanthoderes circumflexus JACQUELIN DU VAL, 1857, in: Sagra, Histoire . . . de l'Ile de Cuba, vol. 7, p. 270; CHEVROLET, 1862, Ann. Soc. Ent. France, ser. 4, vol. 2, p. 247; BATES, 1872, Trans. Ent. Soc. London, vol. 1872, p. 207; BATES, 1880, Biologia Centrali-Americana, Longicornia, vol. 5, p. 140; GAHAN, 1895, Trans. Ent. Soc. London, vol. 1895, p. 130.

Acanthoderes quadrigibba, (*pars*), Duffy, 1960, Monograph of the immature stages of Neotropical timber beetles, p. 214 (larva, habits).

Moderate sized, ground color dark reddish brown. The pubescent pattern of the elytra consists of two white arcuate bands extending from the lateral margins a little behind the humeri to about the center of the disk, two irregular black patches behind the middle with pale brown, black, and white pubescence suffused in patches throughout. The antennae and tibiae are annulated and the apices of the elytra emarginate truncate with the outer angles subdentate. Length, 13–16 mm.

Type locality. Cuba.

Range. West Indies, Mexico to northern South America.

Flight period. March and April (Cocos Island).

Specimens were collected at light and on bark of trees at night by G. Kuschel.

Material examined. 2 ♂♂, Chatham Bay, March 8, 1964 (G. Kuschel); 1 ♂, 3 ♀♀, Wafer Bay, March 1, 1963 (P. Slud).

Acanthoderes cocoensis Linsley and Chemsak, new species.

(Figure 7.)

Male. Form robust, moderate sized, convex above; ground color dark reddish brown, densely clothed with grayish yellow appressed pubescence interrupted by coarse separated punctures. Head with front flat, subquadrate, with a small shallow diamond-like impression between antennal tubercles; antennal tubercles well developed, strongly divergent; punctation minute, obscured by short appressed brownish and yellowish pubescence; frontoclypeal suture with four long erect setae, frontal suture deep; eyes small, rather finely faceted, deeply emarginate, separated above by about diameter of antennal scape; antennae extending about four segments beyond body, segments uniformly clothed with minute yellowish pubescence except base and apex of third and fourth segments and apices of remaining segments which are brownish, the dark bands increasing in length apically, underside of segments with long suberect setae which diminish in number apically; scape extending to about apical one-fourth of pronotum, subequal in length to fifth segment, fourth longer than fifth, third longer than fourth, eleventh slender, shorter than tenth. Pronotum about twice as long as broad, base broader than apex; sides slightly rounded to basal margin, not constricted basally, sides strongly inflated to produce a broad almost obtuse tubercle; disk convex, with three prominent calluses, one median near basal margin and one on each side of middle at apical one-third, punctures coarse, sparse, scattered around dorsal calluses and in a row along basal and apical margins but not extending to sternum; pubescence uniform, dense, recumbent, yellowish and brown with median callus a little glabrous; prosternum narrow, impunctate, intercoxal process broad, expanded apically, coxal cavities closed, pubescence dense, recumbent, yellowish at sides; mesosternal process very broad, episternum of metathorax narrow, pubescence at middle of sternites finer, sparser, and brown; scutellum broadly rounded behind, finely densely pubescent. Elytra over 1½ times as long as broad, tapering apically; humeri well developed; surface convex, even, costae vague, disk with elevated, densely pubescent tubercle on each side at middle on basal one-fourth; punctures coarse, separated, becoming very sparse toward apex; pubescence brownish yellow, dense, recumbent, interrupted by patches of brown pubescence laterally behind humeri and on disk on apical one-half; apices slightly obliquely truncate. Legs with femora strongly clavate, finely clothed with pale recumbent pubescence; tibiae dark brown with small rings of paler pubescence at base and middle. Abdomen densely pubescent along sides, less densely at middle, punctures obsolete; apex of last sternite rotundate-truncate. Length, 10–12 mm.

HOLOTYPE ♂ from Cocos Island, March 8, 1964 (R. O. Schuster); one ♂ paratype from Wafer Bay, Cocos Island, March 1, 1963 (P. Slud).

This species appears to be assignable to the genus *Acanthoderes* in the broad sense. It is distinctive in its small size and untufted front tarsi.

Acanthoderes species.

A broken specimen of what may prove to be an undescribed species of *Acanthoderes* (*sensu latu*) may be briefly characterized as follows: Form large, robust; ground color reddish, pubescence grayish; elytral costae distinct, each elytron with an irregular oblique median dark fascia and a smaller broken apical band; elytral apices truncate.

MATERIAL EXAMINED. A female from Wafer Bay, Cocos Island, March 1, 1963 (P. Slud).

Anisopodus longipes Linsley and Chemsak, new species.

(Figure 5.)

MALE. Form moderately large, body flattened; ground color dark reddish brown, pubescence ochraceous. Head small, front short, quadrate, vertex extending back at right angle from front, antennal tubercles prominent, diverging at right angles from contiguous bases, median line slender, not deeply impressed; genae short with a small obtuse tubercle at apex; pubescence fine, appressed, dense but not concealing surface, punctation minute; eyes large, rather finely faceted, deeply emarginate, lower lobes large, upper lobes separated by about diameter of antennal scape; antennae slender, extending about five segments beyond body, segments three to six paler with dark apices, segments densely clothed with short recumbent pubescence, scape with a few longer suberect hairs beneath, scape subequal in length to third segment, third subequal to fourth, fourth slightly longer than fifth, eleventh slender, subequal to tenth. Pronotum broader across lateral tubercles than long, apex narrower than base, sides diverging from apex to tubercles near base than constricted behind tubercles, lateral tubercles acute, slightly directed backwards; disk flattened, with a slender, elongate glabrous median `callus extending from a little before basal margin to a little beyond middle, each side with a vague oblique callus on apical one-half; punctures rather fine, arranged around glabrous raised areas; pubescence fine, very short, appressed, dense along sides, sparser toward center; prosternum narrow, apically impressed, minutely punctate, finely, densely pubescent; prosternal process flat, expanded apically, coxal cavities closed; episternum of metathorax slender, densely pubescent; scutellum broadly rounded behind, densely pubescent except for median apical spot. Elytra over twice as long as broad, tapering apically; punctures over basal one-half coarse, dense, becoming sparser toward apex; very short recumbent pubescence variegated with darker hairs, each side with a large patch of yellowish pubescence below and behind humeri, each elytron with an indistinct dark angulate postmedian band; apices narrow, emarginate, angles not produced. Legs with hind femora elongate, extending well beyond body, gradually clavate toward apices; front and middle femora clavate, short; hind tibiae elongate, straight, other tibiae shorter and somewhat arcuate; hind tarsi with first segment very elongate, slender; pubescence fine, pale, tibiae dark at apex. Abdomen minutely punctate, finely pubescent; apex of last tergite deeply notched, apex of last sternite shallowly emarginate. Length, 11–14 mm.

Female. Legs with hind femora and tibiae not elongate, femora not extending beyond body. Abdomen with apex of last tergite emarginate, apex of last sternite shallowly emarginate. Length, 9–12 mm.

Holotype ♂, allotype ♀ from Cocos Island, March 8, 1964 (R. O. Schuster); 13 paratypes (8 ♂♂, 5 ♀♀) all from Cocos Island, March 8, 1964 (R. O. Schuster, G. Kuschel), March 1, 1963 (P. Slud), April 16, 1963 (P. Slud).

Anisopodus longipes appears to be closely related to the mainland species *A. xylinus* Bates. The gradual thickening of the elongate hind femora, a character shared by both species, is not common in the genus. *Anisopodus longipes* differs from *A. xylinus* by having darker coloration, by the possession of a postmedian dark elytral band, and by the very prominent yellowish patch of pubescence below and behind the humeri.

Urgleptes kuscheli Linsley and Chemsak, new species.
(Figure 2.)

Male. Color pale brown, elytra and pronotum variegated with patches of dark brown, antennae mostly pale, legs testaceous with dark patches on femora, tibiae dark apically, underside pale brownish. Head small, darker brown, front quadrate, convex; antennal tubercles elevated, widely divergent; eyes small, deeply emarginate, coarsely faceted, separated above by at least twice diameter of antennal scape; punctation minute, finely scabrous; pubescence fine, appressed, golden, front with two very long erect setae along margin of each eye and four more along frontoclypeal margin; antennae slender, extending more than five segments beyond body, segments pale, scape darkened over apical one-half, segments to fifth narrowly darkened at apex, remaining segments slightly darker, scape subequal in length to third and fourth segments, fifth shorter than fourth, sixth to eleventh subequal, shorter than fifth, segments to fourth with several suberect hairs beneath. Pronotum broader than long, sides broadly rounded to acute tubercles near base, than strongly constricted behind tubercles, lateral tubercles directed backward, base shallowly, transversely impressed, apex not impressed; disk convex, surface finely asperate punctate, with a vague median callus near base; pubescence fine, pale, appressed, not obscuring surface; each side of middle with a broad dark brown band extending down sides over lateral tubercles; prosternum narrow, subglabrous, prosternal process laminiform, expanded behind, coxal cavities closed, coxae contiguous; mesosternal process very narrow, punctation of metasternum minute, shallow, vague, pubescence fine, appressed; scutellum rounded behind, sparsely pubescent. Elytra over twice as long as broad, sides subparallel to apical one-third than tapering; dark brown splotches and stripes scattered over surface, over humeri and laterally to apex, near suture behind scutellum and down disk either as narrow lines or as larger spots behind middle; pubescence on paler areas white, subappressed, coarser and longer than dark hairs on dark areas; punctation over basal half coarse, subcontiguous, becoming finer and sparser apically; apices narrowly, slightly obliquely subtruncate. Legs short, front and middle femora strongly clavate, hind femora feebly clavate, tarsi and apical half of tibiae dark brown, femora with a dark band over portion of club. Abdomen finely pubescent; fourth sternite subequal in length to fifth, fifth sternite subtruncate at apex. Length, 3.5 mm.

FEMALE. Fifth abdominal sternite broader than fourth, apex rounded. Length, 3.5 mm.

HOLOTYPE ♂, allotype ♀ from Cocos Island, March 8, 1964, collected on small branches of balsa (*Ochroma lagopus*) (G. Kuschel); one ♂ paratype, same data.

Some variation in the dark elytral coloration is evident in the type series. The types both possess a postmedian brown splotch almost resembling an interrupted fascia. Behind this the apex is dominantly dark with pale irregular variegations. The other male has three irregular, longitudinal, dark stripes over most of the elytral surface.

We take pleasure in naming this species in honor of G. Kuschel who collected much of the material used in this study.

ACKNOWLEDGMENTS

The authors gratefully acknowledge support from the National Science Foundation for this and related studies under grant GB-2326. Dr. G. Kuschel, as a member of the Galápagos International Project, made a special effort to collect Cerambycidae when the Expedition stopped briefly on Cocos Island.

Material collected at the same time by R. O. Schuster was kindly made available by Hugh B. Leech, California Academy of Sciences, San Francisco. Dr. Jerome G. Rozen of the American Museum of Natural History loaned material collected by P. Slud, and E. F. Gilmour sent a copy of his manuscript key to the species of *Anisopodus* which enabled us to confirm our belief that the Cocos Island species was undescribed. To all of the above we extend our thanks.

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 10, pp. 249–254; 1 table January 31, 1966

CERAMBYCIDAE OF THE REVILLA GIGEDO ISLANDS

By

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The Revilla Gigedo Islands, like the Galápagos, 19° to the south, are oceanic and volcanic in origin, arid in climate, and widely separated from the mainland. Unlike the Galápagos, the Revilla Gigedos are only four in number, remote from each other, and arranged in an east–west, rather than a north–south, direction.

Cerambycidae are presently known from two of the islands, Socorro and Clarion (Linsley, 1935, 1942, 1958), based upon collections made by H. H. Keifer and J. R. Slevin as members of the California Academy of Sciences Expedition of 1925 (see Hanna, 1926), and by William A. MacDonald and D. C. Blodget who visited the islands in 1955. The objective of the present report is to summarize these findings and correct nomenclature which has been applied to the species, in order to permit meaningful comparisons with the cerambycid faunas of the Galápagos and Cocos islands.

Flora of the Revilla Gigedo Islands

The flora of the Revilla Gigedo Islands has been analyzed by Johnston (1931). He recognized 37 endemic and 79 nonendemic species and subspecies of plants. Of the nonendemic species, 80 per cent occur also in the Pacific States of Mexico north of Colima; the remainder are either widespread or have West Indian, southern Mexican, or Central American affinities. There are no endemic genera, but among the species, more than half appear to have southern, Galapagean, or West Indian affinities.

Host Plants and Affinities of Revilla Gigedo Cerambycidae

Four species of Cerambycidae have thus far been found on the Islands, two on Socorro and two on Clarion (table 1). Each of these populations is believed

Table 1. *Known Cerambycidae of Revilla Gigedo Islands.*

Name	*Locality*	*Date*	*Host Plant*
Stenodontes dasytomus socorrensis	Grayson Cove, Socorro Island	May	
Nesodes insularis	Clarion Island	May	*Sophora tomentosa, Sapindus sopolaria*
Acanthoderes socorrensis	Grayson Cove, Socorro Island	May	*Hippomane mancinella*
Acanthoderes peritapnoides	Clarion Island	May	*Sapindus sopolaria*

to be endemic at the level of species or subspecies and one is regarded as generically distinct from relatives elsewhere. The ancestors of these four species, by their affinities, might possibly have arrived on the islands from mainland sources on the North American continent (none show close relationship with known species from Cocos Island or the Galápagos). This is almost certainly true of *Stenodontes dasytomus socorrensis,* a population whose insular host is not yet known. Affinities of the other three species are less clear, and can best be discussed in relation to the plants which nourish the larvae.

Host plants have been recorded for three of the four Cerambycidae now known from the Archipelago. Although each of the populations is believed to be endemic, the known host plants comprise widespread species:

Sophora tomentosa Linnaeus (Leguminosae), one of the two recorded hosts for *Nesodes insularis* Linsley. This is a pantropical strand plant of the Old World and West Indies, occurring in the eastern Pacific only on Clarion Island. Here it is reported as growing in dense brush near the ocean, along the beach and on low hills directly behind it, as a shrub with a woody base (Johnston, 1931). *Nesodes insularis*—a flightless species—appears to have affinities with elaphidionine Cerambycidae of the West Indies and Gulf Coast of Mexico and Central America.

Sapindus sopolaria Linnaeus (Sapindaceae), an alternate host of *Nesodes insularis,* is widely distributed in the West Indies also, and occurs along the west coast of America from Baja California southward. It is reported to be the largest shrub on Clarion Island, growing in large thickets near the beach. Ranging from two to three meters in height, it is used as a nest site for the blue-footed boobie (Johnston, 1931). In addition to *Nesodes insularis,* it serves as host for *Acanthoderes peritapnoides*—a species whose phylogenetic affinities, although American, are not entirely clear.

Hippomane mancinella Linnaeus (Euphorbiaceae). This is a widespread shoreline species occurring throughout the West Indies and from southern Mexico (Oaxaca) to Ecuador. In the eastern Pacific, it is known from Socorro Island and the Galápagos. In Grayson Cove it is abundant in small groves, and serves as host for *Acanthoderes socorrensis,* a species with uncertain, but probably Mexican, affinities.

Revilla Gigedo Cerambycidae

Stenodontes dasytomus (Say).

Prionus dasytomus Say, 1823, Jour. Acad. Nat. Sci. Philadelphia, vol. 3, p. 326.
Mallodon dasytoma, LeConte, 1851, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 2, p. 112.
Stenodontes (*Mallodon*) *dasytomus,* Lameere, 1902, Mem. Soc. Ent. Belgique, vol. 9, p. 77.
Stenodontes (*Orthomallodon*) *dasytomus,* Linsley, 1962, Univ. Calif. Publ. Ent., vol. 19, p. 19.

Color reddish brown to dark brown or blackish; surface shining, glabrous. Genae bidentate or tridentate; mandibles not strongly retracted at base, bluntly and broadly tridentate before apex. Antenna attaining basal third of elytra in male, shorter in female. Disk of pronotum with large, polished, sparsely punctate facets. Suture of elytra spinose. Length, exclusive of mandibles, 23–50 mm.

Type locality. Lower Missouri River.

Range. Northern South America to southern United States.

Two subspecies are presently recognized, the nomino-typical form occurring in the southern United States and northern Mexico and *S. d. masticator* (Thomson) from South America to southern Arizona.

The population on the Revilla Gigedo Islands appears to be subspecifically distinct from each of those on the mainland.

Stenodontes dasytomus socorrensis Linsley and Chemsak, new subspecies.

Stenodontes (*Mallodon*) *molarius* Linsley (not Bates), 1942, Proc. Calif. Acad. Sci., ser. 4, vol. 24, p. 83.

Color brown to dark brown. Genae tridentate (third tooth usually vague); gula coarsely, longitudinally rugose. Pronotum with large polished facets usually reunited posteriorly, punctures between facets fine, confluent. Elytra finely and sparsely wrinkled appearing near base. Length, exclusive of mandibles, 30–48 mm.

Holotype ♂, allotype ♀, and 8 ♂ paratypes from Grayson Cove, Socorro Island, May 4, 1925 (J. R. Slevin) and May 11, 1925 (H. H. Keifer), in the collections of the California Academy of Sciences, San Francisco.

This subspecies differs from the nomino-typical form by the tridentate genae, paler brown color, and finer discal punctures of the pronotum. The smaller polished facets and confluent punctation of the pronotum and the slight wrinkling of the elytra distinguish it from *masticator*.

Nesodes insularis Linsley.

Nesodes insularis Linsley, 1935, Pan-Pacific Ent., vol. 11, p. 74, fig.; Linsley, 1942, Proc. Calif. Acad. Sci., ser. 4, vol. 24, p. 83.

Dark brown, irregularly clothed with white, recumbent pubescence. Antennae unarmed, densely pubescent. Prothorax densely punctate with a median glabrous callus; pubescence condensed into irregular white patches. Elytra coarsely, not closely punctured, densely clothed with recumbent white pubescence. Length 11–18 mm.

Type locality. Clarion Island.

Flight period. May.

Host plants. *Sophora tomentosa, Sapindus sopolaria.* The adults bore into the pith of living plants of the host.

This species is distinctive among the Elaphidionini by the absence of spines on the antennae, elytral apices, and femora, the reduced hind wings, and the large prothorax.

Acanthoderes socorrensis Linsley.

Acanthoderes socorrensis Linsley, 1942, Proc. Calif. Acad. Sci., ser. 4, vol. 24, p. 84, pl. 5, fig. 5.

Acanthoderes peninsularis Linsley (not Horn), 1935, Pan-Pacific Ent., vol. 11, p. 74.

Color of integument brown, pubescence dense, appressed, variegated golden and brownish. Pronotum with a large lateral conical tubercle, disk with a narrow glabrous callus extending from base to apex and two pubescent calluses before middle. Elytra finely clothed with golden, pale, and yellowish brown pubescence with an obscure, pale, oblique fascia extending from behind humeri nearly to suture; apices emarginate. Length, 12–14.5 mm.

Type locality. Grayson Cove, Socorro Island.

Host plant. Specimens were reared from *Hippomane mancinella* in May.

Acanthoderes peritapnoides Linsley.

Acanthoderes peritapnoides Linsley, 1958, Bull. So. Calif. Acad. Sci., vol. 57, p. 49, pl. 16.

Form short, robust, color piceous black, antennae, legs, dorsum of head, disk of pronotum, and some sterna reddish; surface subglabrous, pubescence sparse. Pronotum with large lateral tubercles. Elytra with apices and oblique antemedian impressions reddish; coarse punctures sparsely scattered over surface; apices subtruncate. Length, 11.5 mm.

Type locality. Clarion Island.

Host plant. Reared from *Sapindus sopolaria* in May.

The subglabrous integument, piceous coloration, and less robust form will separate this species from *A. socorrensis*.

Acknowledgments

The authors wish to acknowledge the National Science Foundation for support of this and related studies under Grant GB-2326. Material in the collections of the California Academy of Sciences was kindly made available by Hugh B. Leech.

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 11, pp. 255–359; 10 figs.; 5 tables; 23 plates
March 30, 1966

THE COCHLEAR DUCT OF LIZARDS[1]

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[1] This work was supported by United States Public Health Service grants Nos. GM10649-02 and NB-05532-01.

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INTRODUCTION

The reptiles are not only the first vertebrates with a clearly defined cochlear duct, but also are remarkable in that they have experimented with the cochlear duct and have modified almost all its various parts. Among the reptiles we find differences in the overall size of the cochlear duct, in length, width, and configuration of the sound-sensitive cells constituting the papilla basilaris and marked alterations of the limbus, which is the supporting structure of the papilla basilaris. Differences are also noted in the enclosure of the perilymphatic fluid-filled spaces that transmit the sound-pressure waves to the medial aspect of the basilar membrane.

The avian cochlear duct is very similar to that found in the crocodiles. The mammalian duct is apparently also derived from a reptilian type, but is more specialized, elongated, and coiled.

The broad general features of the comparative anatomy of the membranous labyrinth of the vertebrate inner ear have been known for some time and have been most comprehensively presented by Retzius (1881, 1884) and more recently by de Burlet (1934). In 1953, Shute and Bellairs, in a study of the cochlear apparatus of certain gekkonid and pygopodid lizards, demonstrated that a detailed study of the cochlear duct had remarkable taxonomic implications. Recently, Hamilton (1960, 1964), Baird (1960a), and Schmidt (1964) have added much to the knowledge of the anatomy of the lizard inner ear and Wever and Vernon (1956, 1957, 1958, and 1960), Wever *et al.* (1963a, 1963b, and 1964), Wever and Peterson (1963), and Crowley (1964) have indicated something of the various functional capacities of the reptilian cochlea.

It is now obvious that detailed studies of the structure and function of reptilian cochleae will provide valuable information in the fields of bio-acoustics and reptilian taxonomy and phylogeny.

The recent studies of Hamilton and Baird (*op. cit.*) have helped clarify the general anatomical relationships of lizard inner ear structures and the associated anatomical terminology. These studies, as well as those of Schmidt (*op. cit.*), were done largely by the time-honored and necessarily basic method of making serial sections, and from these, reconstructions.

The present approach to the study of the reptilian inner ear is somewhat different in that, in addition to serial sections, the entire cochlear duct has been dissected out of the animal, and its anatomy studied by direct observation of the three-dimensional structure of the intact apparatus. That this is the same approach used by Retzius, in 1884, is apparent if one studies the illustrations of his great work. While he presented the general features of the anatomy of the membranous labyrinth in a variety of lizards (Iguanidae, Lacertidae, Gekkonidae, Chamaeleonidae, Anguidae, and Scincidae), he did not report the detailed anatomy of the cochlear duct in these animals. The object of this paper is to describe and illustrate the gross anatomical features of the cochlear duct of lizards.

Materials and Methods

Since histologic serial sections of the entire posterior cranium are most helpful in an anatomic study of the vertebrate inner ear, lizards from a number of families were sacrificed by decapitation, the heads fixed in a variety of ways, and after decalcification, embedded in paraffin or celloidin and serially sectioned.

After study and reconstruction of serial sections of various lizard inner ears, it became apparent that by careful dissection one could remove the cochlear duct intact from the otic capsule. Trials on freshly sacrificed lizards soon verified the simplicity and great utility of this procedure (see below).

Since the present study is not concerned with the histology of the cochlear duct, but is limited primarily to gross structures, details of histologic preparation will not be presented at this time.

While tissue from freshly sacrificed animals is necessary for histological preparations, museum specimens provide excellent material for the study of gross anatomical features of the otic capsule and its contained structures. Thus, intact cochlear ducts were removed from both live animals and a large variety of specimens in the herpetological collections of the California Academy of Sciences and of the Division of Systematic Biology of Stanford University.

It is possible to remove the cochlear duct from a reptile with only minimal damage to the specimen. A three-sided flap, involving little or no damage to head scales, over the otic area of the left side of the head was folded downward exposing the posterolateral aspect of the cranium. Overlying muscle or extensions from roofing bones were carefully dissected away exposing the lateral aspect of of the otic capsule. The tip of a scalpel or a dental drill was then employed to open the otic capsule exposing the sacculus and cochlear duct. The sacculus was usually removed and the auditory nerve transected at its point of emergence through the medial wall of the capsule; then the cut distal end of the nerve was grasped with fine forceps and the cochlear duct lifted free from the cochlear recess.

In the great majority of museum specimens, the original preserving alcohol or formalin had penetrated the otic capsule in time to preserve even the cellular elements of the papilla basilaris. In large thick-boned specimens such as *Sphenodon, Heloderma,* and *Amblyrhynchus,* some details were indistinct because the preserving agent could not penetrate the capsule fast enough to completely inhibit autolysis.

After removal of the intact cochlear duct, it was stored in 70 per cent ethyl alcohol for further study. The structural details of the cochlear duct were more easily seen if the calcium carbonate crystals were removed from the otolithic membrane overlying the macula lagenae. This was easily accomplished by soaking the specimen overnight in a vinegar–alcohol solution.

Visualization of the details of the papilla basilaris and its supporting limbus required removal of the lateral wall (vestibular membrane) of the cochlear duct with fine forceps and scissors.

All cochlear ducts were photographed in stereocolor and black and white, and scale drawings were made of each specimen. After characteristic family types were established, a professional artist, Mr. Wayne Emery, executed drawings of both the lateral and medial aspects of the cochlea using the actual specimens.

For the present study the following measurements were made of each cochlear duct: the greatest length and width of the entire duct and the limbus, and the lengths of the papilla basilaris and macula lagenae. Measurements were made by means of a calibrated reticule placed in the eyepiece of a dissecting microscope.

The length of the papilla basilaris was estimated to the nearest 0.05 mm. and the approximate area determined by tracing the outline of the papilla basilaris on an appropriately ruled paper, and the areal value determined by use of a Leitz planimeter. While the length of the papilla basilaris was determined for all species studied, the area was calculated for a little less than half the number (see table 2).

Since the macula lagenae is usually curved, its length could only be very generally estimated. The area was not determined in the present study, for this would have required dissection and consequent destruction of the specimens.

In most cases the measurements reported in the tables and graphs are based on one specimen only. That measurements from a single specimen do provide useful data was verified by measuring series of adult specimens of *Cnemidophorus tigris* (25), *Xantusia vigilis* (20), *Mabuya multifasciata* (6), *Gerrhonotus multicarinatus* (6), and *Dipsosaurus dorsalis* (6). In this sampling, no feature of the cochlear duct varied in its measurements more than 15 per cent within one species.

In 25 adults of *Cnemidophorus tigris* varying in snout–vent length from 73 to 105 mm., the cochlear duct length varied from 1.7 to 2.0 mm. (15% variation) and the limbus from 1.2 to 1.4 mm. (14%). There was no correlation between these measurements and snout–vent length of adult animals. The length of the papilla basilaris was very close to 0.8 mm. in all 25 specimens.

To determine the effect of growth on cochlear duct elements within a single species, seven specimens of *Leiolopisma assatum*, ranging from very young (27 mm. snout–vent length) to fully mature animals (53 mm. snout–vent length) were studied. Graph 1 (p. 276) demonstrates that the cochlear duct increases approximately 10 per cent in length and the limbus, 15 per cent, but that the papilla basilaris remains essentially the same length during the postnatal growth of a species. To show the relationship between body size and the length of the cochlear duct and the papilla basilaris in those families where sufficient data were available, such information is presented in graph form (graphs 2–7). While most animals used were adult, if a specimen were immature the dimensions of the cochlear duct and its elements might seem out of proportion to other members of the family. In those families that have but few representatives or where the available material is limited, the above data are presented in table 2 (p. 272).

The present study is based on a gross anatomical examination of the cochlear ducts of 205 species of lizards representing 131 genera and 18 families. Representatives of all living lizard families except the Anelytropsidae, Shinosauridae, and Lanthanotidae were studied.

In addition to the lizards, samples of several families of snakes and turtles have been studied and for purposes of comparison, the cochlear duct of a turtle, a snake, and *Sphenodon* are described and illustrated.

Table 1 is a list of material examined.

Observations

A. General Anatomical Features.

The recent excellent studies of Hamilton (1960, 1964) and Baird (1960a) have greatly clarified the general anatomy of the membranous labyrinth of lizards. For ease of understanding general anatomical relationships, schematic representations of the lateral and inferior aspects of the skull and drawings of the entire membranous labyrinth (lateral and medial views) of *Xantusia vigilis* are presented (figs. 1–4).

The cochlear duct (figs. 3 and 4) is the most inferior portion of the membranous labyrinth and is connected with the sacculus by the sacculo-cochlear

Table 1. *List of materials examined.*

LACERTILIA

Iguanidae

Amblyrhynchus cristatus	(CAS 87102 [59])[1]
Anolis antiquae	(SU 7473 [154])[2]
Anolis biporcatus	(CAS 67165 [65])
Anolis carolinensis	(CAS 63340 [66])
Anolis copei	(CAS 79146 [58])
Anolis cristatellis	(SU 18702 [146])
Anolis equestris	(SU 14608 [232])
Anolis cupreus	(CAS 87836 [132])
Anolis distichus	(SU 14571 [151])
Anolis polylepis	(CAS 79287 [77])
Anolis sallaei	(CAS 68086 [93])
Basiliscus vittatus	(CAS 23)[3]
Brachylophus fasciatus	(CAS 50135 [133])
Callisaurus draconoides	(CAS [16])
Chalaradon madagascariensis	(CAS 54659 [115])
Corythophanes hernandezi	(SU 18344 [193])
Crotaphytus collaris	(CAS [18])
Crotaphytus wislizeni	(No data, CAS [14])
Ctenosaurus pectinata	(CAS [161])
Ctenosaurus similis	(CAS 69291 [171])
Dipsosaurus dorsalis	(CAS [163], + 6 specimens)
Holbrookia texana	(CAS 31260 [39])
Hoplocercus spinosus	(CAS 93805 [70])
Iguana iguana	(CAS [162], + 3 specimens)
Leiocephalus carinatus	(SU 14611 [159])
Liolaemus pictus	(CAS 85249 [99])
Mariguana agassizi	(CAS 62604 [90])
Norops auratus	(CAS 79376 [98])
Oplurus cuvieri	(SU 13950 [191])
Petrosaurus thalassina	(CAS 90946 [96])
Phrynosoma coronatum	(CAS 40170 [56])
Phrynosoma douglassi	(CAS 48854 [204])
Phrynosoma m'calli	(CAS 33657 [222])
Phrynosoma modestum	(CAS 13110 [216])
Phrynosoma platyrhinos	(CAS 65315 [210])
Plica plica	(CAS 14550 [94])
Sauromalus obesus	(CAS [35], + 3 specimens)
Sceloporus magister	(CAS [15 and 19])
Sceloporus occidentalis	(CAS [288], + 4 specimens)
Tropidurus albemarlensis	(CAS 11435 [95])

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[1] The first number is the California Academy of Sciences, Department of Herpetology catalogue number of the specimen. The number in brackets is the catalogue number of the cochlear duct which is preserved separately in the collections of the Department of Herpetology of the Academy.

[2] Stanford University, Division of Systematic Biology catalogue number.

[3] Uncatalogued fresh specimen, cochlear duct only preserved.

Table 1. Continued.

Tropidurus hispidus	(CAS 49413 [102])
Tropidurus peruvianus	(CAS 80905 [103])
Tropidurus semitaeniatus	(CAS 49455 [221])
Tropidurus torquatus	(SU 9450 [236])
Uma scoparia	(CAS 42119 [97])
Urosaurus ornatus	(CAS 35069 [218])
Urostrophus torquatus	(CAS 85236 [181])
Uta stansburiana	(CAS [17])
Xiphocercus valensiennesii	(SU 9307 [199])
AGAMIDAE	
Agama agilis	(CAS 86343 [25])
Agama nupta	(CAS 86509 [165])
Agama persica	(CAS 86522 [202])
Amphibolurus barbatus	(CAS 77569 [160])
Amphibolurus muricatus	(CAS 77618 [172])
Calotes versicolor	(CAS 16880 [219])
Chlamydosaurus kingii	(CAS 77537 [72])
Draco rizali	(CAS 60368 [30])
Gonyocephalus grandis	(CAS [194, 195])
Gonyocephalus modestus	(SU 13555 [150])
Hydrosaurus pustulosus	(CAS 62381 [169])
Japalura polygonata	(CAS 21309 [170])
Japalura swinhonis	(CAS 18088 [174])
Phrynocephalus nejdensis	(CAS 84375 [144])
Sitana ponticeriana	(CAS 94355 [211])
Tympanocryptis lineata	(CAS 77624 [209])
Uromastix loricatus	(CAS 86463 [166])
CHAMAELEONIDAE	
Brookesia superciliaris	(CAS 55118 [43])
Chamaeleo bitaeniatus	(CAS 85766 [42])
Chamaeleo brevicornia	(CAS 54681 [50])
Chamaeleo dilepis	(No data, CAS [9])
ANGUIDAE	
Anguis fragilis	(CAS 66314 [88])
Diploglossus lessonae	(CAS 49540 [61])
Gerrhonotus coeruleus	(CAS 39105 [186])
Gerrhonotus multicarinatus	(CAS [20, 286], + 6 specimens)
Ophisaurus ventralis	(CAS 49063 [60])
ANNIELLIDAE	
Anniella pulchra	(CAS 39198 [44, 45], + 4 specimens)
XENOSAURIDAE	
Xenosaurus grandis	(CAS 87839 [344])
HELODERMATIDAE	
Heloderma suspectum	(CAS [6])
Heloderma horridum	(CAS 53929 [201])

TABLE 1. Continued.

VARANIDAE	
Varanus nuchalis	(CAS 15766 [141])
Varanus punctatus	(CAS 77677 [84])
Varanus salvator	(CAS 61120 [114])
Varanus species	(CAS [284])
LACERTIDAE	
Acanthodactylus cantoris	(CAS 86555 [180])
Eremias argus	(CAS 86904 [188])
Eremias guttulata	(CAS 91601 [51])
Eremias guttulata	(CAS 91599 [52])
Lacerta dugesi	(CAS 94081 [3])
Lacerta dugesi	(CAS 94072 [4])
Lacerta viridis	(CAS [105])
Lacerta viridis	(SU 22995 [106])
Lacerta vivipara	(SU 18472 [104])
Psammodromus algirus	(CAS 92431 [53])
Psammodromus hispanicus	(SU 17279 [235])
Takydromus septentrionalis	(CAS 66112 [46])
TEIIDAE	
Anadia bogotensis	(SU 8282 [229])
Ameiva ameiva	(CAS 7063 [33])
Ameiva aquilini	(CAS 39431 [49])
Ameiva undulata	(CAS 68884 [41])
Bachia peruana	(CAS 93231 [182])
Dicrodon lentiginosus	(CAS 94737 [152])
Cnemidophorus communis	(CAS 58803 [189])
Cnemidophorus gularis	(CAS 34537 [179])
Cnemidophorus hyperthrus	(CAS 8634 [168])
Cnemidophorus maximus	(CAS 46207 [187])
Cnemidophorus melanosthethus	(CAS 39105 [190])
Cnemidophorus ocellatus	(CAS 49555 [178])
Cnemidophorus tigris	(CAS 88334 [1])
Cnemidophorus tigris	(CAS [12, 13, 282])
Cnemidophorus tigris	(CAS [315–340])
Kentropyx calcaratus	(SU 8330 [113])
Neusticurus ecpleopus	(SU 8370 [158])
Pantodactylus species	(SU 17287 [230])
Proctoporus unicolor	(SU 15813 [234])
Tupinambis teguixin	(CAS 89669 [100])
GEKKOTA	
EUBLEPHARIDAE	
Coleonyx species	(CAS 5637 [10])
Coleonyx variegatus	(CAS [304, 305])
Eublepharus species	(CAS 86383 [127])
GEKKONIDAE	
Aristelliger nelsoni	(CAS 39418 [134])
Bavayia sauvagii	(CAS 80835 [116])

Table 1. Continued.

Cosymbotus platyurus	(SU 18566 [148])
Cyrtodactylus annulatus	(CAS 60207 [121])
Cyrtodactylus scaber	(CAS 84532 [118])
Gecko gecko	(CAS [300, 301])
Gecko japonica	(CAS 21749 [139])
Gehyra mutilata	(SU 9149 [156])
Gehyra oceanica	(SU 21778 [157])
Gehyra variegatus	(CAS 76237 [47])
Gehyra variegatus	(CAS 76248 [48])
Hemidactylus frenatus	(SU 9545 [147])
Hemidactylus garnotii	(CAS 47411 [131])
Hemidactylus persicus	(CAS 86454 [128])
Hemidactylus turcicus	(CAS 87114 [354])
Heteronata binoei	(CAS 74805 [126])
Hoplodactylus granulatus	(CAS 47982 [120])
Lepidodactylus lugubris	(SU 9389 [155])
Microgecko helenae	(CAS 93936 [122])
Oedura marmorata	(CAS 75234 [125])
Oedura robusta	(CAS 75671 [137])
Pachydactylus maculatus	(CAS 85889 [109])
Phelsuma madagascariensis	(CAS [302, 304])
Phyllodactylus bauri	(CAS 9745 [124])
Phyllodactylus elisae	(CAS 86352 [110])
Phyllodactylus marmoratus	(CAS 83590 [107])
Phyllodactylus muralis	(CAS 73567 [130])
Phyllodactylus unctus	(CAS 91356 [108])
Phyllurus cornutus	(CAS 44119 [117])
Stenodactylus sthenodactylus	(CAS 84210 [112])
Teratoscincus scincus	(CAS 84648 [119])
Thecadactylus rapicauda	(SU 8335 [73])
Tarentola mauritanica	(SU 18114 [145])
Sphaerodactylidae	
Gonatodes fuscus	(CAS 71228 [111])
Sphaerodactylus argus	(SU 14991 [149])
Sphaerodactylus cinereus	(CAS 39290 [64])
Uroplatidae	
Uroplatus fimbriatus	(SU 13473 [231])
Pygopodidae	
Aprasia pulchella	(SU 16223 [198])
Lialis burtonis	(CAS 77655 [34])
Pygopus lepidopodus	(CAS 77659 [206])
Scincidae	
Ablepharus lineocellatus	(CAS 83798 [81])
Acontias meleagris	(CAS 84188 [225])
Aulacoplax leptosoma	(SU 20822 [228])
Brachymeles gracilis	(CAS 92855 [82])
Brachymeles schadenbergi	(CAS 60493 [205])
Brachymeles tridactylus	(SU 19426 [123])

TABLE 1. Continued.

Brachymeles vermis	(CAS 60721 [220])
Chalcides polylepis	(CAS 92389 [215])
Chalcides sepoides	(CAS [36])
Dasia smaragdinum	(CAS 60500 [69])
Egernia nitida	(CAS 76612 [76])
Egernia striolata	(CAS 83931 [101])
Emoia nigra	(CAS 72238 [142])
Eumeces elegans	(CAS 31899 [38])
Eumeces fasciatus	(CAS 71565 [173])
Eumeces gilberti	(CAS 89417 [75])
Eumeces obsoletus	(CAS 71599 [55])
Eumeces stimsonii	(CAS 21670 [37])
Hemisphaeriodon gerrardi	(CAS 76692 [135])[4]
Leiolopisma assatum	(CAS 68571 [80])
Leiolopisma assatum	(CAS [347–353])
Leiolopisma guichinoti	(CAS 83856 [79])
Leiolopisma noctua	(CAS 64036 [54])
Lygosoma laterale	(CAS 17997 [78])
Lygosoma lentiginosus	(CAS 83737 [214])
Lygosoma verrauxi	(CAS 83738 [212])
Mabuya mabouia	(CAS 71454 [89])
Mabuya multicarinata	(CAS 60435 [74])
Mabuya multifasciata	(CAS 85672 [68])
Mabuya multifasciata	(CAS [299], + 6 specimens)
Nessia monodactyla	(CAS 17164 [207])
Ophiomorus tridactylus	(CAS 84674 [143])
Otosaurus cumingi	(SU 19591 [192])
Rhodona fragilis	(CAS 77196 [67])
Riopa bowringii	(CAS 75671 [136])
Scincus philbyi	(CAS 84585 [85])
Sphenomorphus indicus	(CAS 18685 [86])
Sphenomorphus quoyi	(CAS 76869 [91])
Sphenomorphus variegatus	(CAS 60281 [184])
Tiliqua scincoides	(CAS no number [7, 8])
Trachysaurus rugosus	(CAS 76678 [71])
Tribolonotus gracilis	(SU 13659 [233])
Tropidophorus rivularis	(CAS 62005 [87])
Typhlosaurus cregoi	(CAS 85832 [92])
FEYLINIIDAE	
Feylinia currori	(CAS 55111 [183])
XANTUSIIDAE	
Klauberina riversiana	(CAS 43856 [27])
Klauberina riversiana	(CAS 43848 [28])
Lepidophyma flavomaculatum	(CAS 66489 [63])
Xantusia henshawi	(CAS 64632 [62])
Xantusia vigilis	(CAS [21, 22], + 6 specimens)

[4] It was discovered too late to be incorporated into the body of this paper that the nominal genus *Hemisphaeriodon* has been referred to the synonymy of the genus *Tiliqua*.

Table 1. Continued.

Cordylidae	
Cordylus cordylus	(SU 12086 [158])
Cordylus jonesii	(CAS [290])
Cordylus polyzonus	(CAS 84191 [29])
Gerrhosaurus flavigularis	(CAS [5])
Dibamidae	
Dibamus argenteus	(SU 18762 [83])
Amphisbaenidae	
Amphisbaena fuliginosa	(CAS 71336 [227])
Bipes biporus	(CAS 53726 [224])
Blanus cinereus	(CAS 92400 [226])
Diplometopon zarudnyi	(CAS 84534 [140])
Rhineura floridana	(CAS 14100 [213])
OPHIDIA	
Colubridae	
Pituophis catenifer	(CAS [291])
CHELONIA	
Testudinidae	
Gopherus berlandieri	(CAS [H46])
CROCODILIA	
Alligatoridae	
Alligator mississippiensis	(CAS [164], + 5 specimens)
RHYNCHOCEPHALIA	
Sphenodontidae	
Sphenodon punctatum	(CAS [40])

duct. The latter usually arises from the posteroinferior aspect of the sacculus, but may be more inferomedial in location in some families (Hamilton, 1964).

The cochlear duct in reptiles as exemplified in *Crotaphytus wislizeni* (figs. 5 and 6) characteristically contains two sensory areas. The macula lagenae usually occupies the anterior and anteroinferior portion of the duct, but frequently extends both anterolaterally and anteromedially. The macula lagenae is always covered by an otolithic membrane.

The papilla basilaris is a sensory area usually occupying a position on the medial wall of the cochlear duct and is usually associated with an overlying tectorial membrane. (Outline sketches showing the lateral and medial aspects of the cochlear duct of *Crotaphytus* are presented in figures 5 and 6; figures 7 and 8 are cross sections of the cochlear ducts of *Hemidactylus* and *Sauromalus*.)

The vestibular membrane makes up the lateral wall of the cochlear duct. The medial wall is more complex and in good part is formed of a modified connective

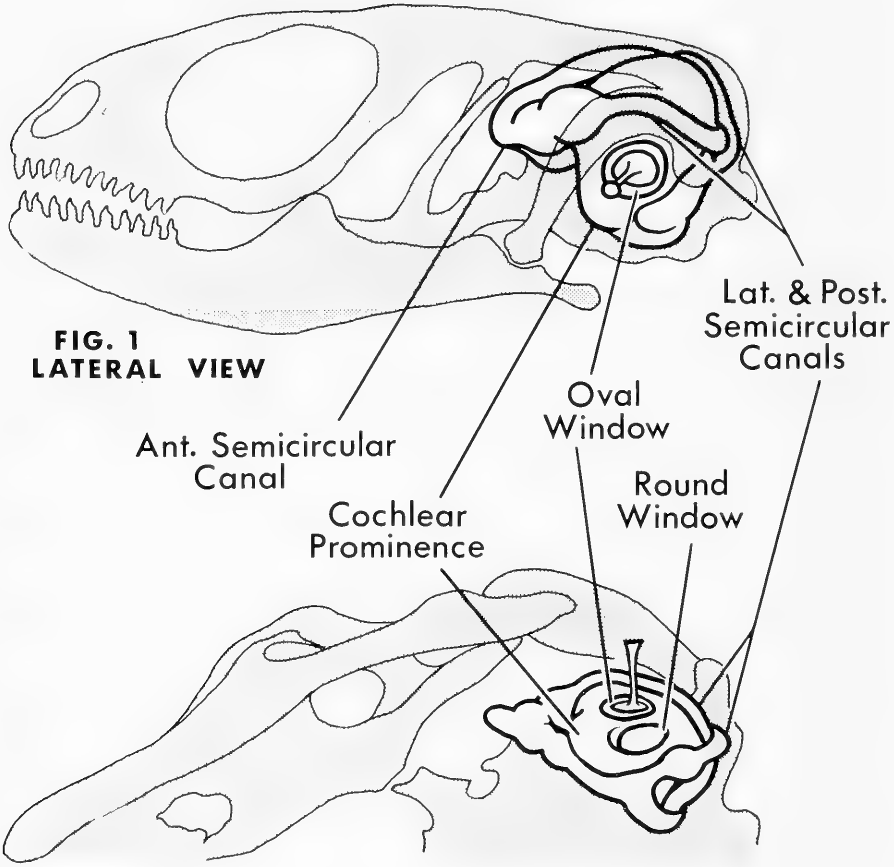


FIG. 1
LATERAL VIEW

FIG. 2
INFERIOR VIEW

Figure 1. Schematic representation of the otic region, *Xantusia*, lateral view.

Figure 2. Schematic representation of the otic region, *Xantusia*, inferior view.

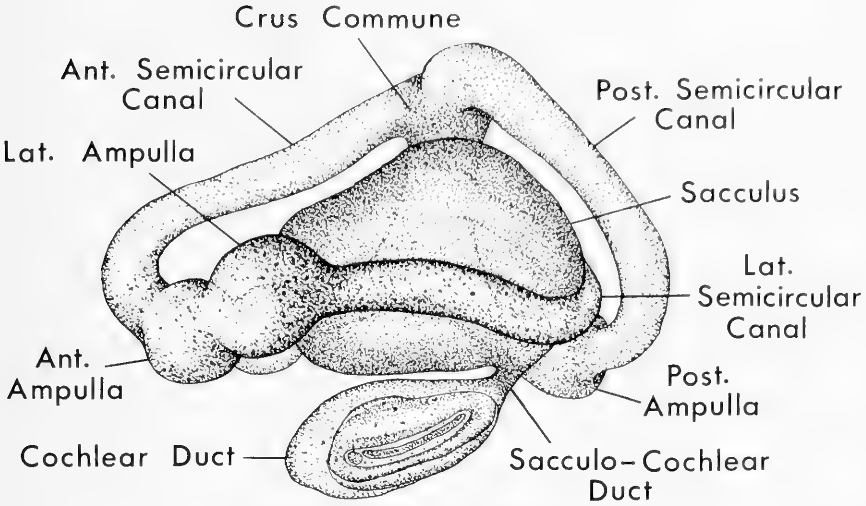


FIG. 3- LATERAL VIEW

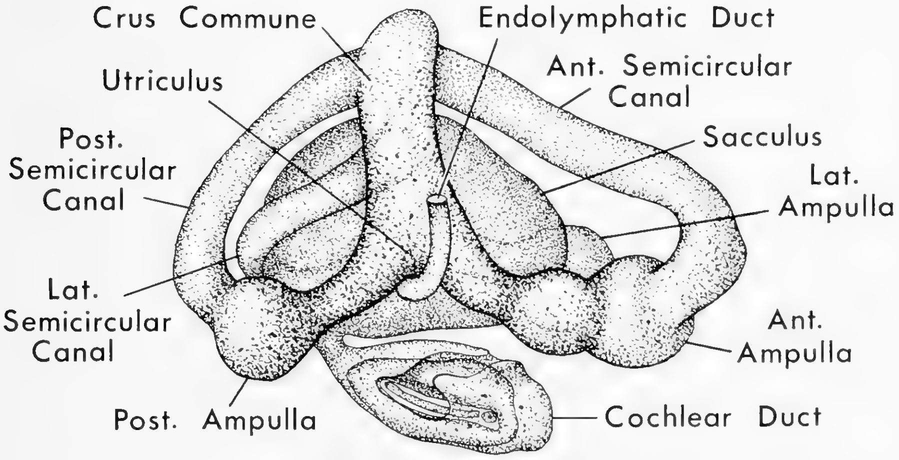


FIG. 4 - MEDIAL VIEW

Figure 3. Left membranous labyrinth, lateral view, *Xantusia vigilis*.

Figure 4. Left membranous labyrinth, medial view, *Xantusia vigilis*.

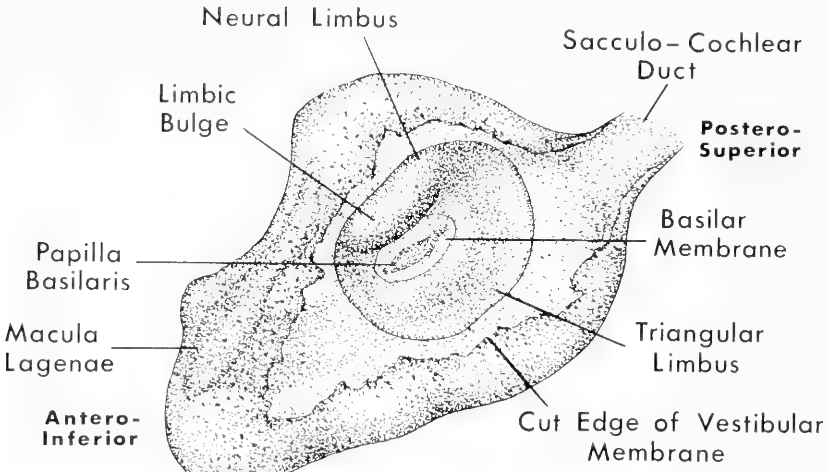


FIG. 5 - LATERAL VIEW

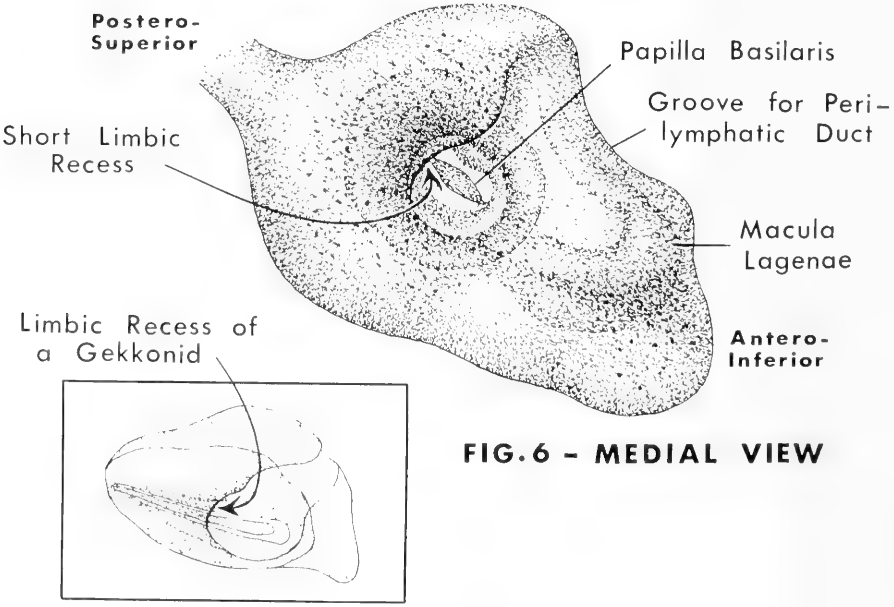


FIG. 6 - MEDIAL VIEW

Figure 5. Cochlear duct, lateral view, *Crotaphytus wislizeni.*

Figure 6. Cochlear duct, medial view, *Crotaphytus wislizeni.*

tissue containing abundant intercellular substance that imparts a flexible quality to this portion of the duct. The supporting tissue is thickened where it surrounds the basilar membrane and is termed the limbus. The anterosuperior portion of the limbus is thicker and larger than the posteroinferior limb and is variously modified and sculptured on both medial and lateral surfaces. Since the auditory nerve is closely apposed to the medial side of the anterosuperior portion of the limbus, it is designated the neural limbus. The lateral surface of the neural limbus may be merely a thin unsculptured plate, be thickened, or may give rise to liplike projections. A tectorial membrane usually arises from the lateral aspect of the neural limbus and overlies the cellular surface of the papilla basilaris.

The medial side of the limbus is differently sculptured in large part to accommodate the perilymphatic duct and sac which conduct sound-pressure waves through the perilymphatic fluid from the perilymphatic cistern to the medial aspect of the basilar membrane (fig. 9). Hamilton (1960, 1964) and Baird (1960a) prefer a different terminology for the various portions of the perilymphatic (periotic) system. Until more extensive studies have been made on the homologies of the structures of the perilymphatic system among different vertebrate groups, I prefer to retain the older terminology.

In some types of cochlear ducts, the perilymphatic sac is not enclosed by any portion of the limbus along the greater part of the medial aspect of the basilar membrane (figs. 6 [not insert], and 8). In other types of ducts, a considerable extent of the basilar membrane on the medial side may be enclosed by connections between the two portions of the limbus (figs. 6 [insert], and 7). Shute and Bellairs (1953) refer to the enclosed area as a limbic recess and the perilymphatic space, a perilymphatic diverticulum. Hamilton (1964) terms the recess, a *furrow*, and that portion of the perilymphatic sac or tympanic scala that extends into this space, an *accessory scala*. For the present, I prefer to use the terminology of Shute and Bellairs (1953).

The posteroinferior part of the limbus is not as much modified as the neural limb (figs. 5, 7, and 8). Because of its approximately triangular shape in cross section it is called the triangular limbus. It should be understood that the limbus is one complete structure varying in shape from a saucer-like plate to an elongated ovoid, and has in its central portion an opening or hiatus across which is stretched the basilar membrane.

Supported on the lateral aspect of the basilar membrane is a thin bar of connective tissue identical in structure to the limbic connective tissue, which in turn supports the papilla basilaris (fig. 7). The limbic hiatus and papilla basilaris vary in size and shape from small circular or ovoid to large elongate structures.

The papilla basilaris may be a simple continuous strip of cells, or may be

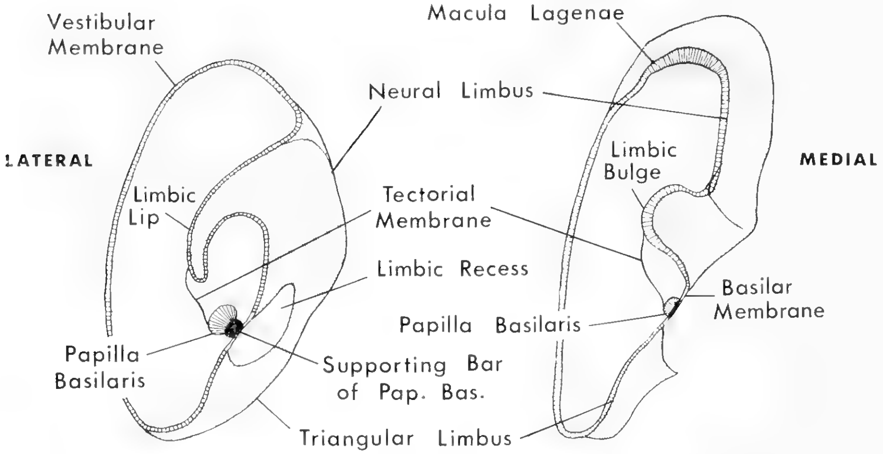


FIG. 7 – Hemidactylus (gekkonid) **FIG. 8 – Sauromalus (iguanid)**

Cross sections of cochlear ducts

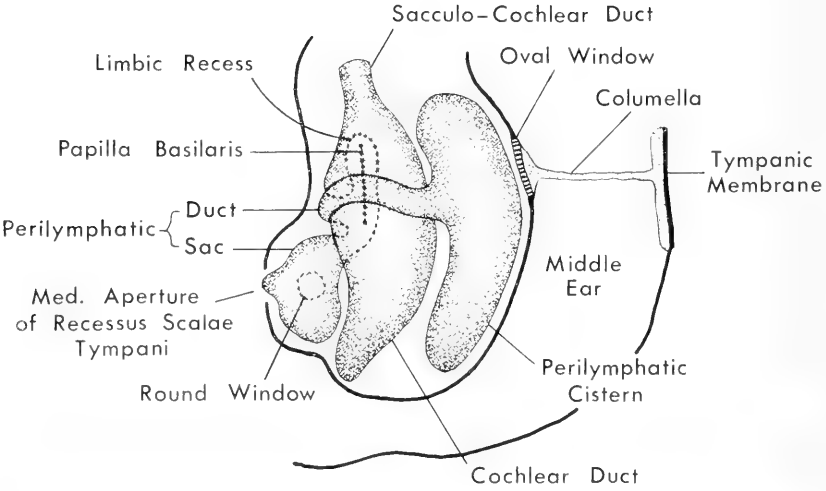


FIG. 9 – Diagrammatic anterior view of left cochlear duct & related structures

FIGURE 7. Cochlear duct, cross section, *Hemidactylus*.

FIGURE 8. Cochlear duct, cross section, *Sauromalus*.

FIGURE 9. Relation of perilymphatic spaces to the cochlear duct.

divided by a limbic connective tissue bar. The papilla may also be evenly contoured, or one end may be widened producing a fusiform-shaped structure.

That portion of the cochlear duct housing the limbus, basilar membrane, and papilla basilaris was termed the *pars basilaris* by Retzius (1884). Since the basilar membrane is only a limited portion of this part of the cochlear duct, I refer to this as the limbic rather than basilar portion of the duct.

The anterosuperior part of the cochlear duct is supported along its anterior edge by the same type of modified connective tissue that makes up the limbus (figs. 5, 6, and 8). This heavy supporting tissue may extend also onto the anterolateral and anteromedial portions of the duct. On the inner luminal surface of this portion of the cochlear duct is a strip of sensory epithelium covered by an otolithic membrane, the macula lagenae. The size and shape of the macula lagenae differs from one lizard family to another. The portion of the cochlear duct housing the macula lagenae may be designated the lagena or lagenar portion of the duct. Reference to figures 5 and 6 and the plates will make it clear, however, that in most lizards, the lagenar and limbic-containing portions of the cochlear duct form a united structure. Thus, while the location of the papilla basilaris and the macula lagenae is definite, there is not a clear-cut distinction between the lagenar and limbic portions of the duct.

B. General Anatomical Characteristics of the Cochlear Duct of Certain Reptilian Orders and Suborders.

1. Order **Rhynchocephalia** (Tuatara) (plate XXI). A striking feature of the cochlear duct of *Sphenodon* is the incomplete fusion between the lagenar and limbic portions of the duct. The duct appears to be made up of two partly joined sacs instead of one completely united structure. There is no specialization of the lateral face of the neural limbus but the medial side is deeply excavated, which imparts a ring or tubular shape to the limbus. The basilar membrane is stretched across the lateral end of the tube-like limbus. Thus, the tubular aspect of the *Sphenodon* limbus is reminiscent of the type of limbus found in amphibians. From this standpoint, the limbus of the *Sphenodon* is more like the amphibian that that of any other reptilian type.

A major difference, however, between the amphibian and *Sphenodon* limbus is the absence in the former of a basilar membrane, and the fact that the papilla basilaris of the amphibian rests on a portion of the limbic wall. The development of a basilar membrane is necessary for direct apposition of the scala tympani to the basilar membrane and appears first in reptiles.

The papilla basilaris seems to be an elongate strip (because of the thickness of the bone of the head, the papilla basilaris was not as perfectly preserved as might be desired). The papilla basilaris is 1.2 mm. and the macula lagenae approximately 2 mm. long (table 2).

TABLE 2. *Snout–vent, cochlear duct, and papilla basilaris length and area in different families of lizards.*

	Snout–Vent (length in mm.)	Cochlear duct (length in mm.)	Papilla basilaris (length in mm.)	Papilla basilaris (area in mm.²)
IGUANIDAE				
Anolis biporcatus	62	1.4	0.60	0.029
Anolis carolinensis	58	1.2	0.45	0.033
Liolaemus pictus	62	1.1	0.30	0.015
Phrynosoma douglassi	78	1.5	0.30	0.017
Tropidurus hispidus	99	1.2	0.35	0.030
Uma scoparia	99	1.0	0.25	0.013
Sauromalus obesus	95	1.8	0.30	0.030
Sceloporus magister	90	1.4	0.35	0.018
Holbrookia texana	65	1.1	0.25	0.011
Iguana iguana	150	2.7	0.60	0.031
AGAMIDAE				
Agama persica	63	1.1	0.30	0.014
Amphibolurus barbatus	140	1.5	0.40	0.026
Calotes versicolor	80	1.2	0.40	0.023
Chlamydosaurus kingi	160	2.2	0.60	0.029
Draco rizali	86	1.4	0.40	0.020
Gonyocephalus grandis	95	1.5	0.60	0.031
Hydrosaurus pustulosus	90	2.4	0.70	0.036
Japalura polygonata	50	1.1	0.30	0.019
Uromastix loricatus	108	2.0	0.25	0.013
CHAMAELEONIDAE				
Brookesia superciliaris	50	1.0	0.15	0.009
Chamaeleo bitaeniatus	72	1.4	0.15	0.011
Chamaeleo brevicornis	80	1.6	0.15	0.013
Chamaeleo diplepis	100	1.6	0.15	0.011
ANGUIDAE				
Anguis fragilis	150	1.2	0.2	0.013
Gerrhonotus multicarinatus	128	1.4	0.4	0.027
Diploglossus lessonae	115	1.8	0.5	0.029
Ophisaurus ventralis	290	1.4	0.3	0.020
Gerrhonotus coeruleus	150	1.2	0.4	0.013
ANNIELLIDAE				
Anniella pulchra	140	1.2	0.2	0.018
XENOSAURIDAE				
Xenosaurus grandis	120	1.9	0.15	0.012
HELODERMATIDAE				
Heloderma suspectum	170	2.4	0.8	0.035
VARANIDAE				
Varanus nuchalis	165	4.0	2.3	0.176
Varanus punctatus	90	1.3	1.0	0.091
Varanus salvator	150	3.6	2.4	0.190
Varanus salvator	120	3.5	2.2	0.138
LACERTIDAE				
Acanthodactylus cantoris	67	1.4	0.40	0.014

Table 2. Continued.

	Snout-Vent (length in mm.)	Cochlear duct (length in mm.)	Papilla basilaris	
			(length in mm.)	(area in $mm.^2$)
Eremias argus	55	1.4	0.50	0.022
Lacerta viridis	95	1.5	0.60	0.030
Lacerta vivipara	61	1.0	0.36	0.017
Psammodromus algirus	70	1.5	0.60	0.023
TEIIDAE				
Anadia bogotensis	58	1.0	0.4	0.014
Ameiva ameiva	150	2.4	1.1	
Bachia peruana	70	1.1	0.55	0.022
Dicrodon lentiginosus	53	2.0	0.90	0.046
Cnemidophorus tigris	90	1.9	0.80	0.048
Kentropyx calcaratus	100	1.9	0.90	0.051
Tupinambis teguixin	140	3.4	1.4	0.125
GEKKOTA				
a. EUBLEPHARIDAE				
Coleonyx species	60	1.2	0.8	0.057
Eublepharus species	90	2.6	1.7	0.115
b. SPHAERODACTYLIDAE				
Gonatodes fuscus	40	1.2	0.7	0.072
Sphaerodactylus argus	32	1.2	0.7	0.043
Sphaerodactylus cinereus	34	1.1	0.7	0.052
c. GEKKONIDAE				
Aristelliger nelsoni	79	2.1	1.2	0.091
Bavayia sauvagii	60	1.8	1.4	0.109
Cosymbotus platyurus	57	1.7	0.9	0.068
Gecko japonica	50	1.7	1.0	0.080
Gehyra multilata	45	1.7	1.1	0.075
Hemidactylus turcicus	55	1.5	0.9	0.046
Microgecko helenae	27	0.9	0.6	0.031
Phyllodactylus bauri	33	1.5	0.9	0.060
Phyllurus cornutus	135	3.8	1.6	0.120
Teratoscincus scincus	90	2.0	1.4	0.084
Gecko gecko	100	3.5	2.0	0.150
PYGOPODIDAE				
Aprasia pulchella	115	0.4	0.25	–
Lialis burtonis	175	2.0	1.4	0.091
Pygopus lepidopodus	150	2.1	1.4	0.103
SCINCIDAE				
Ablepharus lineocellatus	50	1.2	0.75	0.041
Aulacoplax leptosoma	40	1.2	0.8	0.038
Acontias meleagris	110	1.1	0.6	0.053
Brachymeles gracilis	68	1.6	1.0	0.051
Eumeces fasciatus	62	1.5	1.0	0.052
Liolopisma assatum	50	1.4	1.05	0.053
Lygosoma verrauxi	115	1.3	0.7	0.047
Mabuya multifasciata	115	2.0	1.8	0.125
Mabuya multicarinata	80	2.0	1.4	0.077
Nessia monodactyla	80	0.9	0.6	0.040

Table 2. Continued.

			Papilla basilaris	
	Snout–Vent (length in mm.)	Cochlear duct (length in mm.)	(length in mm.)	(area in mm.^{2})
Sphenomorphus quoyi	75	2.1	1.5	0.118
Tiliqua scincoides	90	2.8	1.9	0.162
Typhlosaurus cregoi	153	1.0	0.6	0.042
Feyliniidae				
Feylinia currori	115	1.2	0.7	0.046
Xantusiidae				
Klauberina riversiana	64	1.9	1.1	0.074
Lepidophyma flavomaculatum	80	1.8	1.2	0.096
Xantusia vigilis	40	1.3	0.7	0.047
Xantusia henshawi	55	1.6	0.9	0.062
Cordylidae				
Cordylus jonesii	60	2.2	1.2	0.064
Cordylus polyzonus	60	2.0	1.1	0.080
Cordylus cordylus	60	2.1	1.2	0.096
Gerrhosaurus flavigularis	160	2.4	1.3	0.108
Dibamidae				
Dibamus argenteus	136	0.8	0.15	0.020
Amphisbaenidae				
Amphisbaena fuliginosa	280	1.8	0.2	0.029
Bipes biporus	180	1.4	0.1	0.008
Blanus cinereus	112	0.5	0.1	–
Diplometopon zarudnyi	130	1.4	0.18	0.010
Rhineura floridana	230	0.9	0.25	0.024
Order CHELONIA				
Testudiniidae				
Gopherus berlandieri	150	2.5	0.6	0.073
Suborder OPHIDIA				
Colubridae				
Pituophis catenifer	600	1.5	0.35	0.016
Order CROCODILIA				
Alligator mississippiensis	200 (immature)		4.7	1.32

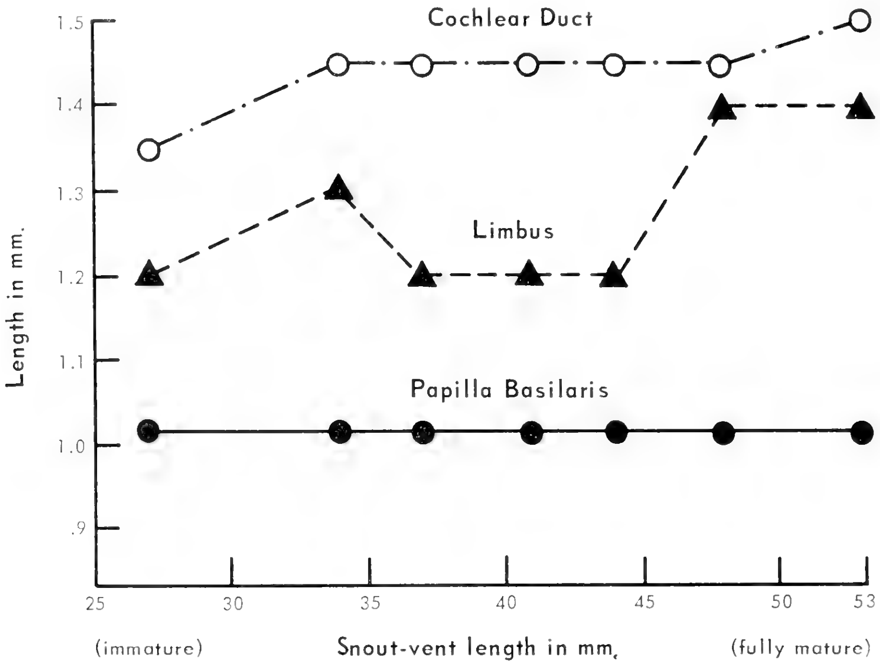
The medial wall of the duct is deeply excavated for reception of the perilymphatic sac and two triangular arms almost close over the perilymphatic duct on the anterosuperior part of the limbus.

2. Order **Chelonia** (turtles and tortoises) (plate XX). While representatives of only four turtle families have been seen (Kinosternidae, Emydidae, Trionychidae, and Testudinidae), the cochlear duct of these types is characterized by fusion of a portion of the saccular wall to the anterolateral aspect of the cochlear duct, a relatively small lagenar sac, lack of limbic specialization, and an ovate papilla basilaris of moderate size (table 2).

3. Order **Serpentes** (snakes) (plate XIX). Representatives of nearly all snake families have been seen. Observations to date indicate some but not outstanding, familial diversity in the cochlear duct of snakes.

Table 3. *Variations in the length and width and length/width ratio of the cochlear duct and limbus and variations in the length of the papilla basilaris.*

			COCHLEAR DUCT			LIMBUS			PAPILLA BASILARIS	
FAMILY	NO. GEN-ERA	NO. SPE-CIES	Length (mm.)	Width (mm.)	(W/L) × 100 (average)	Length (mm.)	Width (mm.)	(W/L × 100) (average)	Length (mm.)	Length in 60–70 mm. specimens
I Iguanidae	28	49	0.9–2.7	0.7– 1.8	54–100(77)	0.6– 1.4	0.4– 1.0	57–100(73)	0.2– 0.75	0.4
II Agamidae	12	17	0.9–2.4	0.8– 1.7	70–114(90)	0.6– 1.7	0.5– 1.3	67–100(81)	0.2– 0.75	0.3
III Chamaeleonidae	2	4	1.0–1.6	0.8– 1.4	57–87 (77)	0.6– 0.75	0.45–0.75	60–100(90)	0.15	0.15
IV Anguidae	4	5	1.2–1.8	0.8– 1.4	67–86 (79)	0.6– 1.1	0.5– 0.7	64–84 (72)	0.2– 0.5	0.4
V Anniellidae	1	1	1.2	1.0	83	0.9	0.7	77	0.2	–
VI Xenosauridae	1	1	1.9	1.8	95	1.0	0.8	80	0.15	–
VII Helodermatidae	1	1	2.4	1.8	75	1.6	1.3	81	0.8	–
VIII Varanidae	1	3	1.3–4.0	0.8– 2.0	50–62 (54)	1.15–3.2	0.7– 1.6	48–61 (53)	1.0– 2.3	–
IX Lacertidae	5	9	1.0–1.5	0.75–1.2	71–83 (79)	0.7– 1.0	0.4– 0.6	50–71 (58)	0.37–0.6	0.4
X Teiidae	10	17	0.9–3.4	0.6– 1.7	50–80 (61)	0.8– 2.2	0.4– 0.8	37–56 (46)	0.4– 1.4	0.75
Gekkonidae XI Gekkota–Eublepharidae Sphaerodactylidae	23	34	0.9–3.8	0.6– 2.3	47–75 (64)	0.9– 2.2	0.35–1.4	37–67 (51)	0.6– 1.7	1.0
XII Pygopodidae	3	3	0.4–2.1	0.4– 1.6	70–100(82)	0.35–1.8	0.35–0.8	44–100(63)	0.25–1.6	–
XIII Scincidae	24	42	0.8–3.8	0.5– 2.6	46–82 (64)	0.7– 3.2	0.3– 1.8	40–77 (57)	0.6– 2.2	1.0
XIV Feyliniidae	1	1	1.2	0.9	75	1.0	0.6	60	0.7	–
XV Xantusiidae	3	4	1.3–1.9	0.6– 1.1	46–61 (51)	1.1– 1.7	0.5– 1.0	43–59 (49)	0.7– 1.2	1.0
XVI Cordylidae	2	4	2.0–2.4	1.0– 1.4	60–64 (62)	1.6– 2.0	1.0	50–63 (60)	1.1– 1.4	1.15
XVII Dibamidae	1	1	0.8	0.5	63	0.6	0.4	75	0.15	–
XVIII Amphisbaenidae	5	5	0.5–1.8	0.4– 0.95	43–80 (64)	0.3– 0.6	0.3– 0.6	83–100(96)	0.1– 0.3	–
XIX Shinosauridae	Not seen									
XX Anelytropsidae	Not seen									
XXI Lanthanotidae	Not seen									

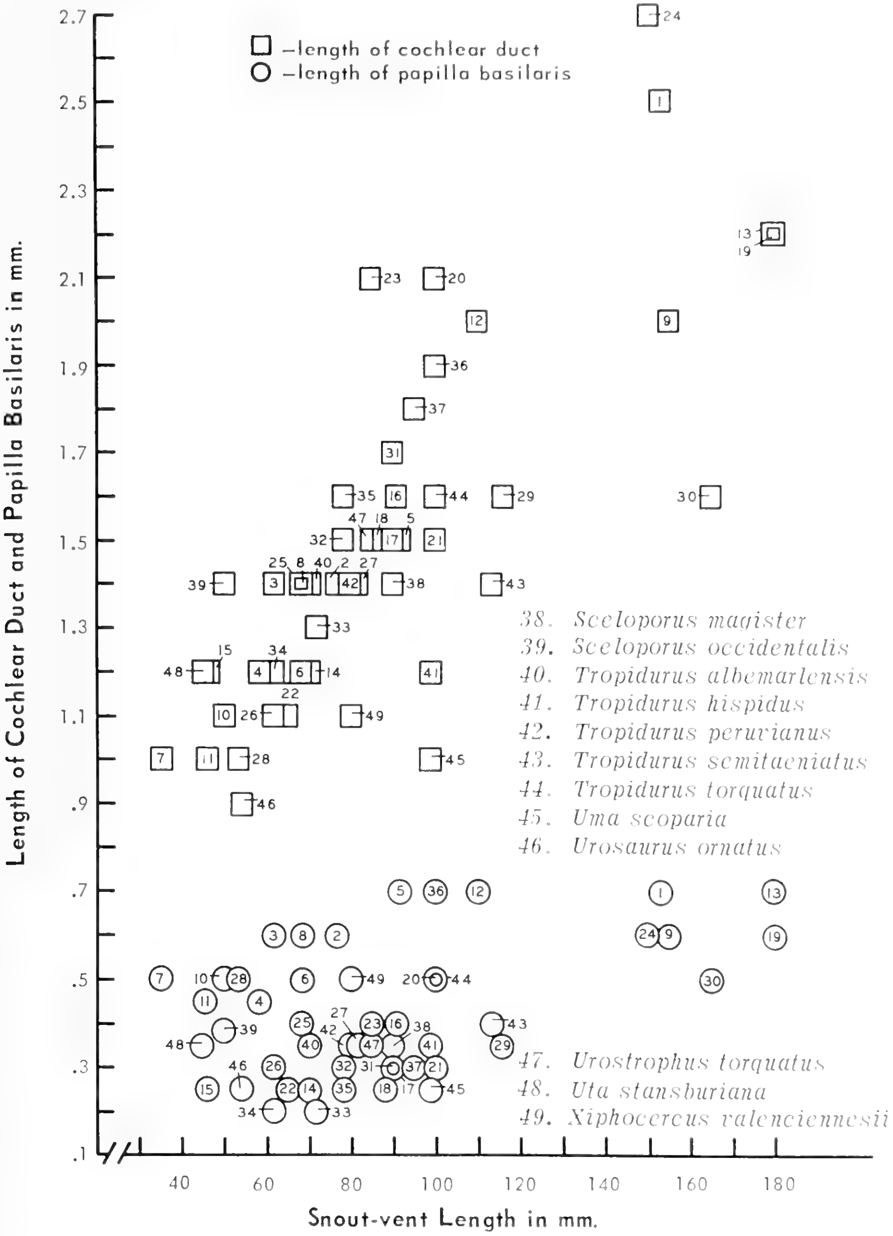


Graph 1. Changes in the length of the cochlear duct, limbus, and papilla basilaris during growth of the scincid lizard, *Leiolopisma assatum*.

→

1. *Amblyrhynchus cristatus*
2. *Anolis antiquae*
3. *Anolis biporcatus*
4. *Anolis carolinensis*
5. *Anolis copei*
6. *Anolis cristatellus*
7. *Anolis cupreus*
8. *Anolis distichus*
9. *Anolis equestris*
10. *Anolis polylepis*
11. *Anolis sallaei*
12. *Basiliscus vittatus*
13. *Brachylophus fasciatus*
14. *Callisaurus draconoides*
15. *Chalarodon madagascariensis*
16. *Corythophanes hernandezii*
17. *Crotaphytus collaris*
18. *Crotaphytus wislizeni*
19. *Ctenosaura pectinata*
20. *Ctenosaura similis*
21. *Dipsosaurus dorsalis*
22. *Holbrookia texana*
23. *Hoplocercus spinosus*
24. *Iguana iguana*
25. *Leiocephalus carinatus*
26. *Liolaemus pictus*
27. *Mariguana agassizi*
28. *Norops auratus*
29. *Oplurus cuvieri*
30. *Petrosaurus thalassina*
31. *Phrynosoma coronatum*
32. *Phrynosoma douglassi*
33. *Phrynosoma m'calli*
34. *Phrynosoma modestum*
35. *Phrynosoma platyrhinos*
36. *Plica plica*
37. *Sauromalus obesus*

Graph 2. Relation between the snout-vent length and cochlear duct and papilla basilaris length in the Iguanidae.



Graph 2. Relation between the snout–vent length and cochlear duct and papilla basilaris length in the Iguanidae.

Like *Sphenodon*, the snake cochlear duct shows incomplete fusion between the lagenar and limbic portions. Whereas in *Sphenodon*, turtles, and most lizards, the limbic portion of the cochlear duct is larger than the lagenar, in snakes, the lagenar sac is considerably larger than the limbic area. There is no marked modification of the lateral wall of the neural limbus, and the medial limbic wall shows no extensive recesses. The papilla basilaris is ovoid to slightly elongate and small in its dimensions (table 2).

4. Order **Sauria** (lizards). In this order I have seen the cochlear ducts of approximately 39 per cent of the living genera (131 of approximately 334 genera), representing 18 families. The most striking feature of the lizard cochlear duct is that it is anatomically distinct for each family and shows considerable modifications of its constituent elements.

General anatomical characteristics of the lacertilian cochlear duct are: (a) usually complete fusion between the lagenar and limbic portions; (b) a limbic portion usually equal to or larger than the lagenar; (c) modification of the neural limbus; (d) a papilla basilaris varying markedly in length and shape; (e) a basilar membrane variously open or closed by the limbus on the medial aspect; and (f) except for the skinks, no marked tendency for bending or coiling of the duct.

5. Order **Crocodilia**. I have seen the cochlear duct of *Alligator mississippiensis*. The duct is considerably elongated and has a half turn or twist. The lagenar area is reduced to a small dilation at the inferior tip of the duct. The papilla basilaris is at least twice as long and its surface area is much greater than that of other reptiles (table 2). There are other modifications of the perilymphatic cistern, duct, and sac but these will not be described in this paper.

C. Anatomical Characteristics of the Cochlear Duct of Lacertilian Families.

The families of lizards are arranged according to my present concept of an increasing degree of complexity of the cochlear duct, except that I treat the dibamids and amphisbaenids last as their relationships are not clear at this time.

1. **Iguanidae** (plate I; graph 2). While the iguanids and agamids show many cochlear duct features in common, nevertheless they each possess distinctive cochlear features. I believe that the duct types found in the members of these two families are generalized or relatively unspecialized.

Features of the iguanid cochlear duct:

a. The cochlear duct is pyramidal in shape, the base broad, and the inferior tip usually pointed, although occasionally rounded. Medial bending of the inferior tip is not marked, but may be prominent in some species. The duct is not as square as is that of the agamid, and not as elongate as that of many other families (see length–width ratios in table 3). The length of the cochlear duct varies directly with the snout–vent length of the species (graph 2).

b. The macula lagenae is large, begins high anterosuperiorly, and runs down the anterior surface of the duct, and at its inferior extremity curves medially. The macula lagenae is two to three times the length of the papilla basilaris.

c. The limbus is ovoid to moderately elongate. Elongation is more marked in the anolids. The neural limbus has a moderate bulge on its lateral face that is bar- or rolling-pin-like in appearance. In the tropidurid iguanids, the neural bar is more undercut than in other iguanids, a feature similar to the agamid lateral neural limbus.

d. In most species, the anterior edge of the duct has only a shallow groove for the perilymphatic duct, while in large species with large ducts, the perilymphatic duct groove is deepened.

e. The medial aspect of the basilar membrane is almost entirely open, but in some species short shallow limbic recesses are present both superiorly and inferiorly. The medial limbic flanges housing the auditory nerve and perilymphatic duct are not prominent.

f. The papilla basilaris is relatively short but increases in length and area in the anolids (table 2 and graph 2). There is not as close a correlation between species size and papilla basilaris length as there is in some other lizard families (compare graphs 2 to 8). The length of the papilla basilaris therefore is probably associated with specific differences other than that of size.

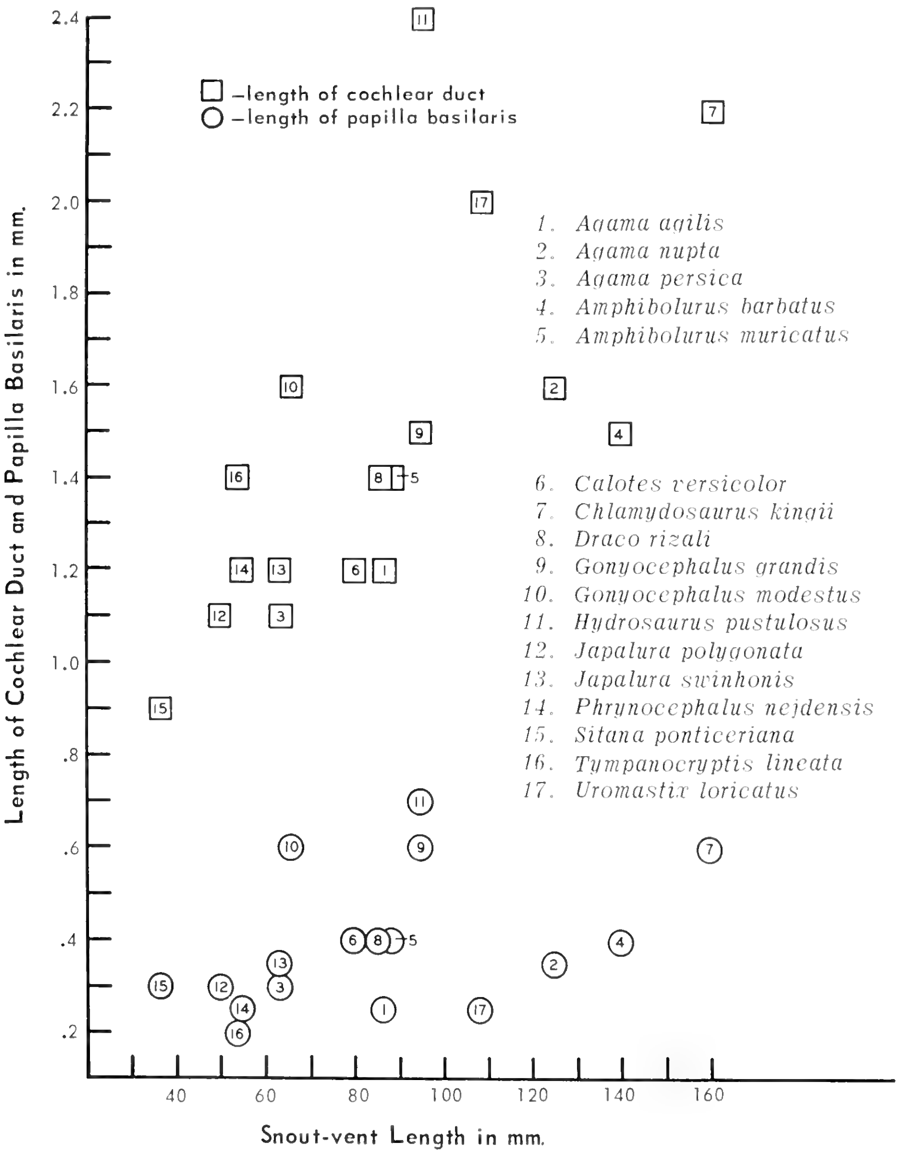
While a detailed analysis of generic differences will be reported in a later paper, a few general observations are noted here. Compared with other iguanids, the limbus and papilla basilaris is longer in anolids; the cochlear duct is more pointed and elongated, and the neural limbic bar better developed in the tropidurids and in *Plica plica*; the neural limbic bar is more prominent in *Sauromalus obesus*; and the limbus and papilla basilaris are relatively short and small in the "earless" lizard, *Holbrookia texana*.

2. **Agamidae** (plate II; graph 3).

a. The cochlear duct is nearly as broad as long and is shaped like a right triangle with the right angle at the posterosuperior corner. The inferior tip is rounded and blunt. There is some correlation between cochlear duct and papilla basilaris length and species size, but there is not as close a correlation as is found among genera in other families.

b. The lagena is relatively large and the macula lagenae two to three times the length of the papilla basilaris.

c. The lateral side of the neural limbus is thickened giving rise to a prominent bar which is more pronounced than the type found in the iguanids, but not as marked as that of the anguids, lacertids, or teiids. The triangular limbus is flared posterosuperiorly.



GRAPH 3. Relation between the snout-vent length and cochlear duct and papilla basilaris length in the Agamidae.

d. The groove for the perilymphatic duct varies from shallow to deep, being deeper in large species with larger and more stoutly constructed ducts.

e. The medial face of the basilar membrane is mostly unenclosed, but there are short superior and inferior limbic recesses. The medial limbic flanges are not prominent.

f. The papilla basilaris is relatively short, either elongate or fusiform, and the enlarged end superior in location. The papilla varies from 0.2 mm. to 0.4 mm. in length; there is some tendency for it to be longer and greater in surface area in larger species (graph 3 and table 2).

While the number of agamid genera so far studied is not large, there is a tendency for the shape of the lagena to vary from genus to genus; in *Sitana ponticeriana*, the lagena is reduced in size, in *Tympanocryptis lineata*, the anterior edge of the cochlear duct, instead of being curved, is straight and set at an angle of 45 degrees to the papilla basilaris. And while a blunt or rounded inferior tip is an agamid characteristic, in *Agama persica* (but not *Agama agilis* or *Agama nupta*), the tip is pointed.

3. **Chamaeleonidae** (plate III).

a. The cochlear duct is characteristically triangular, the length approximately 25 per cent greater than the width. The lagenar and limbic portions form a single unit showing no tendency to separation.

b. The macula lagenae is moderate in size.

c. The limbus is thin and saucer-like in shape. The lateral side of the neural limbus shows only the slightest elevation. The limbic hiatus is relatively large and is circular in outline.

d. The groove for the perilymphatic duct is definite but shallow.

e. The medial aspect of the basilar membrane is open.

f. The papilla basilaris is small and circular to slightly ovoid in shape. There is no indication of variation in papilla size with species size (table 2). An insufficient number of species have been studied to know if there are intrafamilial differences.

4. **Anguidae** (plate IV).

a. The cochlear duct is moderately elongate.

b. The lagenar part of the cochlear is moderate in size and the macular length about twice that of the papilla basilaris.

c. The limbus is ovoid and the central hiatus of good size. The lateral side of the neural limbus shows a prominent projection which is longer than the papilla. The neural limbic projection is much more prominent than that found in the iguanids or agamids, but not quite as well developed nor as shelf-like as that of the lacertids. Because of the development of very elongate body types in the anguids, it is difficult to correlate species size with cochlear duct dimensions.

d. The medial side of the limbus has two quite prominent flanges which partially house the perilymphatic duct. This feature is best developed in the gerrhonotids.

e. The medial face of the basilar membrane is mostly open, but there are short inferior and superior limbic recesses.

f. The papilla basilaris is elongate and modest in its dimensions. In most species there is a small area at the inferior extremity of the papilla that apparently lacks hair cells. In both *Ophisaurus ventralis* and *Anguis fragilis*, the total length of the cochlear duct as well as the length of the macula lagenae and the length and area of the papilla basilaris are relatively small (table 2). This is probably the result of regression or degeneration.

5. **Anniellidae** (plate V).

a. The cochlear duct is somewhat square in shape.

b. The lagenar area is reduced in relation to the limbic portion, and it is probable that the cochlear duct has been shortened largely by a decrease in the dimensions of the lagenar area.

c. The limbus is thin, concave, and eccentrically ovoid. The limbic hiatus is quite large which may be characteristic of either a primitive or a reduced condition. A small bar-like limbic lip forms the anterior edge of the neural limbus. The relative distance of the lip from the papilla basilaris gives the appearance that the neural lip has been displaced in position.

d. The groove for the perilymphatic duct on the medial side of the cochlear duct is narrow and shallow.

e. The medial aspect of the basilar membrane is small and entirely open.

f. The papilla basilaris is ovoid and small (table 2).

6. **Xenosauridae** (plate VI).

a. The cochlear duct appears tall because of the relatively large area above (anatomically dorsal to) the limbus proper. Measurements of the cochlear duct show it to be approximately equal in length and width.

b. The lagenar area is mildly constricted from the limbic portion, a possible result of degeneration of the limbus in this family. The macula lagenae is of moderate size and extent.

c. The limbus is relatively small and almost flat on its lateral face except that there is a moderate elevation at the anterior border adjacent to the lagenar portion. There is no apparent modification of the neural limbus.

d. The groove for the perilymphatic duct is quite deep both anterosuperiorly and on the medial surface of the duct.

e. The medial face of the basilar membrane is open.

f. The papilla basilaris is very small (table 2).

7. **Helodermatidae** (plate VII).

a. The cochlear duct is triangular, and the limbic portion quite large.

b. The lagenar area is less than the limbic, but the macula lagenae is of moderate proportions.

c. The limbus is quite thick. The neural limbus presents a rounded prominence that is more massive than the iguanid lip, and different from the anguid in not being sharply undercut just above the basilar membrane.

d. and e. The groove for the perilymphatic duct and sac is large and shallow and the medial aspect of the basilar membrane mostly open. A short limbic recess is present at the superior end of the basilar membrane.

f. The papilla basilaris is probably elongate (my specimen was not perfectly preserved); it is longer than that found in either the anguid or iguanid lizards (table 2). The nerve supplying the papilla basilaris is bifid, but the papilla does not appear to be divided into two segments.

8. **Varanidae** (plate VIII).

a. The cochlear duct is large and elongated (approximately twice as long as wide); the greater length is due to the large, heavily constructed limbus.

b. The pars lagena is of moderate proportions and the macula lagenae a wide strip covering the anterolateral, anterior, and anteromedial aspect of the lagena.

c. The limbus appears massive and may have a small narrow central bridge dividing the limbic hiatus into two unequal portions. The superior end of the divided hiatus is about twice the length of the inferior portion. In specimens with an undivided hiatus, there is a narrowing of the hiatus in the same area where it is divided in others. Two of my four specimens have a divided hiatus and papilla, and two do not. The lateral face of the neural limbus does not show a definite projection, but is thickened in its midportion above each part of the divided limbic hiatus.

d. The groove for the perilymphatic duct is quite deep.

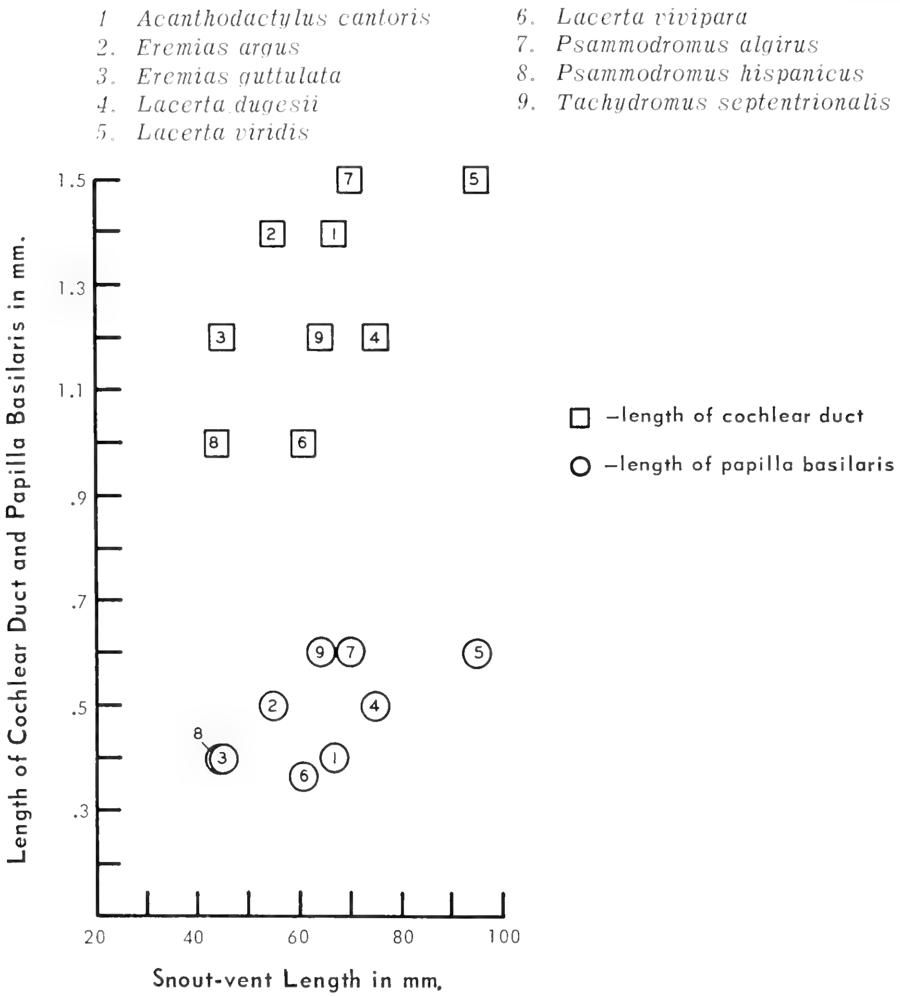
e. The medial face of the basilar membrane is about two-thirds open; a superior limbic recess covers the upper half of the superior portion of the membrane, and a shorter inferior recess covers only 5 to 10 per cent of the inferior part.

f. The papilla basilaris is elongate and may be divided into two unequal portions; the superior part is about twice the length of the inferior. The papilla may or may not be divided. The length of both the cochlear duct and the papilla basilaris is directly related to the size of the species (table 2).

9. **Lacertidae** (plate IX).

a. The cochlear duct is characteristically triangular and the limbic portion markedly posterior (caudal) as well as superior in position.

b. The lagenar portion of the cochlear duct is relatively large and has a



GRAPH 4. Relation between the snout–vent length and cochlear duct and papilla basilaris length in the Lacertidae.

long superior–inferior axis and tends to extend more superiorly than it does in other families. The macula lagenae is correspondingly long, courses down the entire anterior border of the duct, and extends onto the inferior medial wall.

c. The limbus is ovoid–elongate and characterized by a medial bar or bridge dividing the limbic hiatus into two approximately equal halves. The neural lip is a prominent ridge more marked than that of the anguids, but not as well developed as that of the teiids (compare plates IV, IX, and X).

d. The groove for the perilymphatic duct is shallow.

e. The medial face of the basilar membrane is not enclosed and the excavation for the perilymphatic sac relatively deep. Very short superior and inferior limbic recesses are present.

f. The papilla basilaris is divided into two almost equal portions. Each part is slightly fusiform but elongate in shape. The papilla basilaris is both fairly short in length and small in area and seems to vary directly with species size (table 2 and graph 4). Among the lacertid genera studied, there are minor variations in the thickness and shape of the limbic lip, and the exact shape of the lagena.

10. **Teiidae** (plate X).

a. The cochlear duct is elongate. The posterosuperior curve of the limbus projects dorsally and more superiorly than the corresponding lagenar edge. The inferior tip of the duct is pointed and curves sharply in a medial direction. The teiid cochlear duct has expanded both superiorly and inferiorly; the teiids therefore, differ from the gekkonids, in which group the duct expands superiorly, and from the scincids where the duct expands inferiorly and medially.

b. The lagenar portion of the duct is large and well developed; it forms a robust anterior edge. The macula lagenae is always longer than the papilla basilaris.

c. The limbus is one of the most elongate found in the lizards, the length width ratio being 46 per cent (table 3). The limbic hiatus is long and narrow. The lateral face of the neural limbus has a rather heavy umbrella-like projection in the middle 50–60 per cent of its length. The neural limbic lip is considerably shorter and much less delicate and projecting than that of the Gekkota and pygopodids.

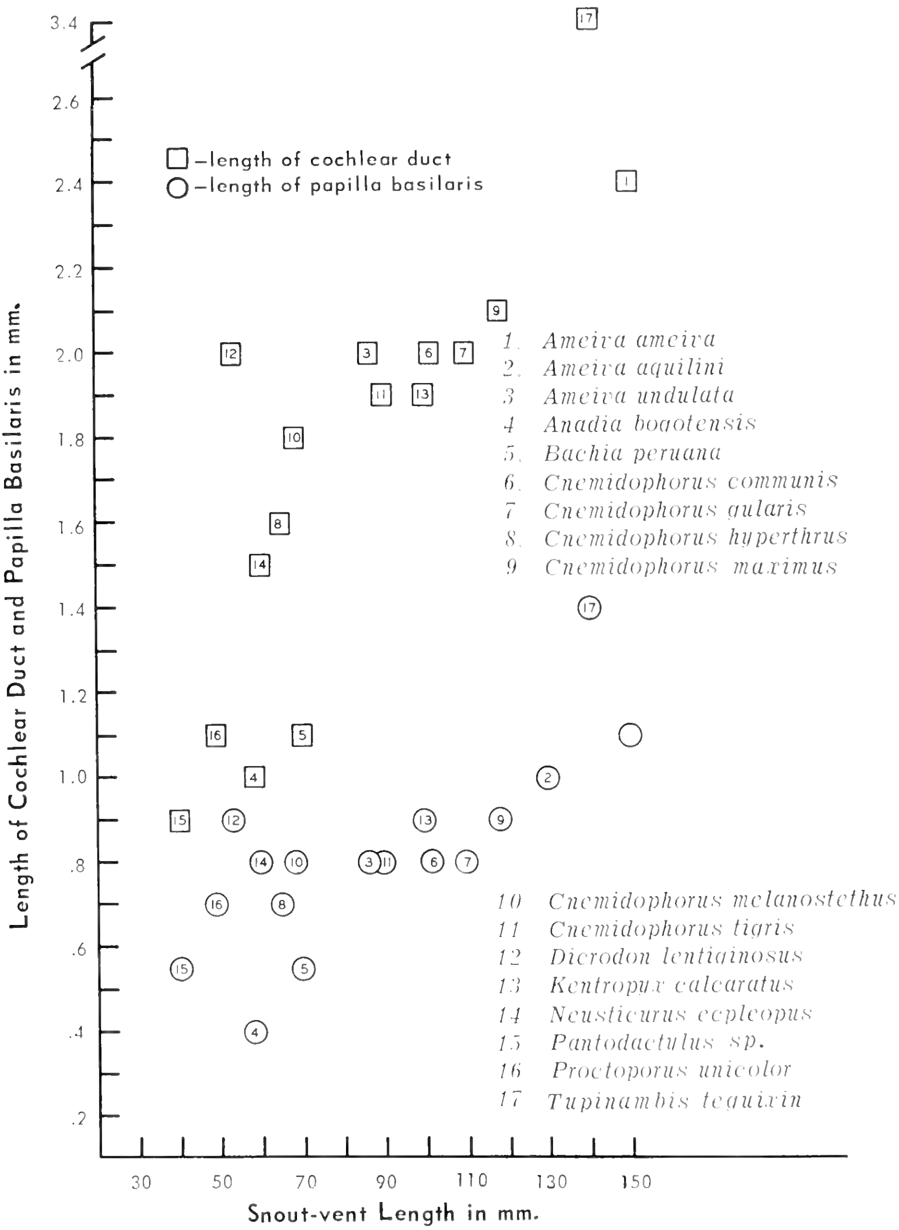
d. The groove for the perilymphatic duct is not well marked.

e. The medial face of the basilar membrane is not enclosed and receives a widely expanded perilymphatic sac.

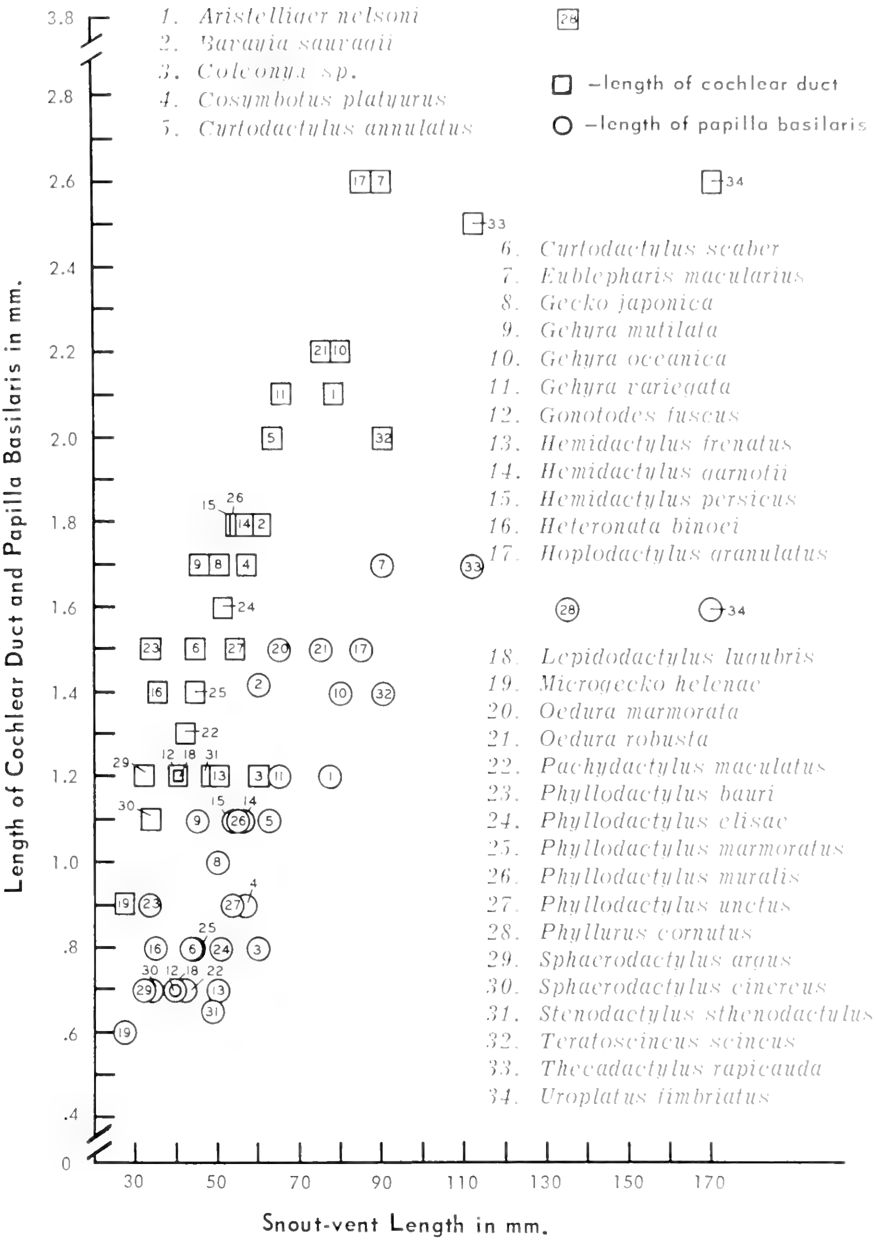
f. The papilla basilaris is moderately long and varies in length and area with the size of the species (table 2 and graph 5). The papilla is slightly expanded inferiorly, and narrowed superiorly. There is usually a break in the papilla basilaris toward the superior tip and the papilla is thus unequally divided with a very short superior portion barely separated from a much longer inferior strip. There is no limbic bridge, however. The tendency towards division of the papilla, together with the development of a thick umbrella-like limbic lip and an open medial basilar membrane are conditions very similar to that found in the lacertids.

Most teiids have robust cochlear ducts, but the microteiids (*Anadia*, *Bachia*, *Pantodactylus*, and *Proctoporus*) show considerable reduction in both the limbic and lagenar portions of the duct.

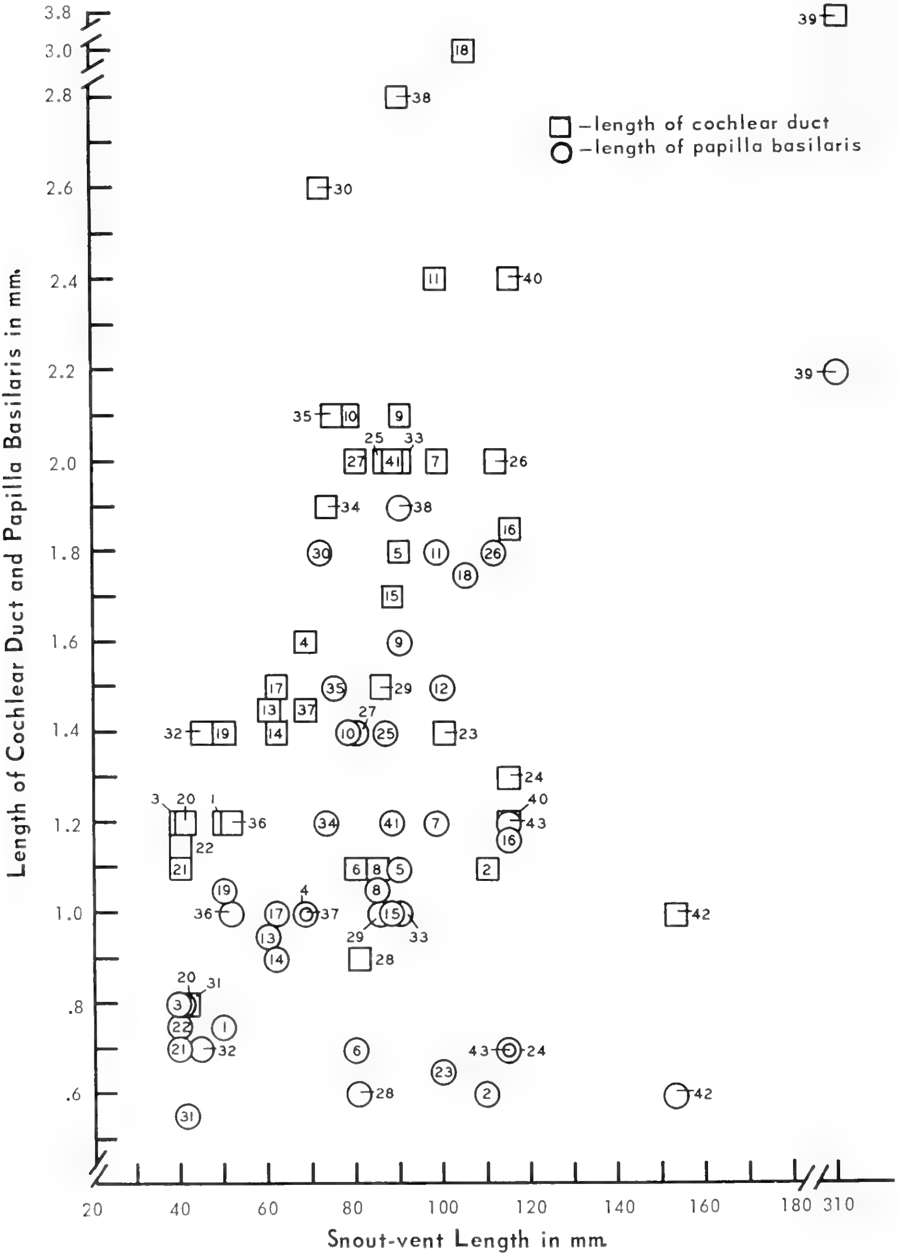
11. **Gekkota** (including **Gekkonidae, Eublepharidae, Sphaerodactylidae,** and **Uroplatidae**) (plate XI; graph 6).



Graph 5. Relation between the snout-vent length and cochlear duct and papilla basilaris length in the Teiidae.



Graph 6. Relation between the snout–vent length and cochlear duct and papilla basilaris length in the Gekkota.

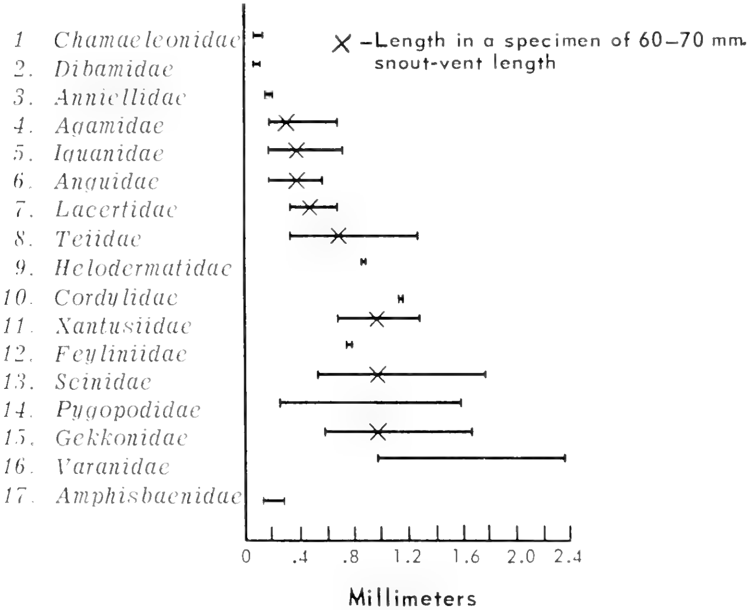


GRAPH 7. Relation between the snout–vent length and cochlear duct and papilla basilaris length in the Scincidae.

1 *Ablepharus lineocellatus*
2. *Acontias meleagris*
3. *Aulacoplax leptosoma*
4. *Brachymeles gracilis*
5. *Brachymeles schadenbergi*
6. *Brachymeles tridactylus*
7 *Chalcides polylepis*
8 *Chalcides sepoides*
9 *Dasia smaragdinum*
10 *Egernia nitida*
11. *Egernia striolata*
12. *Emoia nigra*
13 *Eumeces elegans*
14. *Eumeces stimpsonii*
15. *Eumeces gilberti*
16 *Eumeces obsoletus*
17. *Eumeces fasciatus*
18. *Hemisphaerodon gerrardi*
19. *Leiolopisma assatum*
20. *Leiolopisma guichinoti*
21. *Leiolopisma noctua*
22 *Lygosoma laterale*
23 *Lygosoma lentiginosus*
24 *Lygosoma verrauxi*
25 *Mabuya mabouia*
26 *Mabuya multifasciata*
27 *Mabuya multicarinata*
28 *Nessia monodactyla*
29 *Ophiomorus tridactylus*
30. *Otosaurus cumingi*
31 *Rhodona fragilis*
32 *Riopa bowringii*
33 *Scincus philbyi*
34 *Sphenomorphus indicus*
35 *Sphenomorphus quoyi*
36 *Sphenomorphus tenuis*
37 *Sphenomorphus variegatus*
38 *Tiliqua scincoides*
39 *Trachysaurus rugosus*
40 *Tribolonotus gracilis*
41 *Tropidophorus rivularis*
42 *Typhlosaurus cregoi*
43 *(Feyliniidae) Feylinia currori*

←

Graph 7. Relation between the snout–vent length and cochlear duct and papilla basilaris length in the Scincidae.



Graph 8. Range in length of the papilla basilaris in lizard families.

So far I have not studied a sufficient number of eublepharids and sphaerodactylids to state whether they differ significantly from the gekkonids in cochlear duct characteristics. For the present, I will discuss the Gekkota as a whole.

a. The cochlear duct is relatively large and heavy in appearance. The limbic portion has expanded in a posterosuperior direction and pushed into the saccular area. The pars lagena is also prominent and occupies the anteroinferior portion of the duct. The general form of the duct is elongate, and the inferior tip somewhat pointed.

b. The large macula lagenae lies at an angle of approximately 30 to 40 degrees to the papilla basilaris, whereas in the lacertid–teiid complex, the macula lagenae lies more nearly parallel to the papilla. The most notable difference between the basically similar gekkonids and pygopodids is that the macula lagenae and papilla basilaris are parallel to one another in the pygopodids. (Compare plates XI and XII.)

c. The limbus is large and ovoid–elongate (table 3) and its most outstanding feature is the extension from the neural limbus of a thin awning-like projection curving out over the papilla basilaris. This lateral neural limbic projection is much thinner and more delicate as well as relatively greater in extent than the teiid and lacertid limbic lips.

d. The anteroinferior edge of the cochlear duct is frequently deeply grooved by the perilymphatic duct.

e. Only the inferior third of the basilar membrane is open medially as a long limbic recess houses the superior two-thirds of the membrane.

f. The papilla basilaris is an elongate slightly fusiform structure. The thicker end lies inferiorly and there is no tendency for the papilla to be divided. The length and area of the papilla usually varies directly with the size of the species (table 2 and graph 6).

There is less variation in the cochlear duct of the Gekkota than in any other group of lizards. In fact, the constancy of anatomical detail is remarkable. Only in very small species such as *Heteronata binoei, Microgecko helenae*, and *Sphaerodactylus argus* is the size of the lagenar and limbic areas much reduced. The reduced size of the limbus and lagena in these small species results in a miniaturized and not a degenerate structure.

The cochlear duct of *Uroplatus fimbriatus* differs only in having a somewhat enlarged lagena.

12. **Pygopodidae** (plate XII).

a. The pygopodid cochlear duct is very similar to the gekkonid duct in that it is elongate, heavy, and superiorly expanded. It differs from the gekkonid duct in that the macula lagenae is more parallel to the papilla basilaris. Also, the inferior tip of the pygopodid duct is more rounded. An insufficient number of pygopodid species have been studied to determine cochlear duct and species size relationships.

b. While in the gekkonids, the macula lagenae is usually longer than the papilla basilaris, in the pygopodids, the macula lagenae is usually shorter.

c. The limbus is elongate, superiorly expanded, and the neural limbus bears a delicate awning-like expansion almost identical to that of the gekkonids.

d. The groove for the perilymphatic duct is of moderate depth.

e. As in the gekkonids, the inferior portion of the medial face of the basilar membrane is open and the superior three-quarters enclosed.

f. The papilla basilaris is very slightly fusiform and tapers towards the superior end. Although too few species were studied to be certain, it is probable that the length of the papilla basilaris varies with the size of the species (table 2). The cochlear duct, macula lagenae, and papilla basilaris are reduced in size (miniaturized) in *Aprasia pulchella*.

13. **Scincidae** (plate XIII).

a. The cochlear duct is relatively large and elongate. The limbic portion is relatively much larger than the lagenar. The limbus has expanded inferiorly rather than superiorly as it does in the gekkonids. The limbus also extends medially and is curved or bent in many species. The overall length of the cochlear duct is largely a function of species size (table 2).

b. While the pars lagena is reduced in size, the length of the macula lagenae is not greatly affected. The macula is almost equal in length to the papilla basilaris and is inclined at an angle of 30 to 40 degrees relative to the papilla.

c. The limbus is relatively thick and has an elongate hiatus. The lateral face of the neural limbus does not have a projection like that of many other lizards, but possesses a moderate ridgelike bulge. In agreement with Hamilton (1964) I have so far been unable to demonstrate without doubt the presence of a tectorial membrane in skinks. Overlying the inferior tip of the papilla basilaris is a thickening which is readily apparent on gross observation. On section, this thickened material has an unstructured appearance and stains basophilically; it might be that this is the remnant of the tectorial membrane that somehow was pulled away from its normal site of origin during development.

d. The groove for the perilymphatic duct varies from deep to shallow.

e. The perilymphatic duct sweeps anterosuperiorly over the medial side of the cochlear duct. The superior 40 per cent of the basilar membrane is open, and the inferior 60 per cent enclosed, housing a long limbic recess. The inferiorly directed limbic recess of the skinks is, thus, the opposite of the superiorly directed recess of the gekkonids. This is another reflection of the supposition that the scincid duct developed by inferior, and the gekkonid, by superior growth. Also related to the direction of duct growth is the reduction in size of the gekkonid sacculus as compared with the expansion of the scincid sacculus.

f. The papilla basilaris is as long as that of gekkonids, but in contrast to the gekkonids it does not always vary directly in length with the size of the species (table 2 and graph 7). The papilla is somewhat fusiform and tapers very gradually. While the superior end is wider, there is a very short fusiform expansion at the inferior tip. It is probably acoustically significant that while the scincid limbic recess is inferior in position and the gekkonid superior, it is the narrowest part of the papilla basilaris in both families that is enclosed by the limbic recess.

While still typically scincid in all characteristics, the cochlear duct of such forms (elongate skinks) as *Acontias meleagris, Brachymeles tridactylus, Brachymeles vermes, Nessia monodactyla, Ophiomorus tridactylus, Rhodona fragilis, Typhlosaurus cregoi,* and the lygosomids I have examined, show reduction of both the limbic and lagenar portions.

Even within genera such as in *Brachymeles* and *Lygosoma* there is variation from little or no reduction, to considerable reduction of both lagenar and limbic features. It appears that reduction or degeneration of the cochlear duct in skinks is found in those species that are anatomically modified for burrowing.

The cochlear duct, as well as many other anatomical characteristics, appear to be remarkably plastic in the scincid lizards.

14. **Feyliniidae** (plate XIV).

The feylinid cochlear duct is so similar in all details to the scincid duct that it may be included in that general group. In *Feylinia currori* the duct is scincid, but shows a small degree of reduction in size of all its various features (table 2).

15. **Xantusiidae** (plate XV).

a. The xantusiid cochlear duct is undoubtedly scincid in type, but differs sufficiently to clearly differentiate it from the Scincidae and Feyliniidae. The duct is generally more elongate, there is no tendency to bending, and the superior pole of the duct is more attenuated. The limbic area is greater than the lagenar, and the latter largely occupies the anteroinferior portion of the duct.

b. The macula lagenae is somewhat shorter than the papilla basilaris and a good portion of it is set at almost a right angle to the papilla basilaris. The duct length varies with species size.

c. The limbus is thickened and is similar to that of the scincid, but the hillock or swelling on the lateral neural limbic face is inclined at an angle to the papilla basilaris; the limbic swelling is closer to the papilla at the superior end than it is inferiorly. In other words, the neural limbic bulge inclines dorsally more rapidly than the papilla basilaris does.

d. The groove for the perilymphatic duct is moderate in depth and the opening for the perilymphatic sac on the medial face of the limbus is superior in position and relatively larger than that of the scincids.

e. The inferior 30 to 40 per cent of the basilar membrane is enclosed housing an inferior recess. The inferior limbic recess of scincids extends over nearly 60 per cent of the membrane length.

f. The papilla basilaris is elongate, slightly fusiform, and often has a small separate fusiform expansion at the inferior extremity. An inferior fusiform expansion is often observed in the scincids, but is never separated from the main papilla. Both the length and area of the papilla basilaris vary directly with species size (table 2). Except for size differences, the cochlear ducts of *Klauberina, Lepidophyma,* and *Xantusia* are very similar.

16. **Cordylidae** (plate XVI).

The cochlear ducts of *Gerrhosaurus* and *Cordylus* are nearly identical.

a. The cochlear duct is fairly elongate and both the lagenar and limbic portions are well developed.

b. The macula lagenae is approximately equal to the papilla basilaris in length, and, I would judge, is relatively less reduced than the scincid lagena.

c. The limbus is elongate and probably has expanded in an inferior direction, but not to the degree that occurred in scincid development. The neural limbus is thick (but not as anteriorly extended as the scincid) and has an incipient projection on its lateral face. Thus, the limbic "lip" is more pronounced than the scincid, but less developed than that of the anguid.

d. The groove for the perilymphatic duct is moderate in depth, and not as superiorly placed as the scincid.

e. As in the skinks and xantusiids, the perilymphatic duct approaches the medial limbic hiatus superiorly, but unlike these types that have long inferior limbic recesses, the medial aspect of the basilar membrane of the cordylids is open. Only short, inferior, and superior limbic recesses are present.

f. The papilla basilaris is long. The papilla gradually tapers from the superior to the inferior end and terminates in a fusiform swelling, but is not divided. The length, and to some degree the area, of the papilla basilaris varies directly with species size (table 2).

17. **Dibamidae** (plate XVII).

a. The cochlear duct of *Dibamus argenteus* is somewhat elongate. The anterosuperior surface of the duct appears to be fused to the inferior saccular wall. While a small constriction separates the lagenar and limbic portions of the duct, these areas are not as clearly separated as in the snakes and in *Sphenodon.* The limbic area is greater than the lagenar.

b. The pars lagena and the macula lagenae appear to be reduced in size and, in my opinion, were derived from a once larger and more extensive area. The macula lagenae is but a short strip at the blunt end of the cochlear duct.

c. The limbus is a thin circular plate with a relatively large centrally located ovoid hiatus.

d. and e. The perilymphatic duct occupies a shallow groove on the medial side of the duct and the medial face of the basilar membrane is mostly open. A short limbic recess is located at each end of the basilar membrane.

f. The papilla basilaris is small (table 2) and oval in shape.

18. **Amphisbaenidae** (plate XVIII).

a. The cochlear duct is somewhat elongate and only superfically divided by a slight constriction between the pars lagenae and the limbic portion. There is a tendency for increase in cochlear duct size with increase in species size, although this relationship is difficult to demonstrate in elongated animals (table 2). The cochlear duct of *Blanus* is much reduced.

b. The pars lagenae appears much reduced in size and is represented by the short, blunt inferior extremity of the cochlear duct. The macula lagenae is a short strip located at the blunt inferior extremity of the duct; its long axis is inclined nearly 90 degrees to the papilla basilaris.

c. The limbus is a thin, almost circular, concave plate with a moderate-sized, central, oval-shaped hiatus. The anterior edge of the neural limbus projects laterally forming an overhanging lip.

d. and e. The perilymphatic duct slightly grooves the medial aspect of the cochlear duct and opens into a largely unenclosed sac over the medial face of the basilar membrane. As in *Dibamus,* short inferior and superior limbic recesses are present.

f. The papilla basilaris is small and ovoid (table 2).

The cochlear ducts of *Amphisbaena fuliginosa, Bipes biporus,* and *Diplometopon zarudnyi* are fairly similar. *Rhinuera floridana* differs from those species in that the lagena is somewhat constricted from the limbic area, and the neural limbic lip, instead of being more anteriorly placed, is represented by a bar-like thickening of the entire neural limbus.

Graph 8 (p. 289) is a summary representation showing the range in length of the papilla basilaris in different lizard families.

Plates XXII and XXIII show in summary form, the anatomical relationships of the cochlear ducts in different lizard families.

DISCUSSION

A detailed study of the lizard cochlear duct has two outstanding values. First, the remarkable diversity of structures probably concerned with auditory phenomena may be studied physiologically and hopefully extend our knowledge concerning hearing mechanisms. Second, the relative diversity of cochlear duct anatomy, at least at the familial level of classification, provides us with characters that may contribute to a clarification of some aspects of lacertilian taxonomy and phylogeny.

RELATION OF THE ANATOMY OF THE COCHLEAR DUCT TO ACOUSTICAL PERFORMANCE

Anatomical characteristics that may be related to the acoustic capacity of a particular cochlear duct are the following:

1. *The overall size and configuration of the cochlear duct.* The cochlear duct may be square, triangular, or elongated. Usually the increase in size of the duct is associated with increase in size of the limbus and papilla basilaris, but the total configuration depends on the degree of development of both the lagenar and limbic portions of the duct. While the length of the cochlear duct is directly correlated with the length of the papilla basilaris in birds and mammals, this is not always the case in lizards where the length of the cochlear duct and the papilla basilaris may be independent variables (table 2 and graphs 2–7). However, as is the case in birds and mammals (Schwartzkopff, 1963a), the length of the cochlear duct of lizards usually increases with body size. The absolute length of the cochlear duct is generally greatest in mammals, intermediate in birds, and shortest in reptiles.

While hearing capacity may be related more to papilla basilaris length than cochlear duct length, the factor of overall size and shape of the cochlear duct must be considered in acoustic evaluation.

2. *The relative size of the lagenar portion of the cochlear duct.* A cochlear duct may be relatively large, not because of elongation of the papilla basilaris, but rather because of the shape and length of the macula lagenae. Whether the macula lagenae plays a role in acoustic reception is not known. Afferent nerve fibers from the macula lagenae join nerve fibers from the papilla basilaris, and, according to Hamilton (1963), terminate on small cells in the acoustic area of the brain stem. A similar situation apparently obtains in birds (Schwartzkopff, 1963b). The fact that the macula lagenae is covered by an otolithic membrane would not lead one to suspect that it is an auditory receptor. However, we know that in certain fishes the otolithic membrane-covered macula of the sacculus or utriculus may subserve auditory functions (de Burlet, 1934). Flock (1964), on the other hand, states that Lowenstein has demonstrated that the peripheral (and possibly auditory) portions of these sensory areas in fishes may remain uncovered by the otolithic membrane.

While the possible role of the macula lagenae in auditory reception in reptiles remains to be determined, the size and configuration of the pars lagenae and particularly the macula lagenae certainly affect acoustic reception. In Evans' (1936) study of the cochlear–lagena ratio, he attempted to determine what proportion of the entire cochlear duct was occupied by the macula lagenae and what by the papilla basilaris. Neither from Evans' data, nor from the figures of Retzius (1884) can one determine these values. These values can be obtained only by reconstruction of the entire duct or by gross anatomical study (see p. 271).

3. *The shape and size of the limbus.* The limbus varies in shape from a thin saucer-like plate to a thick elongated structure. Thin platelike limbi are usually associated with small ovoid papillae basilares, and the large limbi with longer and better developed papillae.

4. *The development of a lateral projection or lip from the neural limbus.*

This structure is somewhat variable within lizard families, but on the whole, characteristically different from family to family. The possible significance of the limbic prominence or lip is that it alters the manner in which the tectorial membrane is related to the hair cells of the papilla basilaris, and the extent to which endolymph is enclosed between the tectorial membrane and the neural limbus.

While the great majority of lizards possess a tectorial membrane, it is very odd that some skinks, and possibly other scincomorphic lizards may have lost the tectorial membrane. This feature demands further and very careful study, both to determine if and in what species the tectorial membrane is absent, and to assess the functional significance of this phenomenon. Histological and ultrastructural studies of the relationship of hair cells to the tectorial membrane should reveal further adaptations of acoustical significance.

5. *The size and shape of the papilla basilaris.* The papilla varies from small ovoid aggregates of sustentacular and hair cells, to elongated, fusiform, or divided structures. It is probable that differing auditory capacities, either in pitch or intensity discrimination (Schwartzkopff, 1963a) are related at least in part to the size, shape, and structure of the papilla basilaris.

Graph 8 and table 3 summarize variations in the length and areas of the papilla basilaris in representatives of different lizard families.

6. *The basilar membrane.* This structure varies both in size and shape and usually corresponds to the size and extent of the papilla basilaris, but may vary in extent independently of the degree of development of the papilla basilaris.

7. *The papillar bar.* Underlying the supporting cells of the papilla basilaris is a variously thick bar of modified connective tissue identical to that of the limbus. This bar lends rigidity and support to the overlying supporting and sensory cells of the papilla. This structure may serve to dampen sound waves in acoustic reception. The only previous mention of this structure I have seen, occurs in figure 16 (f), table VIII of Retzius (1884), where he illustrates a "Firste" (bar or ridge) underlying the papilla basilaris of *Lacerta ocellata.*

8. *The development of limbic recesses.* In some types of cochlear ducts the entire medial face of the basilar membrane is not enclosed by any portion of the limbus. In others, various parts of the basilar membrane are enclosed by the limbus. Projecting into the limbic recesses are extensions of the perilymphatic sac. Such enclosed portions of the perilymphatic sac (perilymphatic diverticuli or accessory scalae tympani) which are conducting sound-pressure waves to the basilar membrane may act to intensify or concentrate acoustic energy; thus these portions may play an important part in auditory reception.

It is also possible that sound energy may be transmitted directly across the cochlear duct, rather than all the energy being carried by the perilymphatic duct to the basilar membrane (see discussion in Baird, 1960a).

9. *The number of hair cells,* the innervation of the hair cells, the number of

cochlear ganglion cells, the number of connections of the cochlear nuclei cells, as well as the role of mid- and forebrain centers are certainly all related to hearing capacity but are as yet unstudied in reptiles.

Table 4 summarizes some anatomical differences in the cochlear duct that may be related to the acoustical capacity in different lizard families.

To date, most of our information concerning the acoustical capacities of reptilian cochlear ducts have been derived from studies of cochlear potentials in the laboratory of E. G. Wever and his associates. Table 5 summarizes some of the data derived from these studies.

While both the number of species as well as the number of individual animals so far studied is relatively small, it appears that the iguanids and lacertids are intermediate to relatively poor in their acoustical responses. The anguids, while sensitive at low ranges of pitch, are not very sensitive about 1,000 cps. and the teiids and gekkonids, of all lizards so far examined, are the best performers.

This information correlates well with the anatomical information presented in tables 2, 4, and 5 where it can be seen that the iguanids and lacertids (poor to intermediate performers) have relatively short papillae basilares as well as small papillary areas. It is particularly significant that while but a single specimen of *Anolis carolinensis* was studied by Wever and others (1963a) it gave a better performance than other iguanids. This correlates well with the fact that among the iguanids, the papilla basilaris of the anolids is both longer and greater in area (table 2).

As might be expected, a teiid (*Cnemidophorus tessalatus*) was a better performer than the above types, and members of the Gekkota were very good. Both the teiids and Gekkota have papillae of fair length and area. It is interesting that *Gecko gecko* whose papilla basilaris is twice the length and triple the area of *Coleonyx variegatus* performed less well than the latter species.

Certainly many factors other than papilla basilaris length and areas are important in determining auditory capacity, and further anatomical and neurophysiological studies of lizard cochleae should be of great value.

For the present, one might conjecture that on the basis of anatomical development, at least four categories of relative hearing capacity might be expected among different lizard families. These are:

A. Relatively poor, undeveloped, or regressed.

    Chamaeleonid
    Anniellid
    Xenosaurid
    Dibamid
    Amphisbaenid

B. Fair.

    Iguanid

Agamid
Lacertid

C. Moderately well to good.

Anguid
Anolid iguanians

D. Good to very good.

Teiid
Gekkotid
Pygopodid
Varanid
Scincid
Xantusiid
Cordylid

An artificial division such as this presupposes that the length and area of the papilla basilaris, the type of limbic lip and disposition of the tectorial membrane, and the development of limbic recesses are related to hearing capacity. Other factors of importance are the variations in middle ear anatomy, the detailed structure of the papilla basilaris, and the central nuclei and their connections.

The only lizards known to have developed vocality and auditory communication are geckos (Evans, 1936); thus, it is not surprising that this group has an "advanced" type of cochlear duct.

Since other lizards with seemingly advanced types of cochlear ducts (teiids, scincids, xantusiids, cordylids, and varanids) apparently have not developed a voice, it seems likely that they use their hearing ability for defensive or foraging activities. One might imagine that a skink resting in an underground burrow, or a xantusiid hidden between the leaves of a rotting Joshua tree log, are easily capable of perceiving the sounds made by insect or termite activity in their immediate vicinity.

Beach (1944), in a discussion of hearing in reptiles, cites three studies relative to lizards. Kuroda (1923) found modifications of certain visual reflexes in *Tachydromus tachydromoides* in response to stimulus with a bell or Galton whistle. Beatty (1932) working with *Lacerta viridis,* observed responses to auditory stimuli, and Berger (1924), with *Lacerta agilis* and *Lacerta vivipara,* found that specific eye reflexes, a modified respiratory rhythm, and trained learned responses could be induced by loud noises as well as tonal stimuli.

Evans (1936) also comments on an extremely interesting and significant observation of G. M. Allen who described a case of vocal expression in the skink, *Mabuya bensonii,* the sounds being a series of bark-like staccato noises.

It is well known that alligators are vocal (Beach, 1944), and possess a better developed cochlear duct than lizards; the duct is longer, partially twisted, and

Table 4. *Some anatomical differences in the cochlear duct that may be related to the acoustical capacity in different families of lizards.*

FAMILY	*MACULA LAGENAE*	*LIMBUS*	*LATERAL–NEURAL LIMBIC MODIFICATION*	*PAPILLA BASILARIS*	*LIMBIC RECESSES*
I Iguanidae	Large, long, 2 to 3 times length of papilla basilaris	Small to moderate in size	Thickened bar	Relatively short, but elongate	Very short inferior and superior recesses
II Agamidae	"	"	Thickened bar; slightly better developed inferiorly	"	"
III Chamaeleonidae	Moderate	Reduced to thin saucer-like plate	None	Small circular to ovoid in shape	None
IV Anguidae	Moderate, 2 to 3 times length of papilla basilaris	Moderate, ovoid, large basilar membrane	Somewhat prominent, elongate, sharply undercut bar	Short to moderate, slightly fusiform, elongate	Very short superior and inferior recesses
V Anniellidae	Reduced	Reduced to thin saucer-like plate	Anterior edge forming bar-like projection	Small, ovoid	None
VI Xenosauridae	Moderate	"	None	Small, ovoid	None
VII Helodermatidae	Moderate	Moderate, thick	Rounded prominence	Moderate, elongate	Short superior recess
VIII Varanidae	Moderate	Large, elongate, sometimes divided hiatus	Thickened neural ridge	Elongate, sometimes divided (longer superior portion)	Relatively long superior and short inferior recesses
IX Lacertidae	Moderate to relatively large	Moderate, ovate, divided hiatus	Prominent, fairly thick ridge projecting from anterosuperior middle part of neural limbus	Elongate, divided; two portions approximately equal in length	Very short superior and inferior recesses
X Teiidae	Large	Large, elongate	Prominent, thick process projecting from mid 50–60% of limbus	Moderate to elongate, slightly fusiform	None

Table 4. *Continued.*

FAMILY	*MACULA LAGENAE*	*LIMBUS*	*LATERAL–NEURAL LIMBIC MODIFICATION*	*PAPILLA BASILARIS*	*LIMBIC RECESSES*
XI Gekkota	Large	Large, ovate to elongate	Thin, extensive awning-like process extending over papilla basilaris	Elongate, slightly fusiform	Long superior recess ($^{2}/_{3}$ basilar membrane recessed)
XII Pygopodidae	Moderately large	"	"	"	Long superior recess ($^{3}/_{4}$ basilar membrane recessed)
XIII Scincidae	Moderate, except in some reduced species	Large, shows lateral curvature	Ridge-shaped thickening	Elongate, slightly fusiform	Long inferior recess ($^{3}/_{5}$ basilar membrane recessed)
XIV Feyliniidae	Moderate, though reduced	Reduced scincid	Ridge-shaped thickening	Similar, but slightly shorter and thicker than scincid	Long inferior recess ($^{3}/_{5}$ basilar memberane recessed)
XV Xantusiidae	Moderate	Relatively large, elongate	Ridge-shaped thickening	Elongate, slightly fusiform	Long inferior recess ($^{3}/_{10}$ to $^{2}/_{5}$ basilar membrane recessed)
XVI Cordylidae	Moderate	Moderately large, elongate	Slightly projecting ridgelike thickening	Elongate, slightly fusiform	Short inferior and superior recesses
XVII Dibamidae	Relatively short	Thin, saucer-like plate	Very small lip	Small, ovoid	Shallow and short recesses
XVIII Amphisbaenidae	Relatively short	Thin, saucer-like plate	Anterior edge forming bar-like lip	Small, ovoid	Shallow and short recesses

TABLE 5. *Summary of auditory responses in various reptiles obtained by the cochlear potential method.*

SPECIES	*GENERAL RANGE (cps)*	*RANGE OF GREATEST SENSITIVITY (cps)*	*SOURCE*
Crocodilia			
Caiman sclerops	20 to 6,000	100 to 3,000 (very sensitive)	Wever and Vernon, 1957
Chelonia			
Emydidae			
Clemmys insculpta *Chrysemys picta* *Pseudemys scripta*	up to 3,000	*Clemmys* very sensitive up to 500 (sensitivity in range of –40 to –60 db.)	Wever and Vernon, 1956
Ophidia			
Colubridae			
Pituophis m. melanoleucus *Thamnophis s. sirtalis* *Thamnophis s. sauritus* *Natrix sipedon pictiventris*	to 700	100 to 500 (moderate sensitivity; –20 db.)	Wever and Vernon, 1960
Lacertilia			
Iguanidae			
Uma notata *Sceloporus clarkii* *Urosaurus ornatus*	Decreased sensitivity below 700 or above 2,000	700 to 2,000 (moderate sensitivity; –20 db.)	Wever and Peterson, 1963
Sauromalus obesus	"	400 to 4,000; peak at 2,500	Wever *et al.*, 1963a
Anolis carolinensis		400 to 3,000 (good sensitivity; –30 db.)	Wever *et al.*, 1963a
Lacertidae			
Eremias velox	1,000 to 3,000	500 to 1,000 (low sensitivity; +35 db.)	Wever *et al.*, 1963a
Anguidae			
Gerrhonotus multicarinatus	Decrease below 1,000 or above 2,000	300 to 500 (very sensitive)	Crowley, 1964
Teiidae			
Cnemidophorus tesselatus	Up to 17,000 to 19,000!	400 to 4,000 (moderate sensitivity)	Wever *et al.*, 1963a
Gekkota			
Gecko gecko	100 to 7,000	200 to 400 (decrease above 3,000)	Wever *et al.*, 1963b
Hemidactylus turcicus	100 to 10,000	(moderate sensitivity)	Wever *et al.*, 1964
Coleonyx variegatus	100 to 10,000	400 to 1,000 (very sensitive)	Wever *et al.*, 1964

in *Alligator mississippiensis* the papilla basilaris is two to five times the length and 10 to 30 times the area of most well developed lizard papillae (table 2).

Bellowing has been reported in certain turtles (Kelemen, 1963) but the cochlear duct of these species has not been studied.

The Relation of Cochlear Duct Anatomy to Lacertilian Classification

Probably the outstanding feature of the cochlear duct of lizards is that the duct is recognizably distinct in every family of lizards so far studied. And even though the degree of variation is considerable within some families, it is always possible to define the cochlear duct characteristics of any particular family. When the degree of intrafamilial variation is relatively large, the data on differences may be useful in intrafamilial classification. These features will be discussed in detail under family headings.

Shute and Bellairs (1953) were probably the first to recognize the taxonomic significance of the lacertilian cochlear duct, and since then, Baird (1960a), Hamilton (1960, 1964) and Schmidt (1964) have verified this observation. Also, the studies of Hamilton and Baird have shown that detailed analysis of the perilymphatic spaces, and variation in other parts of the membranous labyrinth are all important in the ultimate analysis of lacertilian classification and phylogeny. Wherever useful, all anatomic, physiologic, biochemical, or behavior information should contribute to the solution of taxonomic and phylogenetic relationships.

While the following tentative groupings are based to a large degree on the anatomy of the cochlear duct many relationships are strengthened or basically indicated by the general features of lacertilian classification as set down by Camp (1923), McDowell and Bogert (1954), and Romer (1956).

This scheme does not imply a phylogeny, but groups families according to the anatomical similarities of their cochlear ducts.

I. Iguanidae
   Agamidae
II. Chamaeleonidae
III. a. Anguidae
   b. Anniellidae
   c. Xenosauridae
   d. Helodermatidae
IV. Varanidae
V. Lacertidae
   Teiidae
VI. Gekkota
   Pygopodidae
VII. a. Scincidae
   b. Feyliniidae
   c. Xantusiidae
   d. Cordylidae
VIII. Dibamidae
IX. Amphisbaenidae

I. Iguanidae
Agamidae

The cochlear duct of this assemblage, while fairly large, has a relatively small but thickened limbus and does not possess a distinctive limbic lip. The macula lagenae is relatively long and the papilla basilaris, short. The main difference between the ducts of the iguanids and agamids is the exact shape of the duct and the nature of the neural limbic thickening.

The cochlear duct of this group does not have marked specializations of any one feature and may be considered generalized, or unspecialized.

From a study of the cochlear ducts of 49 species representing 29 genera of iguanids, the ducts of the anolids differ from most other iguanids in having a more elongate limbus and a longer papilla basilaris. Both the length and area of the anolid papilla basilaris are approximately double that of other similarly sized nonanolid iguanids. The genus *Tropidurus* has an unusually pointed duct and a high bar-like neural limbic thickening.

The cochlear ducts of the three Old World lizard genera, *Brachylophus, Chalarodon,* and *Oplurus,* are characteristically iguanid.

At the present time, I am unable to relate the structure of the iguanid–agamid cochlear duct to that of any other assemblage.

II. Chamaeleonidae

The cochlear duct of the true chamaeleons shows no separation of lagenar and limbic portions, is triangular in shape, and the outstanding features, a thin platelike limbus and a small circular papilla basilaris. While the duct is characteristic for this family, it is not sufficiently similar to that of any other group to indicate a clear-cut relationship.

Unlike the interpretations of Hamilton (1964) and Schmidt (1964), I believe the chamaeleonid cochlear duct is degenerate and not primitive. A small limbus and papilla basilaris do not necessarily indicate a primitive condition, but may represent a regressed or degenerate state. Similar regressed conditions are seen also in *Anniella* and *Xenosaurus* (see below).

While there is insufficient evidence on the basis of cochlear duct anatomy alone to relate the Chamaeleonidae to the Agamidae, it is entirely conceivable that the chamaeleonid duct could result from regression of the agamid type.

It is particularly interesting that a group (Chamaeleonidae) that has developed visual acuity to a high degree (Walls, 1942, p. 625) should either not have developed or have experienced degeneration of the auditory organ.

III. a. Anguidae

The development of a prominent neural limbic thickening probably indicates some advance in cochlear duct construction. However, the papilla basilaris and macula lagenae remain relatively short. The above-mentioned "advance" may correlate with the greater auditory acuity in the lower ranges of pitch discrimination and the short papilla with relatively poor performance in the higher ranges (table 5).

I consider the cochlear duct of anguids more advanced than the iguanid–agamid type, but not as advanced as that found in the teiids, gekkonids, and skinks.

Hamilton (1964) states that the cochlear duct of *Anguis* approaches a primitive state. This is not the case, for the duct of *Anguis fragilis,* while reduced, shows all the characteristics of an anguid lizard.

It is interesting that *Anguis fragilis* and *Ophisaurus ventralis* show reduced features in both the lagenar and limbic portions of the cochlear duct. These species are burrowing forms and like many burrowing skinks and *Anniella* have lost the external ear opening and show degenerative cochlear duct changes.

III. b. **Anniellidae**

The macula lagenae and papilla basilaris both appear to be regressed structures in the cochlear duct of *Anniella pulchra.* Further, the small anteriorly placed limbic lip might represent the remnant of a once larger projection. I believe this is another example of degeneration of the cochlear duct that is associated with the assumption of a burrowing habitus.

While the cochlear duct of *Anniella* does not show close anatomical affinities with any other group, it is conceivable that it could result from the degeneration of an anguid-like structure.

III. c. **Xenosauridae**

The limbic portion of the cochlear duct of *Xenosaurus grandis* is markedly reduced, while the lagenar area remains moderate in proportion. Like *Anniella,* the duct of *Xenosaurus* is very different and I find no definite clues to suggest its taxonomic relationship.

It is conceivable that the duct of *Xenosaurus* could be derived from either iguanid or anguid stock; because of other anatomical features (Camp, 1923; Romer, 1956), however, I include it among the anguinomorphs.

III. d. **Helodermatidae**

The limbus of *Heloderma* is heavier and the neural limbic thickening better developed than that of the iguanids, but not as well developed as that of the anguids. The papilla basilaris is longer than either the iguanid or anguid. While the helodermid duct could have been derived from either the iguanid or anguid type, on the basis of other anatomical features (Romer, 1956), I tentatively include it in the anguid group.

IV. **Varanidae**

The cochlear duct of the varanids is moderately advanced; the duct is large and elongate, the papilla basilaris is long and frequently divided, and a moderately long limbic recess is present.

While the lacertids are the only group having a clearly divided papilla basilaris, the varanids show a variable tendency in this direction, and the teiids and scincids show what I interpret as remnants of such a condition. For the present, the significance of a divided papilla basilaris is not clear.

It is interesting that the nerve to the papilla basilaris in *Heloderma* is bifid, while the papilla is not divided. However, the much thickened neural limbus of *Heloderma* is reminiscent of that of *Varanus*. Thus, as in certain other anatomical characters (McDowell and Bogert, 1954) the helodermids, varanids, and anguids are probably related.

V. Lacertidae
Teiidae

The cochlear duct of these two families, while distinctive for each, show definite similarities. This is to be expected in two families that share many common anatomical attributes.

The cochlear duct of the teiids is generally larger and the limbus and papilla basilaris longer than that of the lacertids. While the papilla is not divided in the teiids as it is in the lacertids, a constriction near the superior end in the teiids indicates that it may have been divided at an earlier state of development.

The limbic lip while slightly different in each of these two families is generally similar in appearance. Neither family has developed a limbic recess of significant size.

As far as the anatomy of the cochlear duct is concerned, the lacertid–teiid complex cannot be associated clearly with any other group of lizards.

VI. Gekkota (including Gekkonidae, Eublepharidae, Sphaerodactylidae, Uroplatidae)
Pygopodidae

While I have studied the cochlear duct of 19 genera of gekkonids, I have seen but two genera of Eublepharids (*Coleonyx* and *Eublepharis*) and two genera of sphaerodactylids (*Gonatodes* and *Sphaerodactylus*). I have also seen *Uroplatus* and three genera of pygopodids.

The gekkonid duct seems to be remarkably stable, and except for increase in the length of the cochlear duct, limbus, and papilla basilaris in relation to body size, the anatomical details are remarkably constant throughout this group. On the basis of cochlear duct anatomy alone, the Gekkota comprise a uniform group.

Hamilton (1960) in his studies on the morphology of the inner ear of certain gekkonid lizards which takes into account other structures than the cochlear duct, concludes that there are more fundamental differences within this assemblage than I could find. Until more genera and species are studied, and more quantitative comparisons are made, further discussion at this time would not seem fruitful.

The pygopodid cochlear duct is remarkably similar to the gekkonid. The main differentiating feature seems to be the angle of inclination of the macula lagenae to the papilla basilaris. While I have seen the ducts of only three pygopodid genera, these are anatomically very similar and differ mainly in size relationships. The cochlear duct of *Aprasia pulchella* is somewhat reduced in size, and is essentially a miniaturized replica of an advanced pygopodid duct.

On the basis of the marked development of the limbic lip, the increase in length and area of the papilla basilaris, and the development of a long superior limbic recess, the gekkonids and pygopodids in relation to other lizards have an advanced type of cochlear duct. These are not the only advanced types of cochlear ducts among the lizards, however, inasmuch as the scincids and xantusiids have evolved advanced types too that are somewhat different in anatomical details (see below).

It is interesting that a group (gekkonids) that displays many so-called primitive anatomical features, should have evolved a fairly advanced cochlear apparatus.

Hamilton (1964) has noted also that the development of the gekkonid duct was posterosuperiorly and at the expense of the sacculus, whereas the lengthening of the scincid duct was anteroinferiorly and not at the expense of the sacculus.

At the present, I am unable to relate the cochlear duct of the gekkonid–pygopodid complex to that of any other living group.

VII. a. **Scincidae**

The scincid cochlear duct is an advanced structure that is narrowed, elongated, slightly curved (incipient coiling?), and has a relatively long, slightly fusiform papilla basilaris, and an extensive inferiorly directed limbic recess. The lateral neural limbic wall, while having a thickened ridge, does not develop a lip as do the lacertids, teiids, gekkonids, and pygopodids. Retzius (1884, p. 100) is of the opinion that the scincid cochlear duct is the most highly developed type found in the saurians and represents an important transitional stage from the lizard to the crocodilian type.

Whether the lack of a limbic lip affects the auditory capacity of the scincids is unknown as these forms have not been studied acoustically. While other factors may be of much greater importance, the crocodiles and birds, like the scincids, do not possess a limbic lip, and apparently achieve greater auditory powers by means of an increase in the length and area of the papilla basilaris.

Study of graph 7 shows that there is a great range of cochlear duct and papilla basilaris length in the skinks. This variability correlates with certain anatomical changes that are related to the variety of life modes that are found in the skinks. For the present it appears that in species of skinks modified for burrowing, and where there have been changes in the external ear, the cochlear duct shows degenerative changes.

While an extensive analysis of correlative changes in the scincid cochlear duct will be undertaken in a future paper, it is noteworthy that even with a considerable degree of anatomical change, such as occurs in *Acontias,* some species of *Brachymeles, Nessia, Rhodona,* the lygosomids and the typhlosaurids, the cochlear duct, while also showing reduced features, is always recognizably scincid. No family of lizards has what we may without doubt interpret as a "primitive" cochlear duct; regression or reduction of the duct has in fact occurred and might mislead one to believe that an evolutionary primitive structure is present. Application of the term "primitive" to an obviously degenerate state is a contradiction in fundamental meaning.

VII. b. **Feyliniidae**

The cochlear duct of *Feylinia currori,* while reduced in many features, is undoubtedly scincid.

VII. c. **Xantusiidae**

In most regards, the cochlear duct of the xantusiids is very similar to that of the scincids. The differences in the neural limbic ridge, the limbic recess, the shorter macula lagenae, together with other anatomical features indicate the separate familial status of the xantusiids, but suffice to show the close affinities of this group to the scincids. The differences between the cochlear ducts of *Klauberina, Lepidophyma,* and *Xantusia* are related mainly to the size of the animal and not to any structural differences in the ducts.

VII. d. **Cordylidae**

The relationship of the cordylids to the scincoid lizards is not as easy to demonstrate as is that of the scincids and xantusiids to one another. The cochlear duct is not as elongated as the scincid, and while the neural limbic ridge is better developed in the cordylids, there is little closure of the medial aspect of the basilar membrane. The sacculus of the cordylids is also not as large as that of the scincids indicating a lesser degree of ventral expansion.

The relatively long papilla basilaris and the lack of a definite limbic lip, together with other anatomical characteristics (Romer, 1956) would indicate a scincid relationship of the cordylids.

VIII. **Dibamidae**

The cochlear duct of *Dibamus argenteus* is probably a degenerate structure and while it superficially resembles the duct of the amphisbaenids one cannot say that these two groups are related to one another, or to any other group, on the basis of cochlear duct anatomy alone.

IX. **Amphisbaenidae**

It is difficult to be certain whether the cochlear duct of the amphisbaenids is degenerate or specialized. It certainly is not primitive.

The limbus is a thin saucer-like plate, similar to that of the chamaeleonids, *Anniella*, or *Xenosaurus* in which the cochlear duct is probably regressed or degenerate. The lagenar portion of the duct in the amphisbaenids seems to be more obviously degenerate. If this is the case, then, it is highly likely that the limbic portion has also been reduced from some better developed precursor. While the cochlear duct may have arisen by reduction of a once more fully developed type, it might be considered that the auditory apparatus is a specialized one representing an adaptation to a burrowing habit. Camp (1923) is of the opinion that the outer ear of amphisbaenids is not a degenerate structure, but a highly specialized one.

The fact that the lagenar and limbic portions of the duct are well joined speaks somewhat against ophidian relationship, but further studies in this direction are certainly indicated as *Typhlops* has a cochlear duct somewhat similar to that of the amphisbaenids (unpublished observations). Baird (1960b) concludes that the auditory apparatus found in typhlopid snakes is a specialized adaptation for burrowing.

It may well be that the amphisbaenids are not lacertilians and either belong to another or a separate order.

The cochlear ducts of anelytropsids, shinosaurids, or *Lanthanotus* have not been studied.

SUMMARY

The gross morphology of the cochlear duct of 205 species, representing 131 genera and 18 families of lizards was studied. While the cochlear duct differs considerably in its morphology from one family to another, it is sufficiently stable at the family level of classification to be diagnostically characteristic for any one family. The degree of intrafamilial variation is different from one family to another. Morphological variations occur in the shape and size of the entire duct, and in the relative sizes of the lagenar and limbic portions of the duct. The limbus undergoes modifications of both surfaces, forming thickenings, projections, or lips on its lateral face, and recesses on the medial aspect. The macula lagenae varies greatly in length and area. The papilla basilaris may be short, elongate, circular, ovoid, fusiform, entire, or divided, and varies in total length and area. In most lizard families the size of the cochlear duct and limbus, and the length and area of the papilla basilaris varies directly with species size; in others, correlation between size of duct elements and species size is not as marked.

The auditory capacity of a particular cochlear duct is probably related to many of the above anatomical differences. These are discussed in relation to acoustical studies that have been made on reptilian cochleae.

The morphological features of the cochlear duct in certain families is indicative of close taxonomic relationships. The most clear-cut anatomical

similarities between the cochlear ducts of different groups are exemplified in the iguanid–agamid, lacertid–teiid, gekkonid–pygopodid, and scincid–xantusiid associations.

In other families, cochlear duct morphology in itself, is not greatly helpful in revealing interfamilial taxonomic relationships.

Various elements of the cochlear duct may undergo regressive changes in species of some families. In no case, however, does regression or degeneration progress to the degree that the familial status of a particular cochlear duct is in doubt. In some very small species, miniaturization of the duct may occur.

Both interfamilial and intrafamilial relationships of the cochlear duct are discussed.

Acknowledgments

The author is first of all indebted to Professor Francis A. Sooy, Chairman of the Department of Otolaryngology of the University of California School of Medicine, San Francisco, for his suggestion that this study be undertaken and for his enthusiastic appreciation and support throughout the progress of the work.

Without the great generosity and continuous stimulation and help of Dr. Alan Leviton, Curator of Amphibians and Reptiles, California Academy of Science, San Francisco, this study would not have been possible.

It was also my good fortune to be afforded the cooperation, interest, and skill of Mr. Wayne Emery of the Department of Medical Illustration of the University of California School of Medicine, San Francisco, who faithfully studied reptilian anatomy and executed the figures and drawings for this paper.

Mrs. Helen Burn, associate specialist, of the Department of Otolaryngology has been of great assistance in the solution of many technical problems.

Miss Michiko Kasahara has been involved in all phases of this work and has contributed especially in the photographic aspects of this paper.

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NOTE CONCERNING THE VIEWING OF BLACK-AND-WHITE STEREOPHOTOGRAPHS

An understanding of the anatomical details of the lizard cochlear duct is best achieved by three-dimensional visualization of the intact structure. To accomplish this stereophotographs of the cochlear duct are presented.

While stereocolor transparencies are superior to black-and-white stereophotographs, their cost of publication is high, and for the time being black-and-white stereophotographs are presented.

The use of black-and-white stereophotographs was common in the latter part of the nineteenth and early part of the twentieth centuries, but is used much less often today.

de Burlet (1934) very effectively illustrated his excellent articles on the ear of vertebrates with stereo black-and-white photographs.

Since color transparency stereo pairs are easily viewed in readily available special viewers, difficulty in achieving a full three-dimensional effect is rarely experienced. The viewing of black-and-white stereophotographs, on the other hand, is more difficult and requires some special practice or the acquisition of a stereoscopic viewing device.

Judge (1926, pp. 78–79), in a discussion on the viewing of stereograms, states: "It is possible to experience stereoscopic, *i.e.*, relief and perspective, effects without the aid of the camera, or stereoscope, as will be appreciated from the following simple test.

"Draw two circles or black dots about ¼ inch diameter at a horizontal distance apart of about 2 inches; it will render the test easier if these are drawn near the top edge of a sheet of white paper. If the eyes be focused on these dots in the ordinary way, both will be seen distinctly, but if the paper be held at about 15 to 18 inches from the eyes, and the dots be observed with the eyes accommodated for a long range, or infinity, they will be found to merge into a single central dot; in most cases there is also a fainter or ghost image on each side. It is better to hold the paper in front of the eyes at the distance mentioned and whilst still looking at a distant object to slowly move the paper upwards, and without altering the position of the eyes to look at the dots; they will appear to travel inwards and to merge.

"Some persons are able to merge objects in this way without difficulty, and can view stereoscopic prints without the aid of a stereoscope. It is also possible by 'crossing' the eyes, or squinting, to obtain a stereoscopic effect when viewing a 'pair' of illustrations and without the aid of any viewing apparatus.

"The principle to be observed when viewing stereoscopic prints or illustrations is for the right eye to see only the print taken with the right-hand lens, and the left eye that with the left lens. Both views should appear superposed. Unless the observer is able to merge the views in the manner previously indicated, he will find it impossible to concentrate the attention of each eye on its respective illustration, so that some artificial aid becomes necessary."

One of the simplest methods of viewing a stereogram is that illustrated by Judge in his figure 43 (figure 10) and consists of a vertical black screen S placed in front of the two views A and B of the stereogram, and moved backwards or forwards until it just about occupies the position indicated. It will be

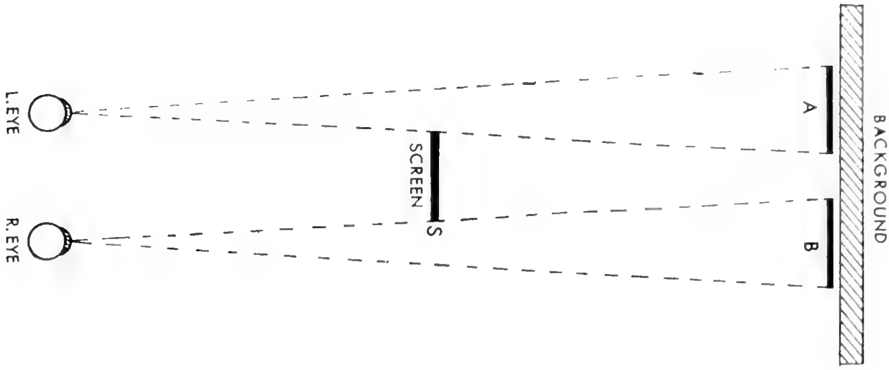

Figure 10. A simple method of viewing stereograms (from Judge, 1926).

evident that the black screen S prevents the right eye from seeing the left view and the left eye from observing the right view. "A convenient way to carry out this method, or rather to practice it, is to place the two reduced width stereoscopic prints against a book on a table and to bend a piece of tin or cardboard in the form of an angle arranged at the required level, near the edge of the table. After a certain amount of practice, the screen S can be dispensed with in many cases."

If one desires, a stereopticon, or stereoscopic viewing device may be purchased.

PLATE I

Family IGUANIDAE

Crotaphytus wislizeni (CAS [14])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 23
Stereopair × 26 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been partly cut away from the lateral face of the duct. The sacculo-cochlear duct lies to the right. The limbus and papilla basilaris are centrally placed. The macula lagenae courses down the anterior (left slope) edge and then onto the medial surface of the duct; this can be seen best in the photographs. A portion of the medial wall of the sacculus is present in the photograph, but not in the drawing.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 23
Stereopair × 26 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The course of the macula lagenae can be visualized better in this view. Note the nerve branches supplying the macula lagenae.

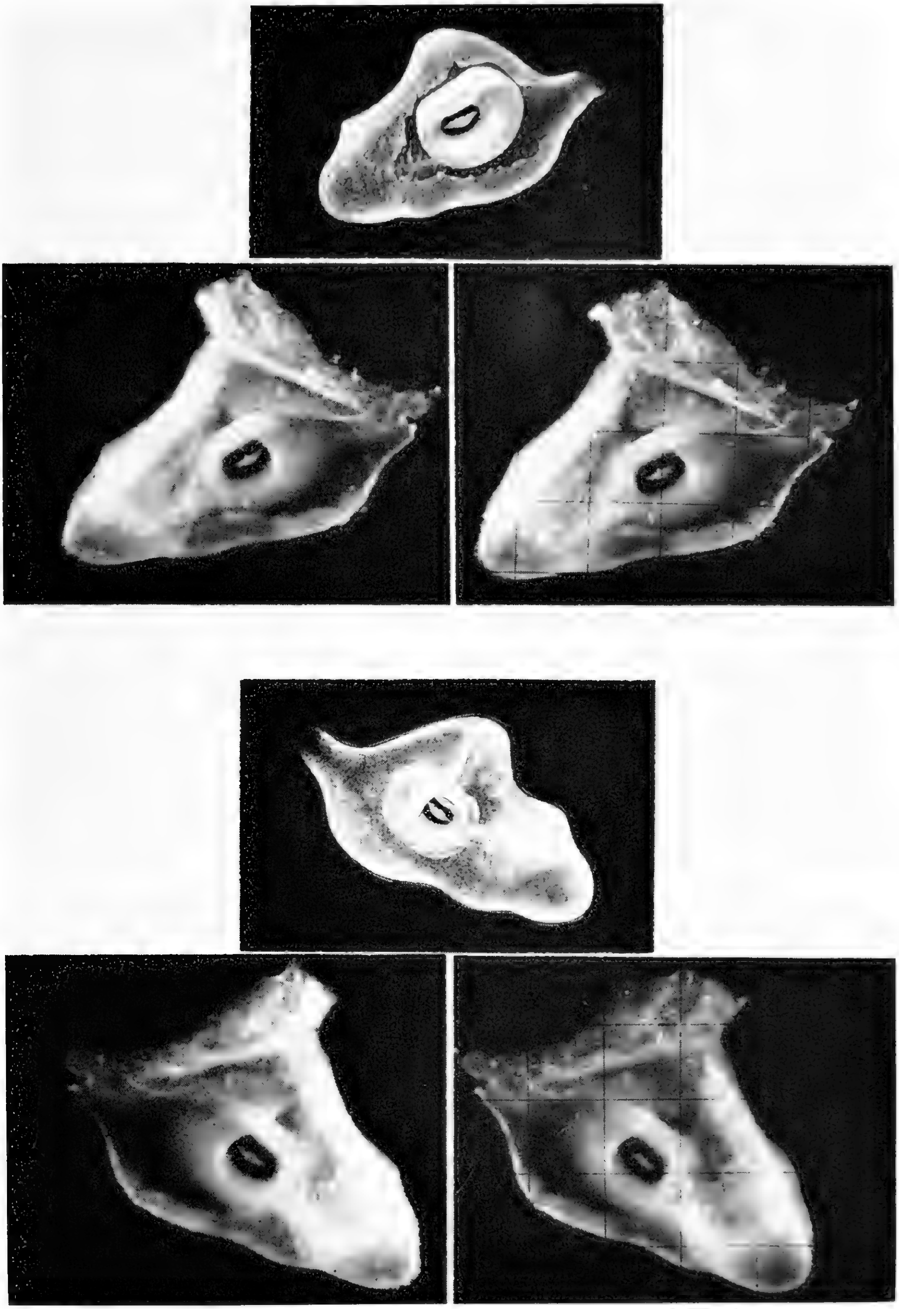

Plate I. The cochlear duct of *Crotaphytus wislizeni* (Iguanidae).

PLATE II

Family AGAMIDAE

Agama agilis (CAS 86343 [25])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 23
Stereopair × 32 (one grid division = 0.25 mm.)

Posterosuperior is to the right, and anteroinferior to the left. Most of the vestibular membrane has been removed. The sacculo-cochlear duct is seen in the drawing, but not in the photograph. The course of the macula lagenae down the anterior (left slope) aspect of the cochlear duct is best seen in the medial view. The bright area in the upper right part of the stereopair is a portion of the macula of the sacculus.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 23
Stereopair × 32 (one grid division = 0.25 mm.)

Posterosuperior to the left, anteroinferior to the right. The macula lagenae passes down the anterior (right slope) of the duct and then curves onto the medial wall. Very short limbic recesses are present. The nerves to the macula lagenae have been torn away just before they supply the length of the macula lagnae.

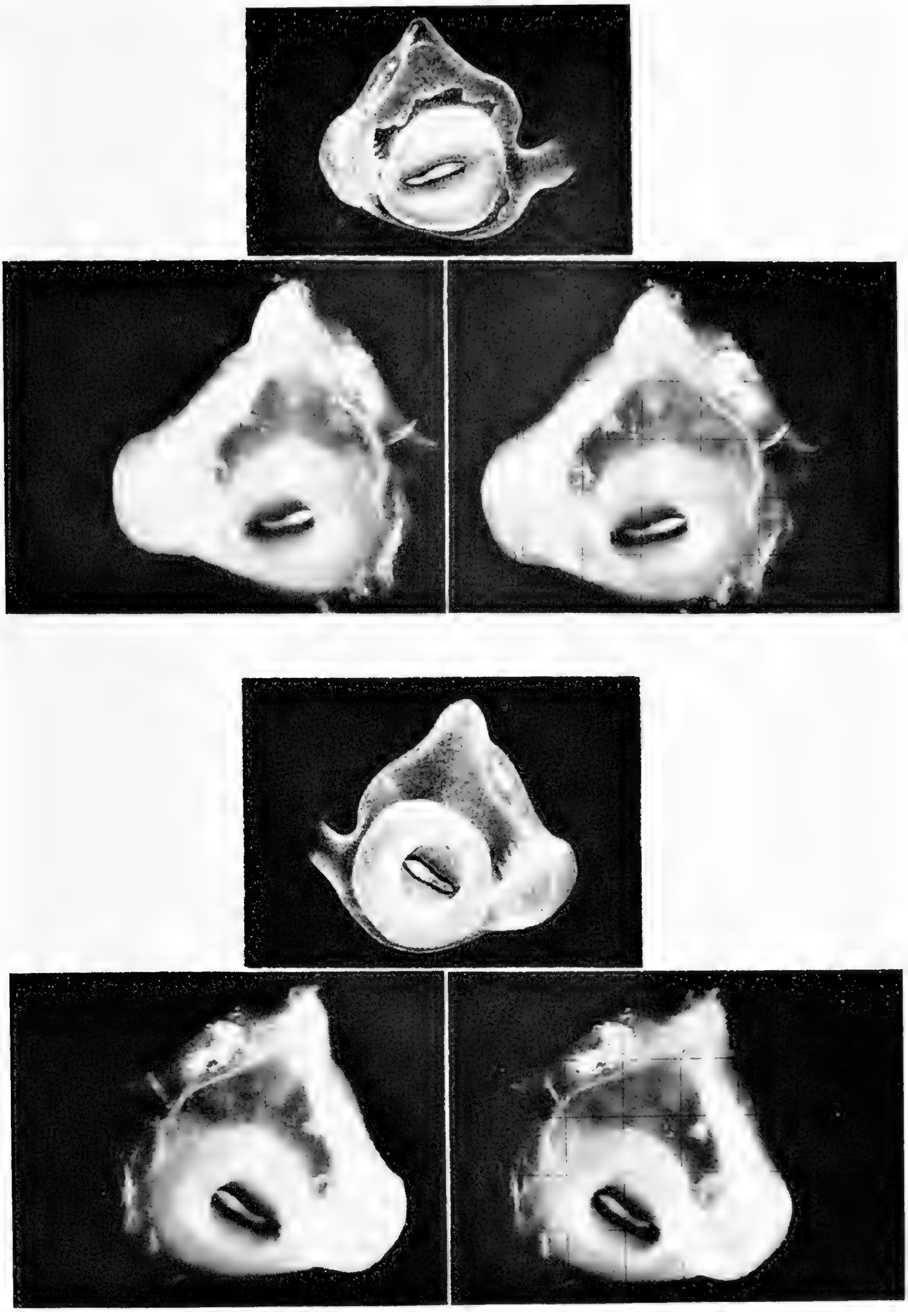

Plate II. The cochlear duct of *Agama agilis* (Agamidae).

PLATE III

Family CHAMAELEONIDAE

Chamaeleo sp. (CAS [311])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 28
Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The sacculus remains attached to the cochlear duct in the photograph, but is not represented in the drawing. The vestibular membrane has not been removed. The thin saucer-like limbus is clearer in the drawing. The nerve to the papilla basilaris is seen in the photograph, but it has not been included in the drawing. The nerve to the papilla basilaris in this specimen is divided into a larger posterior, and a smaller anterior branch. The course of the macula lagenae down the anterior (left) duct wall and then onto the medial wall may be observed in both lateral and medial views.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 28
Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is at the top, and anteroinferior at the bottom. A short superior limbic recess is visible. A small divided nerve supplies the papilla basilaris; multiple nerve branchlets supply the macula lagenae.

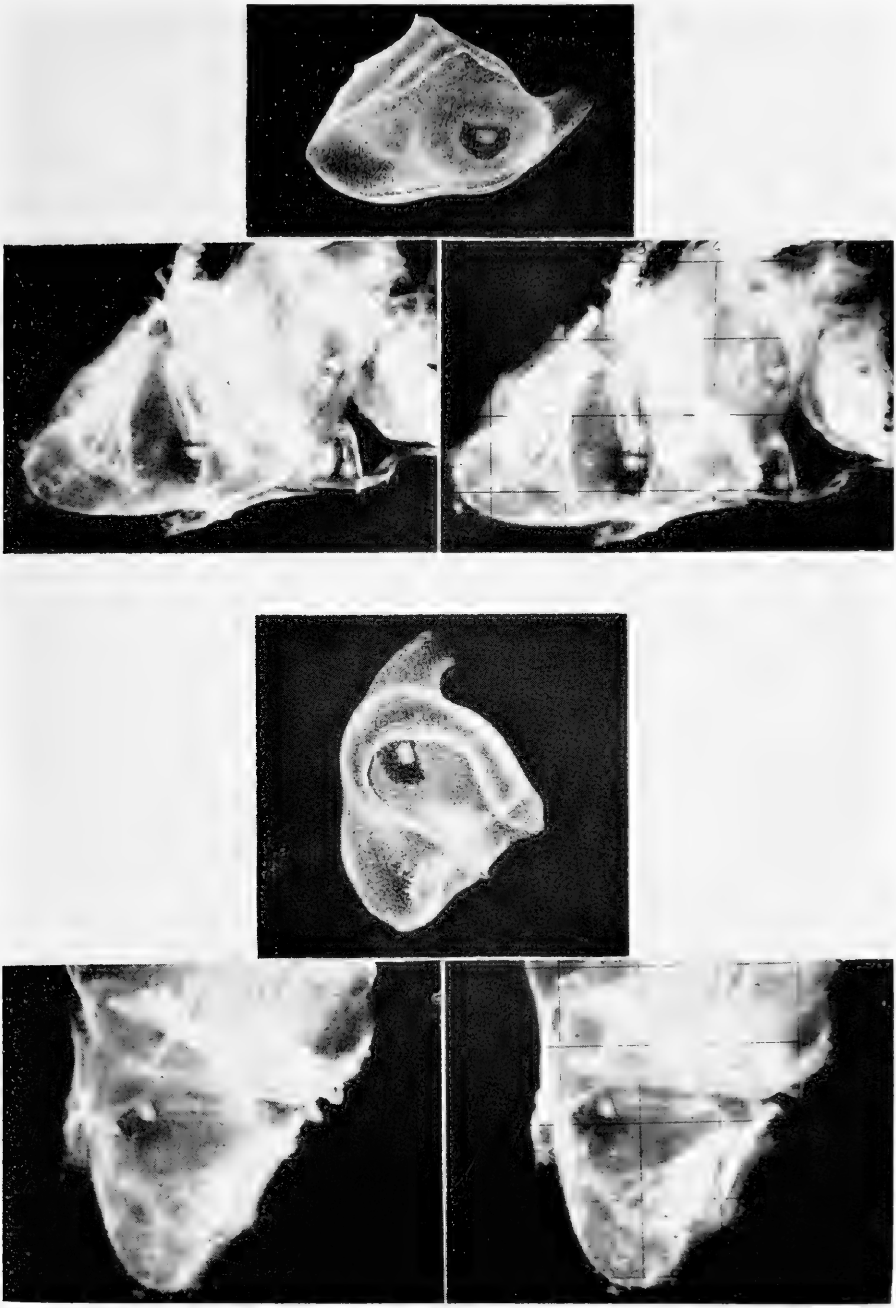

Plate III. The cochlear duct of *Chamaeleo* sp. (Chamaeleonidae).

PLATE IV

Family ANGUIDAE

Diploglossus lessonae (CAS 49540 [61])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 22
Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior is to the left. The vestibular membrane has been partially removed. While the nerves are not depicted in the drawing, three main branches are seen in the photographs. The nerve to the right supplies the crista of the posterior ampulla (cut off). Centrally, behind the neural limbus, is the nerve to the papilla basilaris, and above and to the left is the nerve to the macula lagenae. The macula lagenae is seen on the anterosuperior (upper left) and medial parts of the cochlear duct.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 22
Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior is to the right. The three nerve branches mentioned above are better seen on the photographs of the medial side of the duct. The flanges housing the perilymphatic duct are quite prominent.

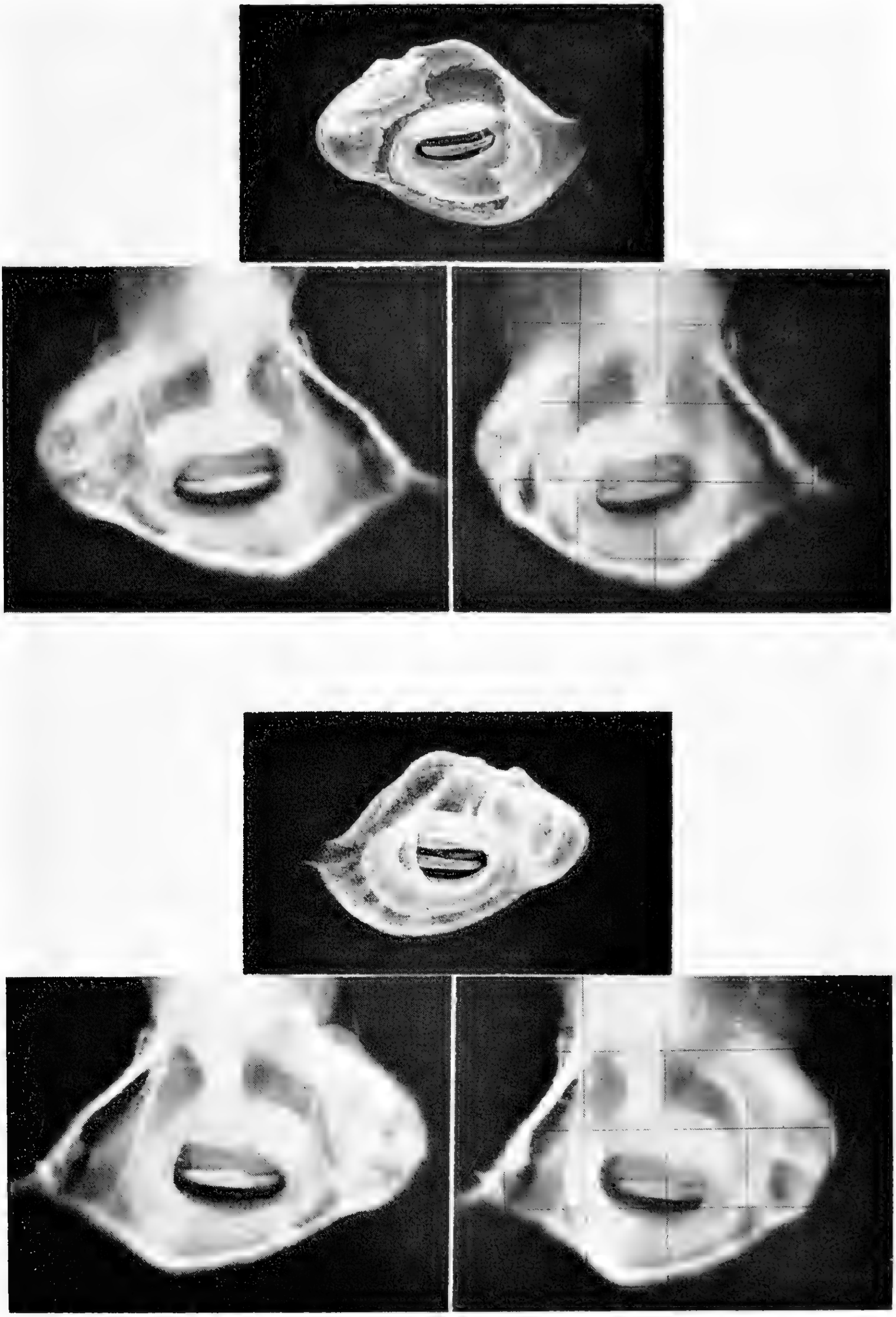

Plate IV. The cochlear duct of *Diploglossus lessonae* (Anguidae).

PLATE V

Family ANNIELLIDAE

Anniella pulchra (CAS 17848 [343])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing ×29
Stereopair × 36 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. In the photograph the nerve to the papilla basilaris courses down the medial side of the neural limbus.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 29
Stereopair ×36 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The lagena lies to the right (anteroinferior) and the opaque white structure within its cavity is the otolithic membrane overlying the macula lagenae. The heavy opaque structure at the top of the photograph is the posterior branch of the auditory nerve, but only the division supplying the papilla basilaris is present.

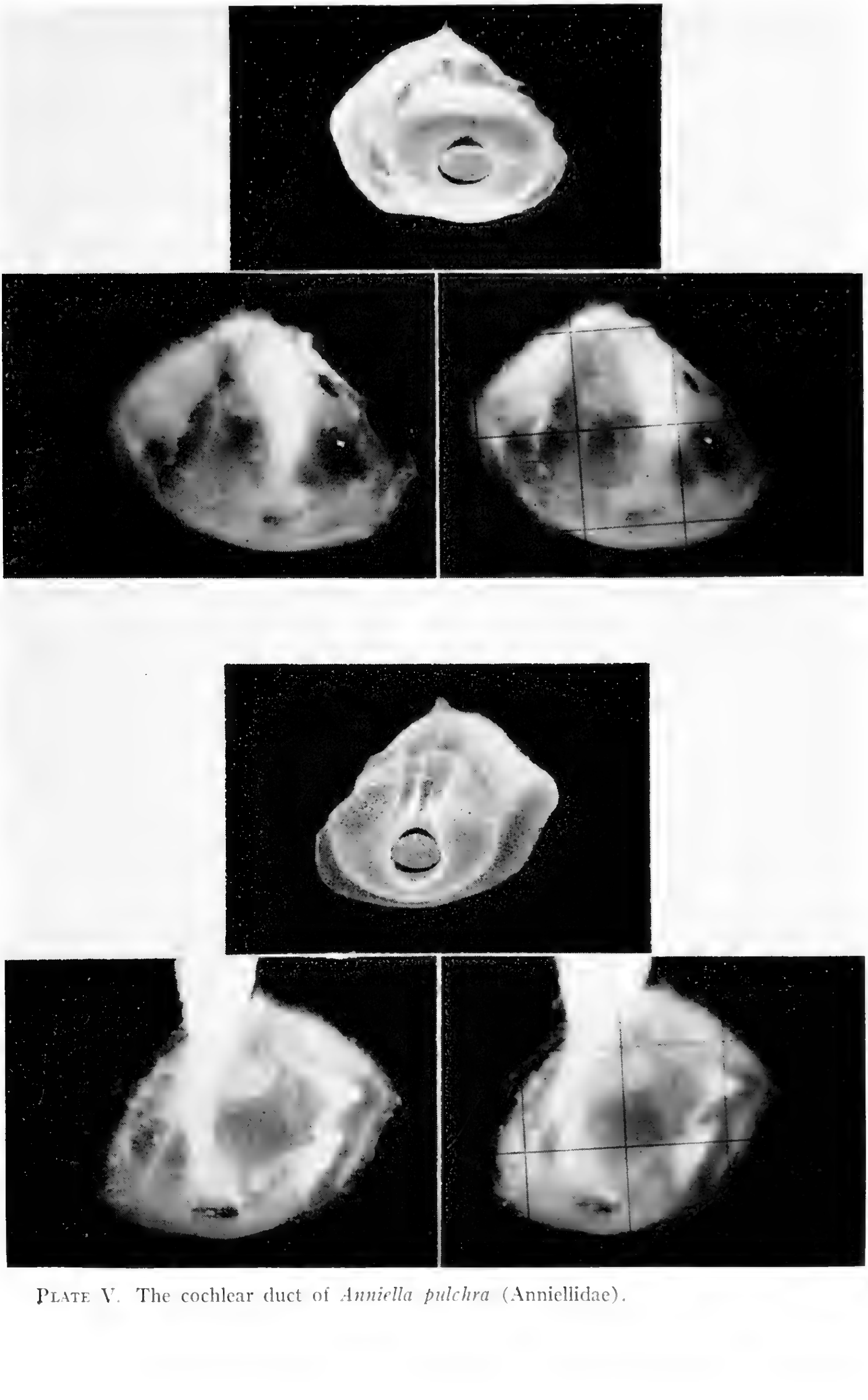

Plate V. The cochlear duct of *Anniella pulchra* (Anniellidae).

PLATE VI

Family XENOSAURIDAE

Xenosaurus grandis (CAS 87839 [344])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 19
Stereopair × 19 (one grid division = 0.58 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane is intact. The opaque white elongate structure on the right edge of the photograph is the nerve to the crista of the posterior ampulla. To the left of this is the long slender nerve to the papilla basilaris. The groove on the upper left corner (anterior edge) of the duct is for the perilymphatic duct. The macula lagenae extends in an arc-like fashion from the anterolateral to the anteromedial portion of the duct.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 19
Stereopair × 19 (one grid division = 0.58 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The nerve branches to the macula lagenae spread out to supply this structure. The nerves to the papilla basilaris and the posterior crista are also quite evident in the photographs.

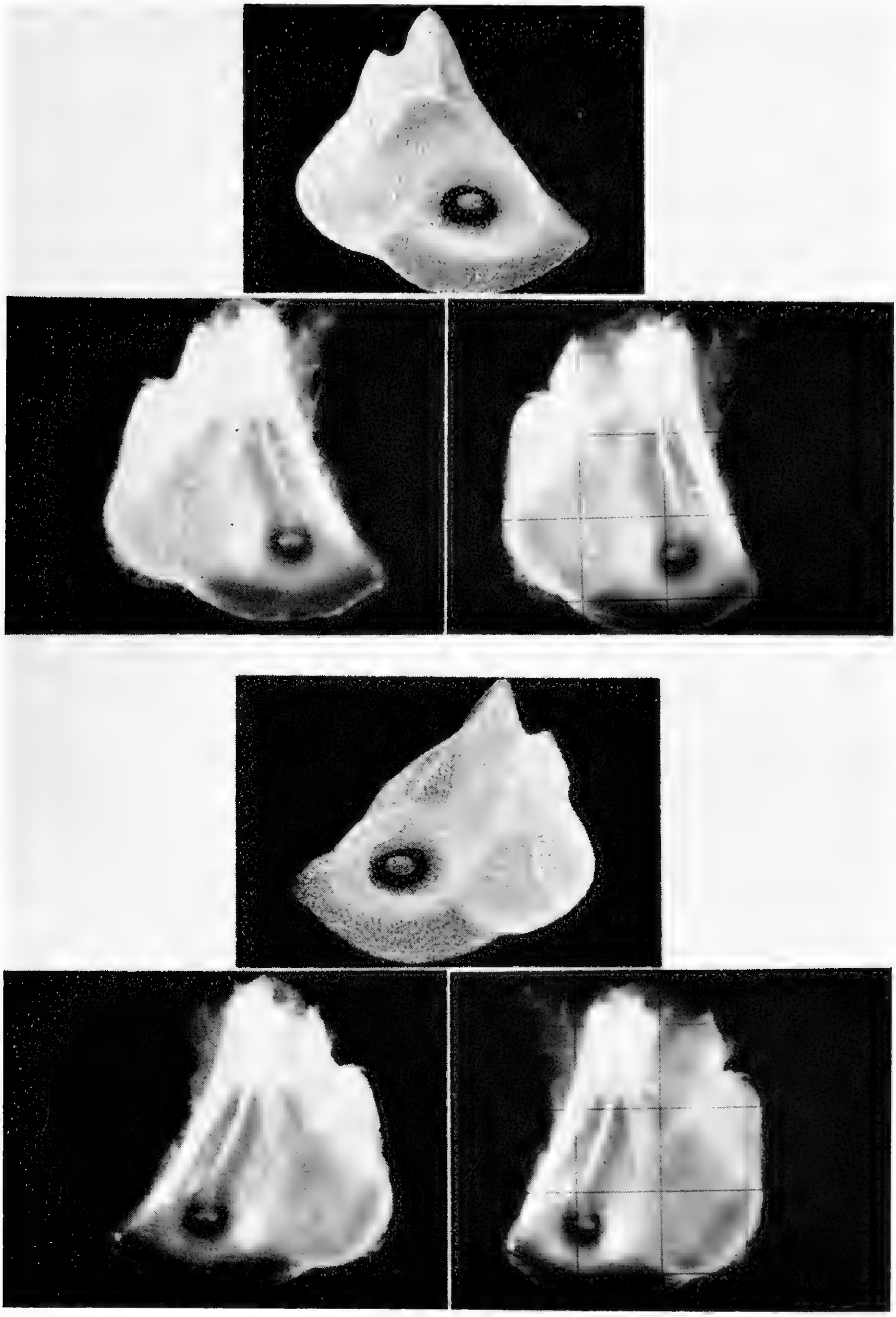

PLATE VI. The cochlear duct of *Xenosaurus grandis* (Xenosauridae).

PLATE VII

Family HELODERMATIDAE

Heloderma suspectum (CAS [6])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 14
Stereopair × 18 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The opaque white structure in the upper midportion of the photographs is a portion of the auditory nerve; the branch to the posterior ampulla has been cut off, but the branches to the papilla basilaris and macula lagenae remain.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 14
Stereopair × 18 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The large nerve branch to the papilla basilaris is visible in the upper central portion of the photographs. Note that this nerve branch is bifid just before it enters the basilar membrane. A short superior limbic recess is present.

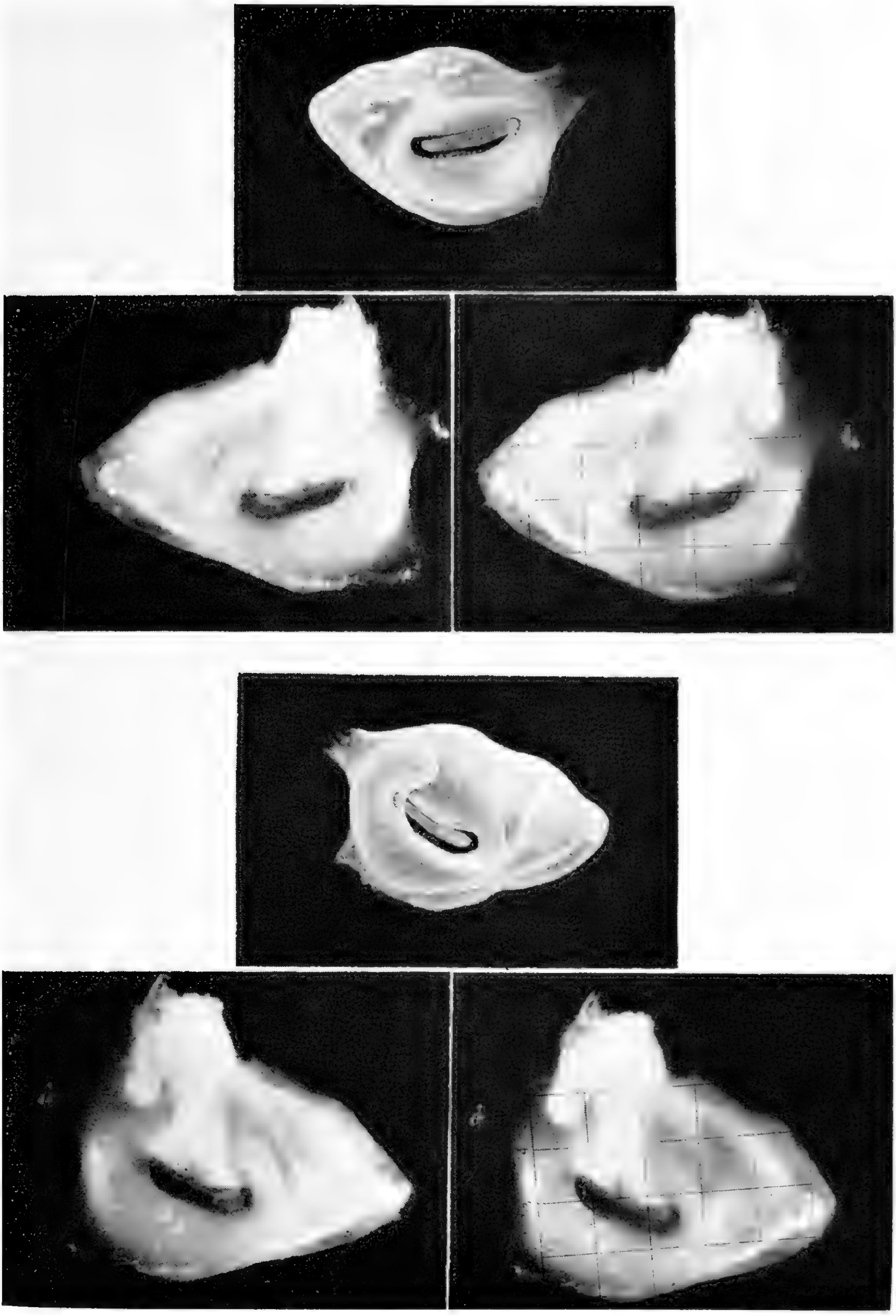

Plate VII. The cochlear duct of *Heloderma suspectum* (Helodermatidae).

PLATE VIII

Family VARANIDAE

Varanus sp. (CAS [24])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 12
Stereopair × 19 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. A divided papilla basilaris is clearly evident in this specimen. In some specimens the papilla is not divided. The neural limbus has no lip, but is thickened. The macula lagenae runs down the anterior (left) edge of the duct and then onto the medial wall of the lagena.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 12
Stereopair × 17 (one grid division = 0.58 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The macula lagenae can be seen running down the anterior wall (right edge) of the duct. A moderately long superior and a short inferior limbic recess are present.

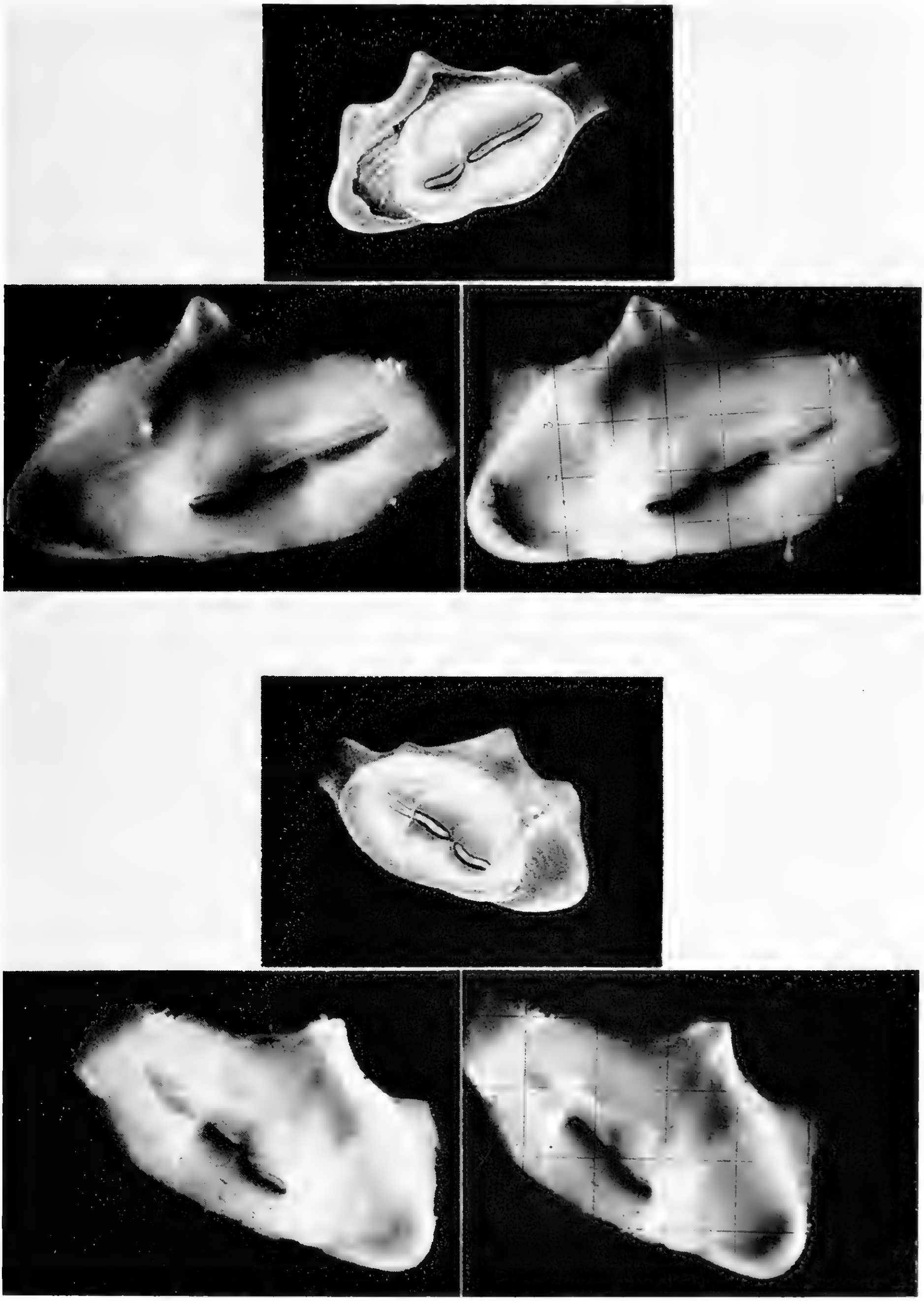

PLATE VIII. The cochlear duct of *Varanus* sp. (Varanidae).

PLATE IX

Family LACERTIDAE

Acanthodactylus cantoris (CAS 86555 [180])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 33
Stereopair × 40 (one grid division = 0.25 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The macula lagenae passes along the inner anterior wall (from right to left, upper edge of the figure) and onto the inferior medial wall of the duct. The nerves supplying the macula lagenae are well shown in the medial view. A well developed limbic lip, and a divided limbic hiatus and papilla basilaris are clearly evident.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 33
Stereopair × 40 (one grid division = 0.25 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The nerves to the macula lagenae and short superior and inferior limbic recesses are evident.

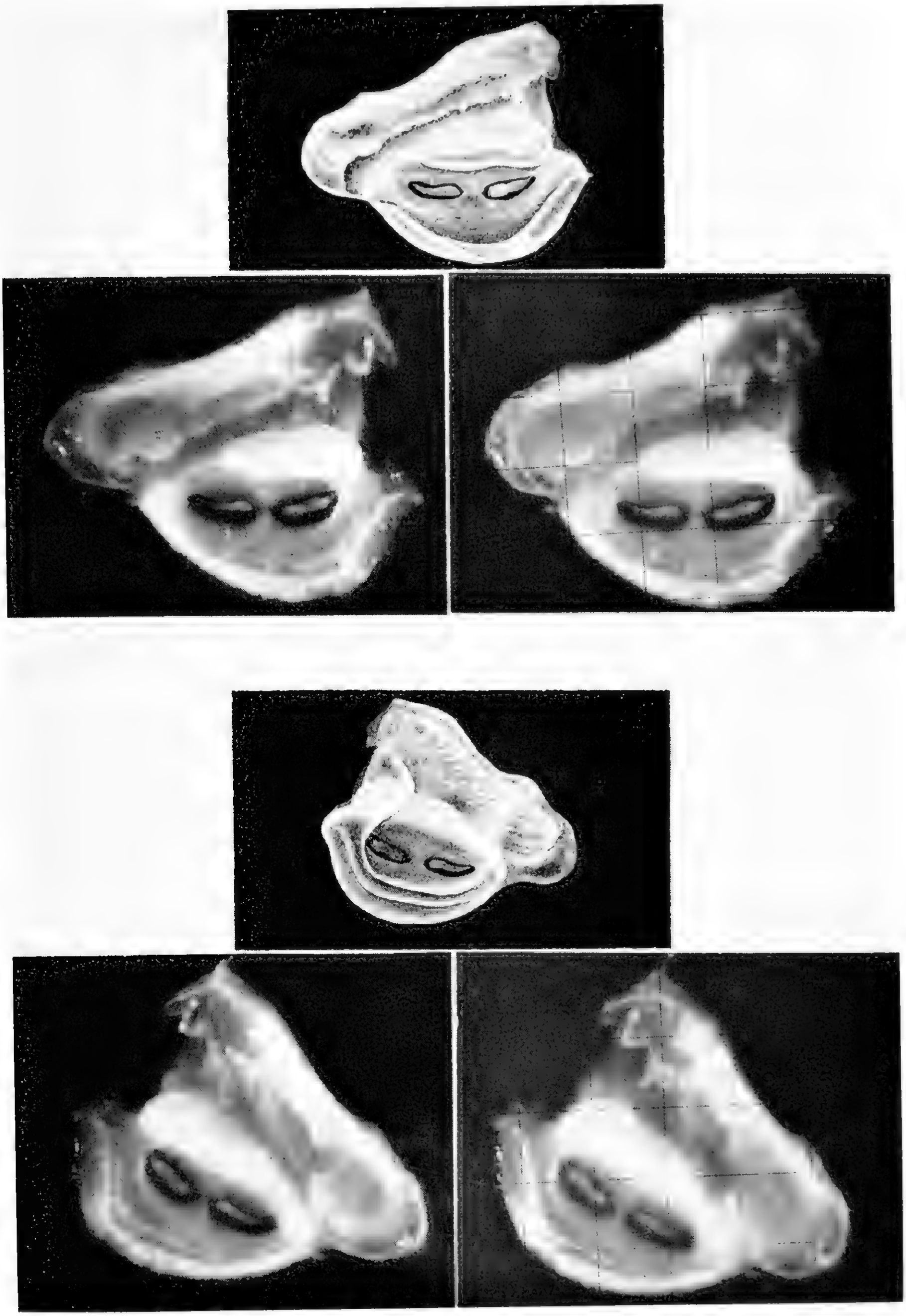

Plate IX. The cochlear duct of *Acanthodactylus cantoris* (Lacertidae).

PLATE X

Family TEIIDAE

Cnemidophorus tigris (CAS 88328 [2])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 18
Stereopair × 26 (one grid division = 0.25 mm.)

Posterosuperior is to the upper right, and anteroinferior to the lower left. The vestibular membrane has been removed. The posterosuperior tip (upper right end) of the limbic lip is broken in the photographed specimen. The macula lagenae runs down the inner aspect of the anterior (left) edge of the duct. Its medial portion is better seen in the medial view below. The calcium carbonate in the otolithic membrane overlying the macula lagenae has been removed with weak acid.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 18
Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the upper left, and anteroinferior to the lower right. The macula lagenae courses along the anterior (right slope) edge of the duct, and then curves onto the inferior medial wall. Short superior and inferior limbic recesses are visible.

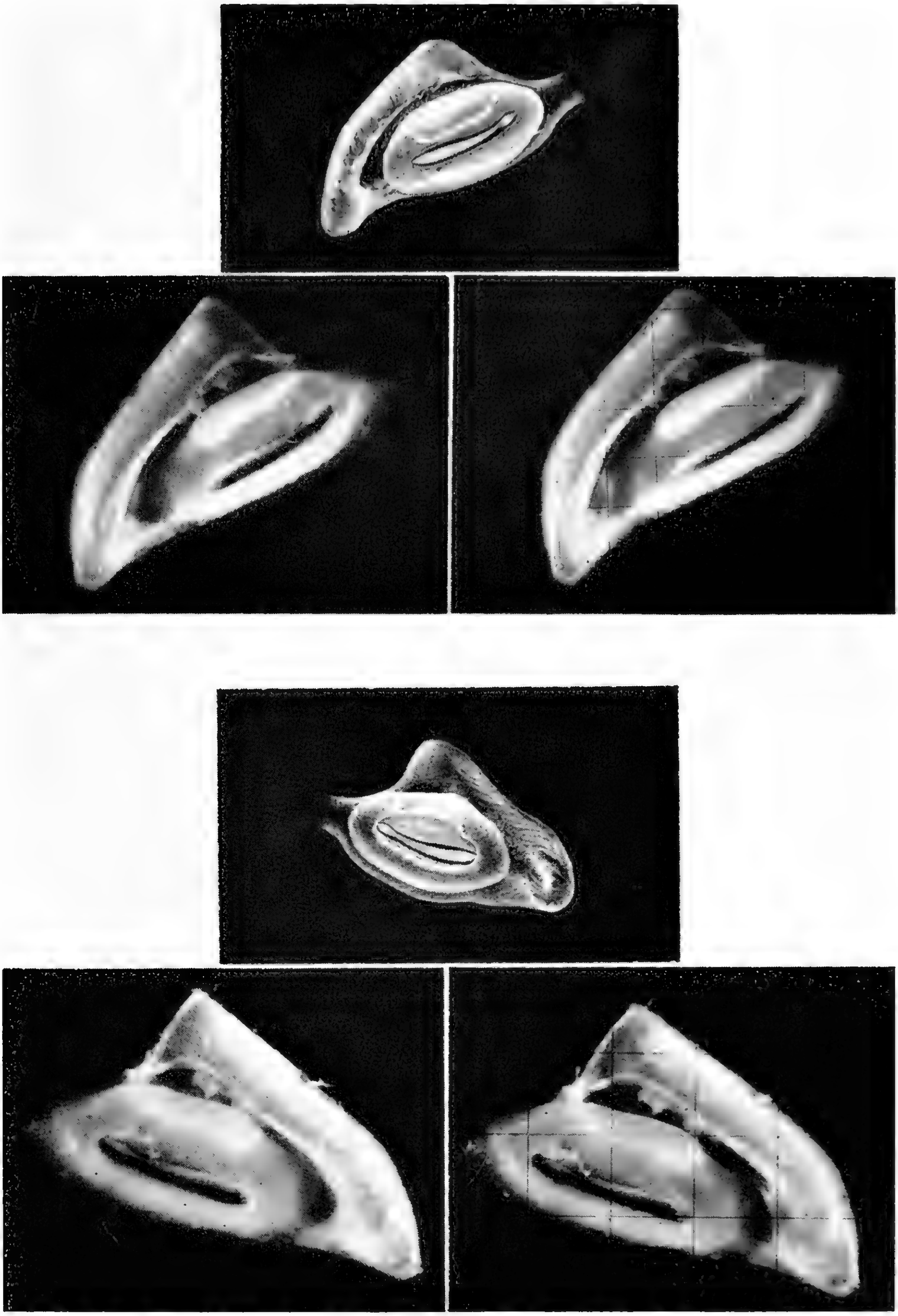

Plate X. The cochlear duct of *Cnemidophorus tigris* (Teiidae).

PLATE XI

Family GEKKONIDAE

Drawing: *Hemidactylus persicus* (CAS 86454 [128])

Photographs: *Cosymbotus platyurus* (SU 18566 [148])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 27
Stereopair × 33 (one grid division = 0.39 mm.)

Posterosuperior is to the upper right, and anteroinferior to the lower left. The vestibular membrane has been removed. The macula lagenae runs down the inner anteroinferior (left) edge of the duct. In the stereophotos, the tectorial membrane extends inferomedially from the tip of the limbic lip over the papilla basilaris (compare with fig. 7).

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 27
Stereopair × 33 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior to the lower right. A relatively long superiorly directed limbic recess is apparent (compare with fig. 6 [insert]).

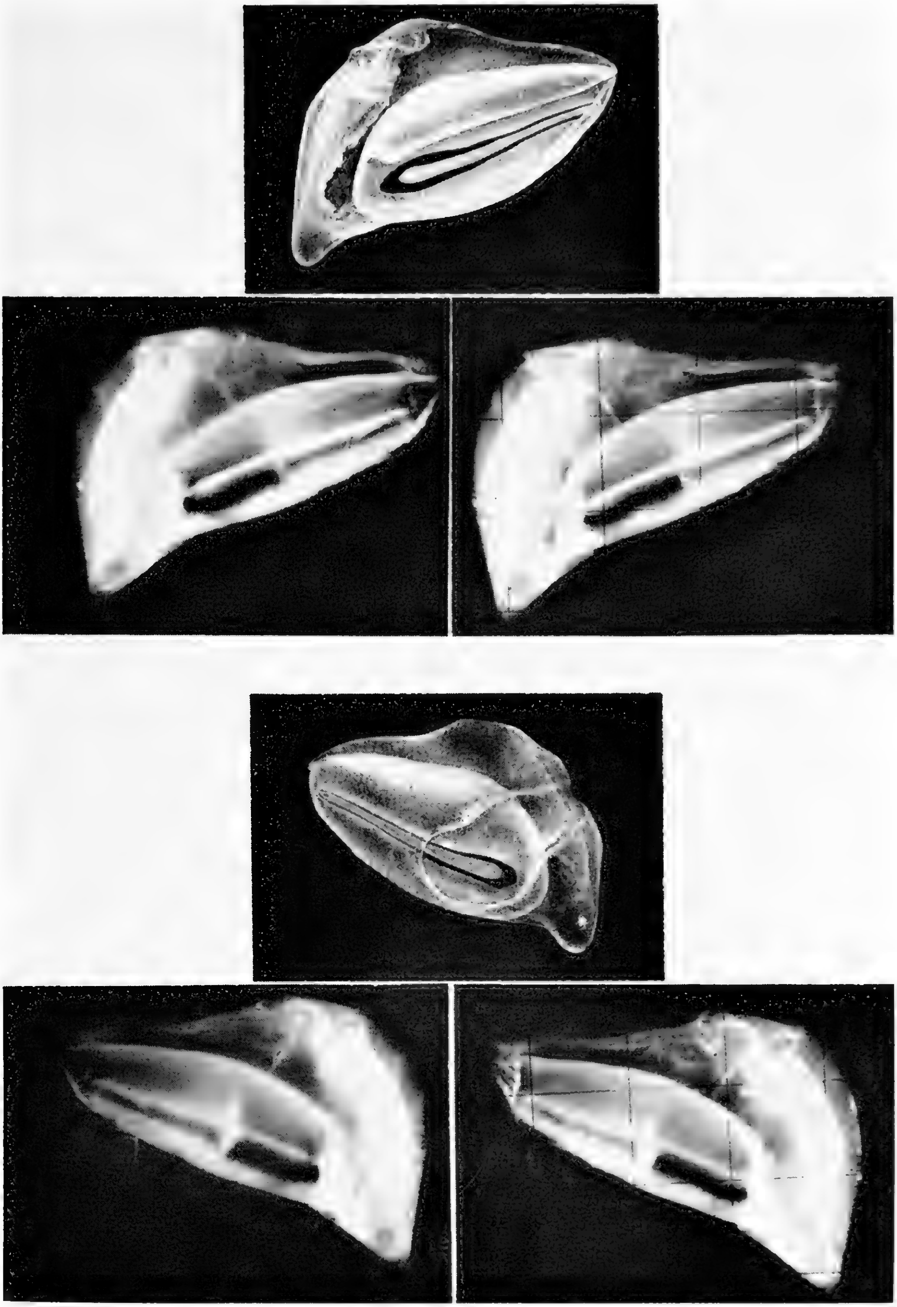

Plate XI. The cochlear duct of *Hemidactylus persicus* (Gekkonidae).

PLATE XII

Family PYGOPODIDAE

Lialis burtonis (CAS 77655 [34])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 18
Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The macula lagenae is a curved band running along the inner anterior edge of the duct. Note that the macula lagenae is nearly parallel to the papilla basilaris. The extensive awning-like limbic lip is clearly apparent.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 18
Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The groove for the perilymphatic duct courses around the anterior (middle top of photographs) edge of the duct and onto its medial surface. Note the long superiorly directed limbic recess.

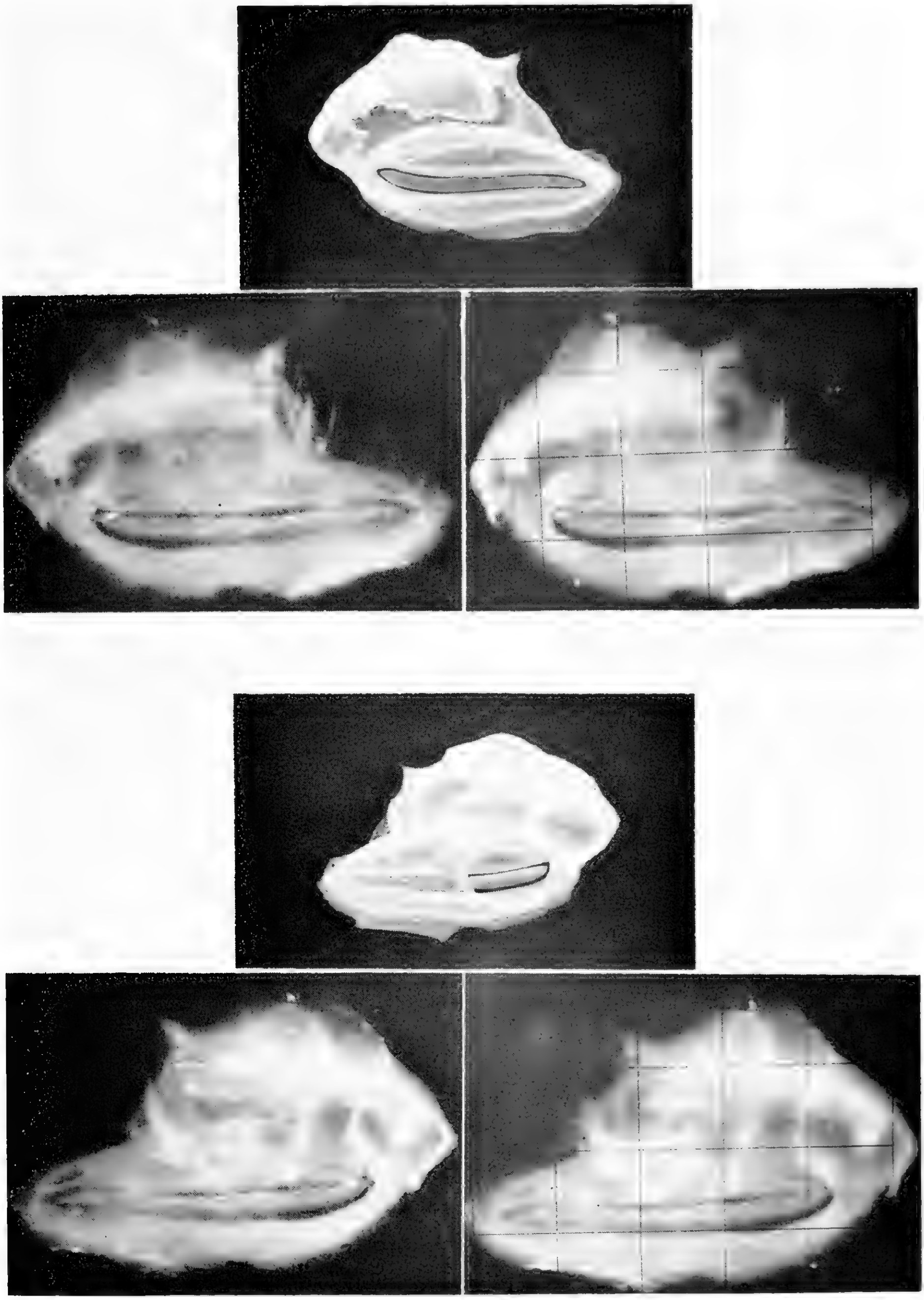

Plate XII. The cochlear duct of *Lialis burtonis* (Pygopodidae).

PLATE XIII

Family SCINCIDAE

Mabuya multicarinata (CAS 60435 [74])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 19
Stereopair × 27 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The macula lagenae is seen coursing from anterosuperior to anteroinferior (upper left) and then onto the inferomedial portion of the duct. The limbus is convex, with the convexity directed laterally (toward the viewer).

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 19
Stereopair × 27 (one grid division = 0.39 mm.)

Posterosuperior is to the upper left, and anteroinferior to the lower right. There is a slight tear between the anteroinferior tips of the pars lagena and the anteroinferior end of the limbus in the stereophotographs. The nerve to the papilla basilaris fans out as it supplies the papilla. The inferiorly directed, relatively long limbic recess is better seen in the drawing. The groove on the midportion of the duct houses the perilymphatic duct.

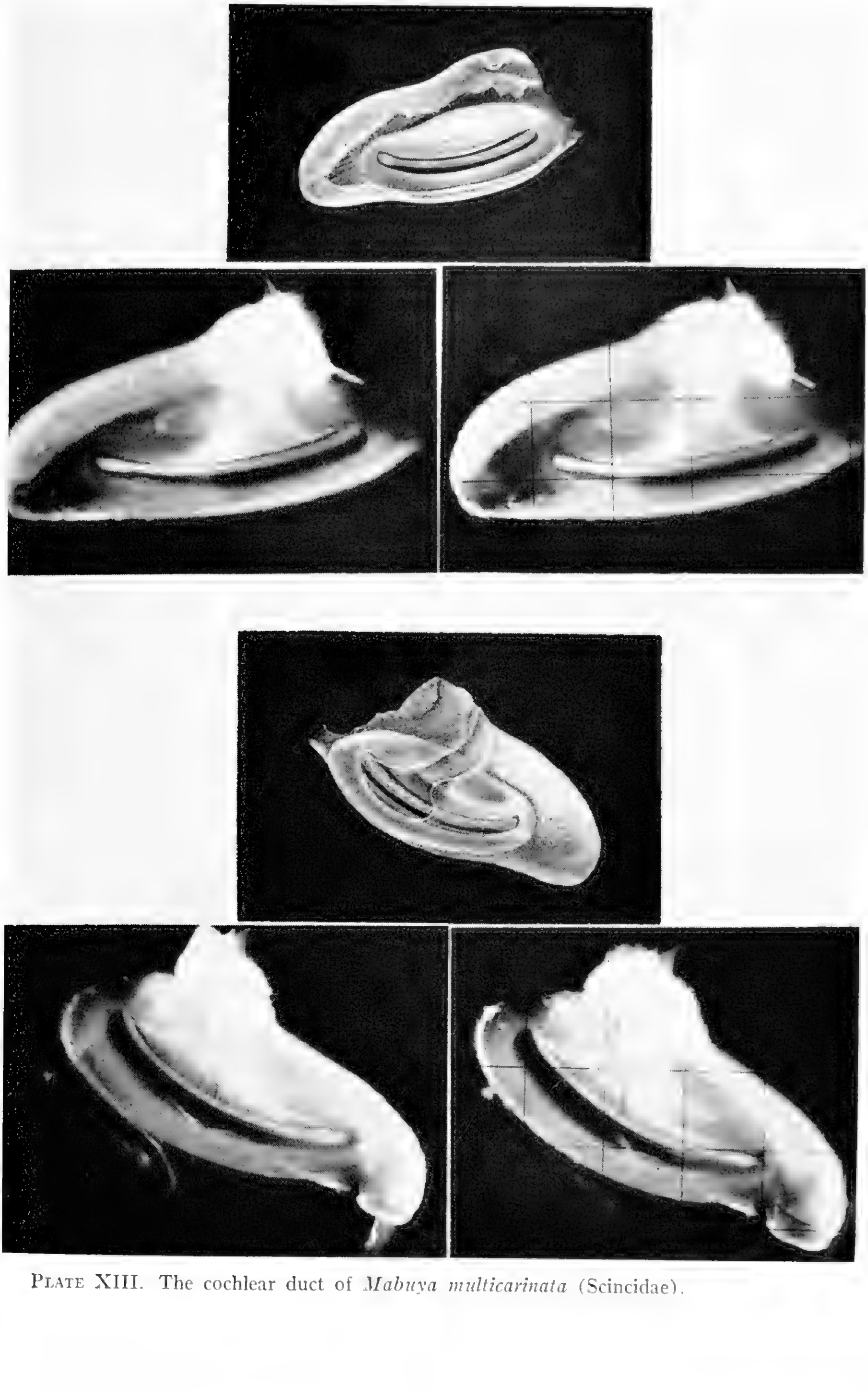

Plate XIII. The cochlear duct of *Mabuya multicarinata* (Scincidae).

PLATE XIV

Family FEYLINIIDAE

Feylinia currori (CAS 55111 [183])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 29
Stereopair × 38 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The anterior (lagenar) edge of the duct has a right-angle bend in its midportion. The greater portion of the macula lagenae occupies the anteroinferior end of the lagenar portion of the duct. A certain amount of precipitated protein and cellular debris obscures the details of the lateral side of the limbus in the photographs.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 29
Stereopair × 38 (one grid divsion = 0.39 mm.)

Posterosuperior is to the lower left, and anteroinferior to the upper right. The perilymphatic duct courses superiorly on the medial face of the cochlear duct. Note the long inferiorly directed limbic recess.

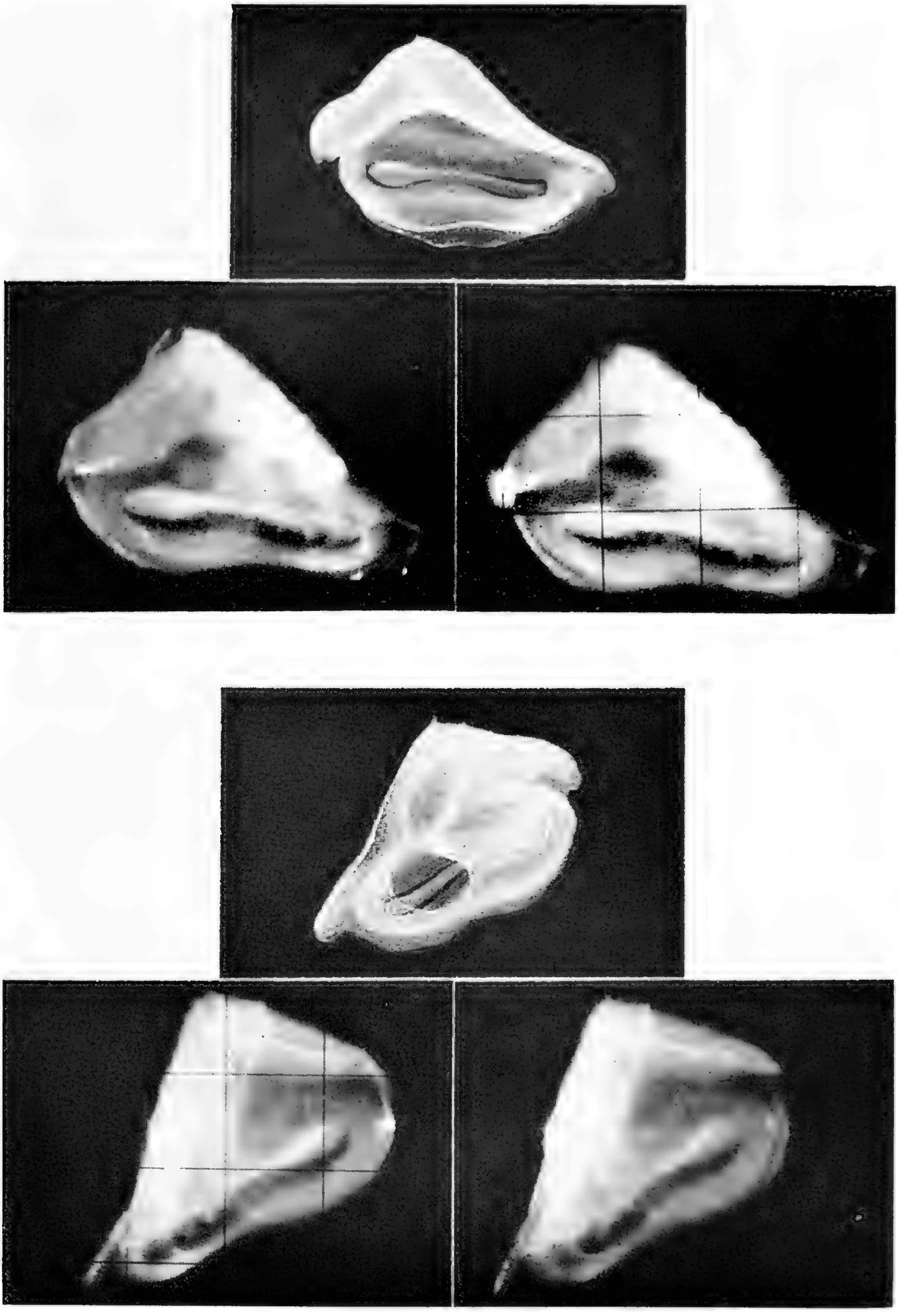

Plate XIV. The cochlear duct of *Feylinia currori* (Feyliniidae).

PLATE XV

Family XANTUSIIDAE

Klauberina riversiana (CAS 43848 [28])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 22
Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the upper right, and anteroinferior to the lower left. The vestibular membrane has been removed. The macula lagenae courses along the inner anterior (left) portion of the duct. The inferiormost portion of the macula lagenae is almost at a right angle to the papilla basilaris. The inferior tip of the papilla basilaris is separated from the superior portion.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 22
Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the upper left, and anteroinferior to the lower right. There is a relatively long inferior limbic recess (lower right). In the photograph the nerve to the papilla basilaris spreads out as it supplies the papilla. The nerve to the macula lagenae courses anteroinferiorly (to the right). Comparison of plates 13 and 15 reveals the striking similarities between the xantusiid and scincid cochlear ducts.

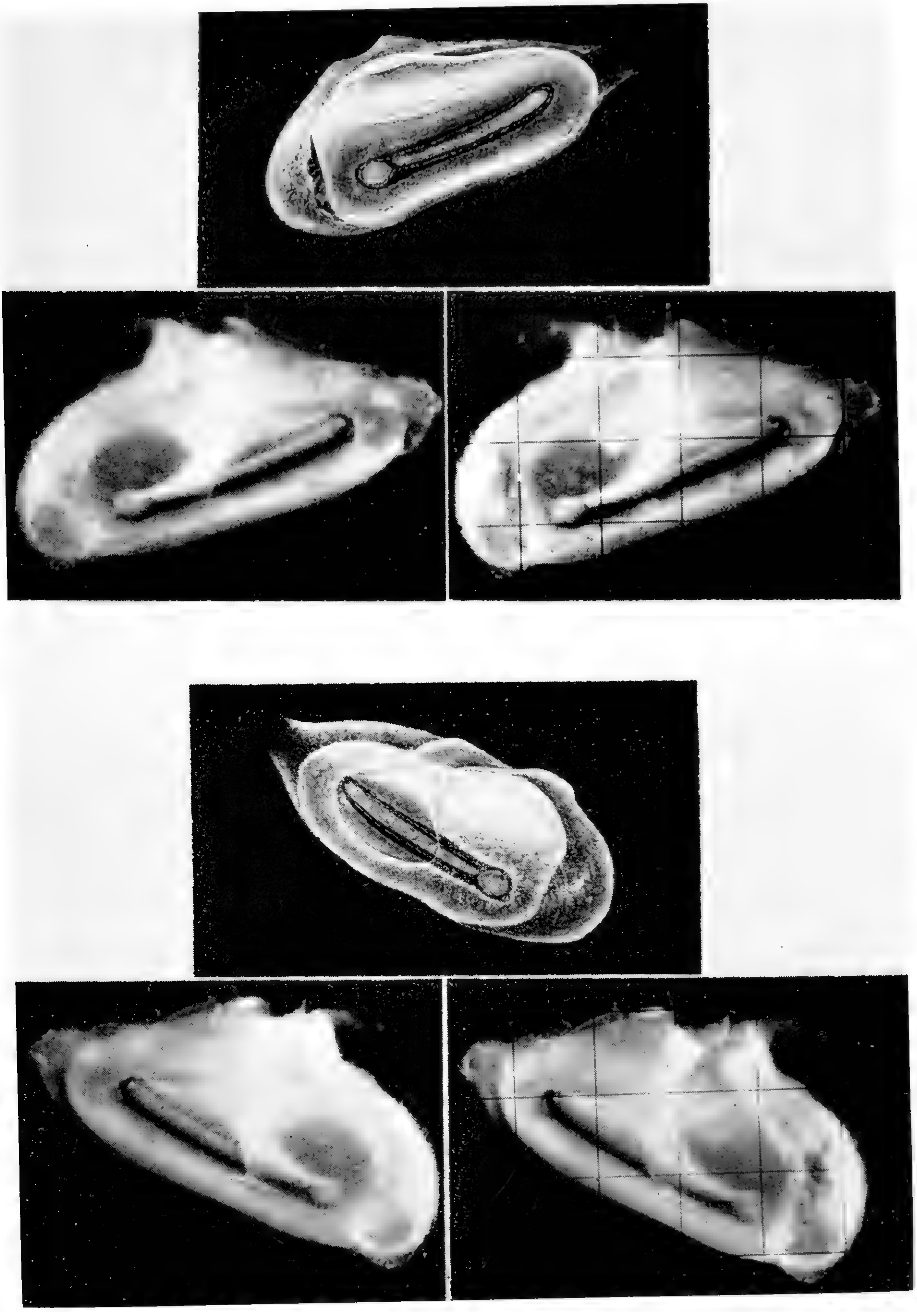

Plate XV. The cochlear duct of *Klauberina riversiana* (Xantusiidae).

PLATE XVI

Family CORDYLIDAE

Cordylus jonesii (CAS [290])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 18
Stereopair × 20 (one grid division = 0.58 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. A portion of the saccular wall is attached to the cochlear duct in the photographs. The macula lagenae courses down the anteroinferior edge of the duct. The nerve to the papilla basilaris fans out to supply the papilla.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 16
Stereopair × 20 (one grid division = 0.58 mm.)

Posterosuperior is to the upper left, and anteroinferior points downward. The nerve to the posterior ampulla has been cut off while the nerves to the papilla basilaris and macula lagenae are present in the photographs. Short superior and inferior limbic recesses are best demonstrated in the drawing.

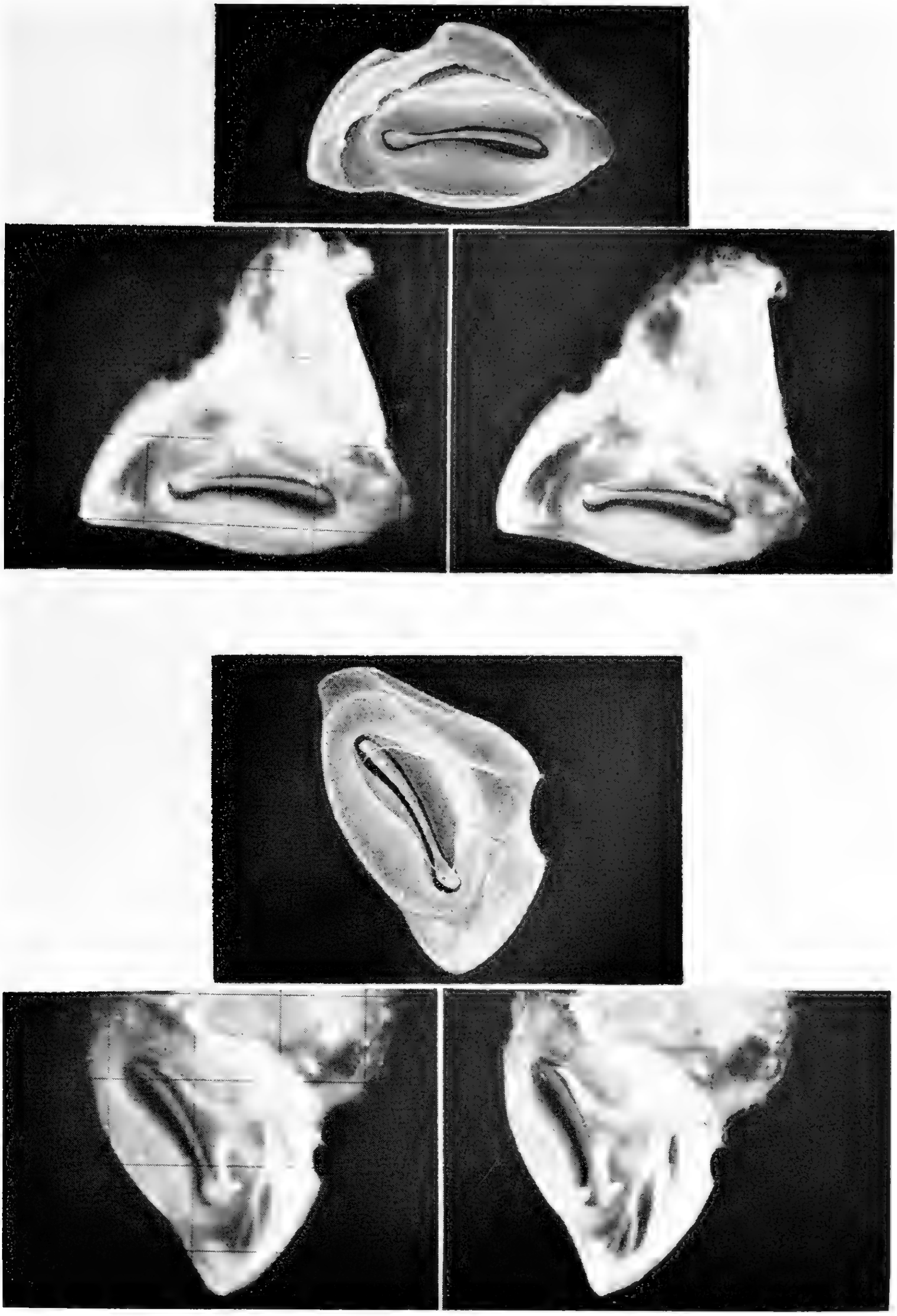

Plate XVI. The cochlear duct of *Cordylus jonesii* (Cordylidae).

PLATE XVII

Family DIBAMIDAE

Dibamus argenteus (SU 18761 [341])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 39
Stereopair × 33 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed in the drawing, but is intact in the photographs. A portion of the posterior semicircular canal and the posterior ampulla is present in the photographs. The inferior wall of the sacculus seems to be fused to the anterosuperior wall of the cochlear duct. A larger portion of the saccular wall is shown in the photograph. The small lagena forms the left (anteroinferior) end of the duct.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 39
Stereopair × 33 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior to the right. Note the groove for the perilymphatic duct on the medial face of the duct and the nerve branch supplying the papilla basilaris in the photographs.

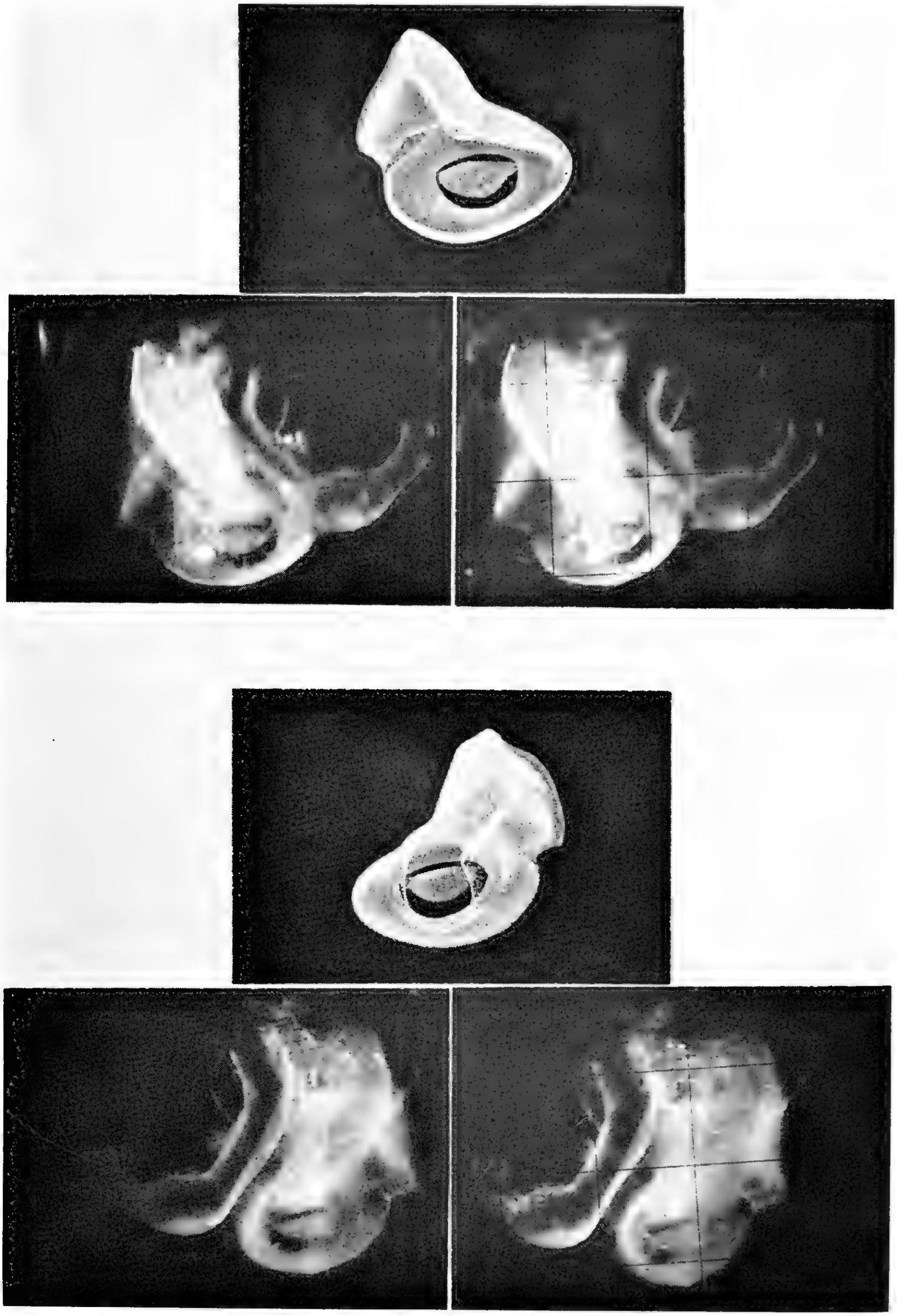

Plate XVII. The cochlear duct of *Dibamus argenteus* (Dibamidae).

PLATE XVIII

Family AMPHISBAENIDAE

Amphisbaena fuliginosa (CAS 71336 [227])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 22
Stereopair × 29 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane is intact. The macula lagenae lying on the left (anteroinferior) end of the duct is covered by an opaque white otolithic membrane. In most other specimens the calcium carbonate which was present in the otolithic membrane was dissolved away with weak acid, as it usually obscures the general structure. The limbic lip lies at the upper (anterior) edge of the neural limbus.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 29
Stereopair × 36 (one grid division = 0.39 mm.)

Posterosuperior is to the left, anteroinferior to the right. The white elongate structure on the right-hand side of the photograph is the nerve to the macula lagenae. The perilymphatic groove and part of the medial portion of the basilar membrane is obscured by a membrane in the photograph.

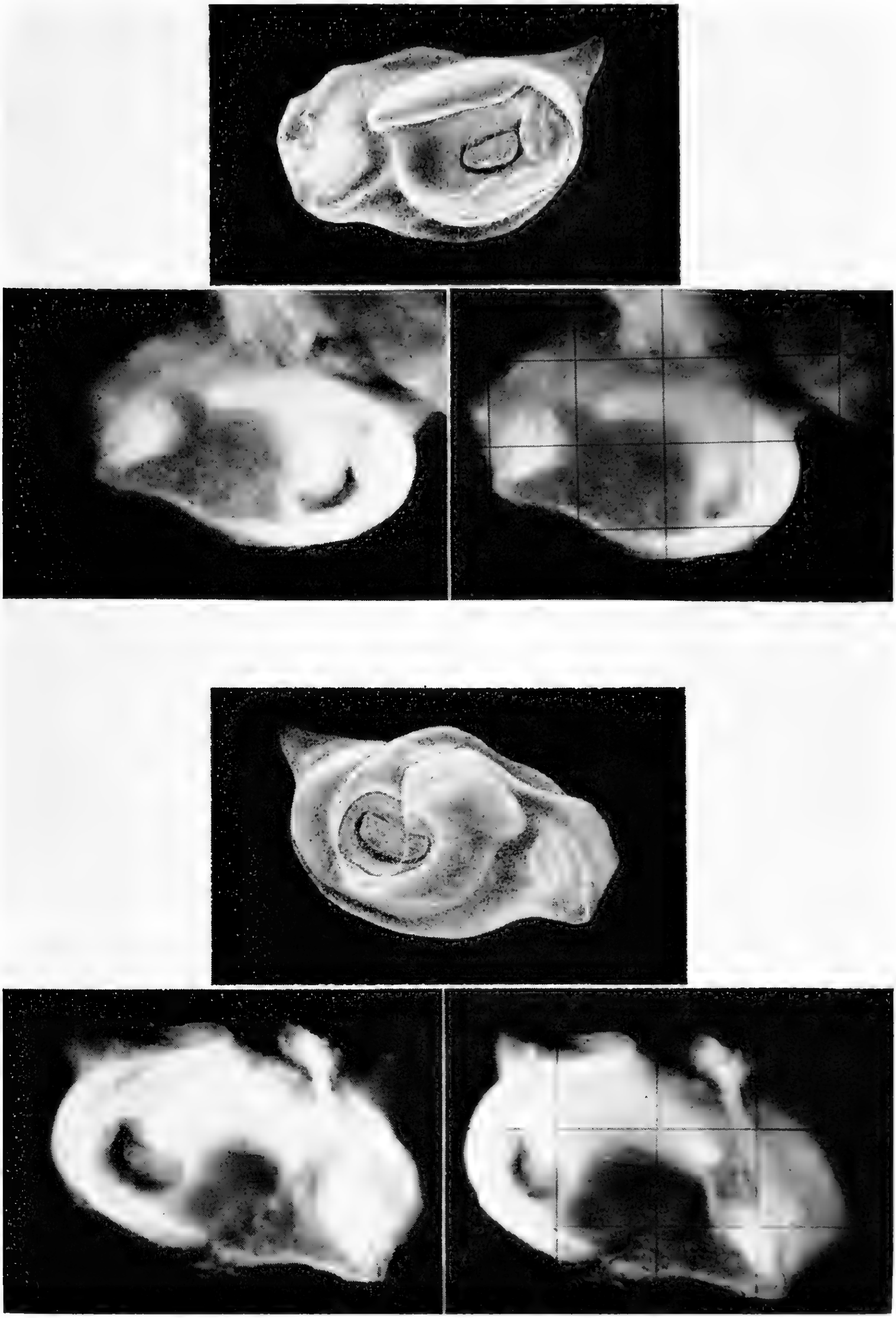

Plate XVIII. The cochlear duct of *Amphisbaena fuliginosa* (Amphisbaenidae).

PLATE XIX

ORDER OPHIDIA

Family COLUBRIDAE

Pituophis catenifer (CAS [291])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 22
Stereopair × 29 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The large lagenar sac lies to the left and the smaller limbic portion of the duct to the right. The apparent shelflike projection above the neural limbus seems to be an area of fusion between the sacculus and the anterior edge of the neural limbus. In the photograph, the distal, broken end of the nerve to the papilla basilaris is seen. The outlines of the perilymphatic duct sweeping from the lateral surface of the duct around to the medial aspect of the basilar membrane are evident in both lateral and medial views. The macula lagenae is an opaque white band on the anterior and medial inner surfaces of the lagenar sac.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 22
Stereopair × 29 (one grid division = 0.39 mm.)

Posterosuperior is to the upper left, and anteroinferior to the lower right. The course of the perilymphatic duct sweeps from the right upper side of the photo over to the medial aspect of the papilla basilaris. The nerves to the macula lagenae supply the band-like macula lagenae.

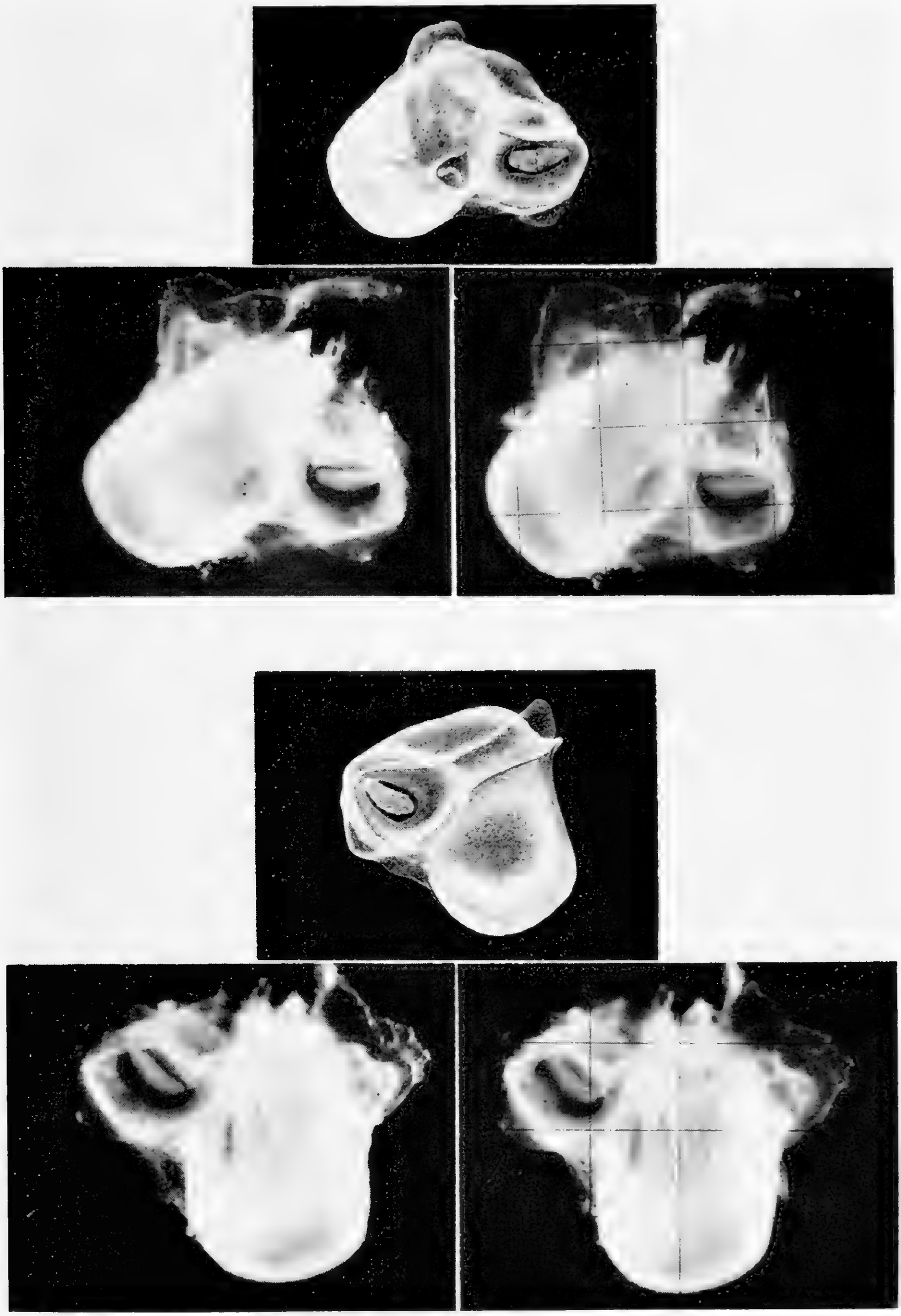

Plate XIX. The cochlear duct of *Pituophis catenifer* (Colubridae).

PLATE XX

SUBORDER CHELONIA

Family TESTUDINIDAE

Gopherus berlandieri (CAS [46])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 12
Stereopair × 12 (one grid division = 0.58 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The inferior wall of the sacculus (sac-like structure situated above in the drawing) remains attached (it seems to be fused) to the anterosuperior wall of the cochlear duct. The solid white structure running posterior (downward) in the photograph is the nerve to the crista of the posterior semicircular canal. The fuzzy processes surrounding the cochlear duct are trabecular connective tissue strands that attach the cochlear duct to the periosteum of the otic capsule. The ovate papilla basilaris is seen in the lower midportion of the pictures.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 12
Stereopair × 12 (one grid division = 0.58 mm.)

Posterosuperior is above, and anteroinferior below. The structure projecting to the left in the photograph is the nerve to the posterior crista. The nerves to the papilla basilaris and macula lagenae are also quite obvious in the photograph. The cavity in the midportion of the photograph is the groove for the perilymphatic duct as it sweeps around from the lateral to the medial surface (right side of the photograph) of the duct and then becomes the scala tympani portion of the perilymphatic sac where it lies over the basilar membrane.

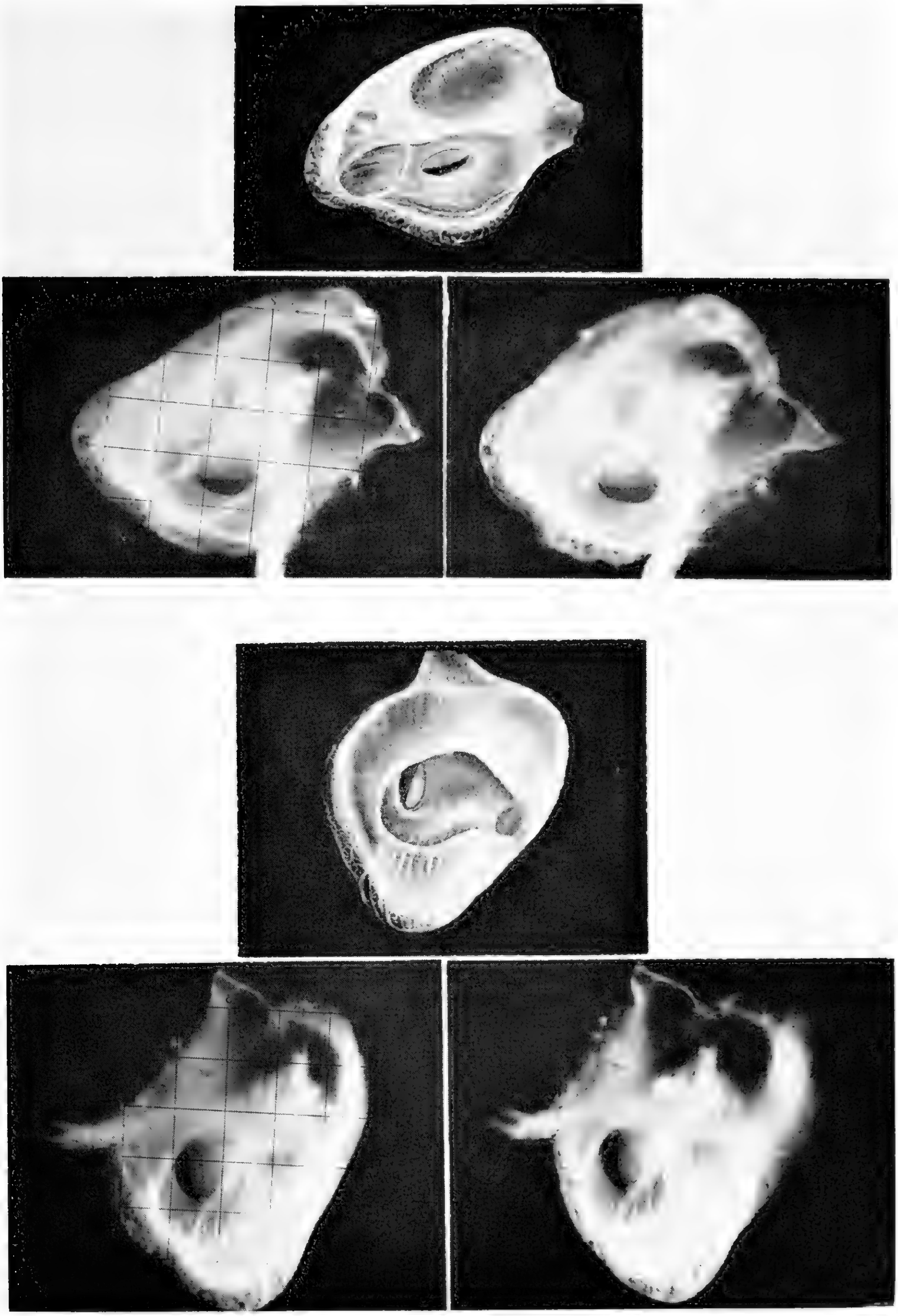

Plate XX. The cochlear duct of *Gopherus berlandieri* (Testudinidae).

PLATE XXI

ORDER RHYNCHOCEPHALIA

Family SPHENODONTIDAE

Sphenodon punctatum (CAS [40])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 9
Stereopair × 13 (one grid division = 0.76 mm.)

Posteroinferior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The sac-like pars lagena lies to the left and the limbic portion to the right. The basilar membrane is stretched across the lateral end of a tubelike limbus. The papilla basilaris has not been well preserved, but the residual outlines may be made out. The macula lagenae sweeps around the midportion of the lagena as a band-like area running from the lateral to the anterior and then onto the medial aspect. This is better seen in the medial view. Debris from the otolithic membrane lies within the lagenar sac.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 9
Stereopair × 13 (one grid division = 0.76 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The medial side of the limbus appears as a tubelike or deeply excavated pocket with the basilar membrane stretched across its lateral end. Two triangular arm-like processes almost close over a portion of the back of the limbus. The perilymphatic duct opens into the scala tympani portion of the perilymphatic sac above (anteromedial) these two arms and the large medial opening is the site of connection of the scala tympani with the perilymphatic sac proper.

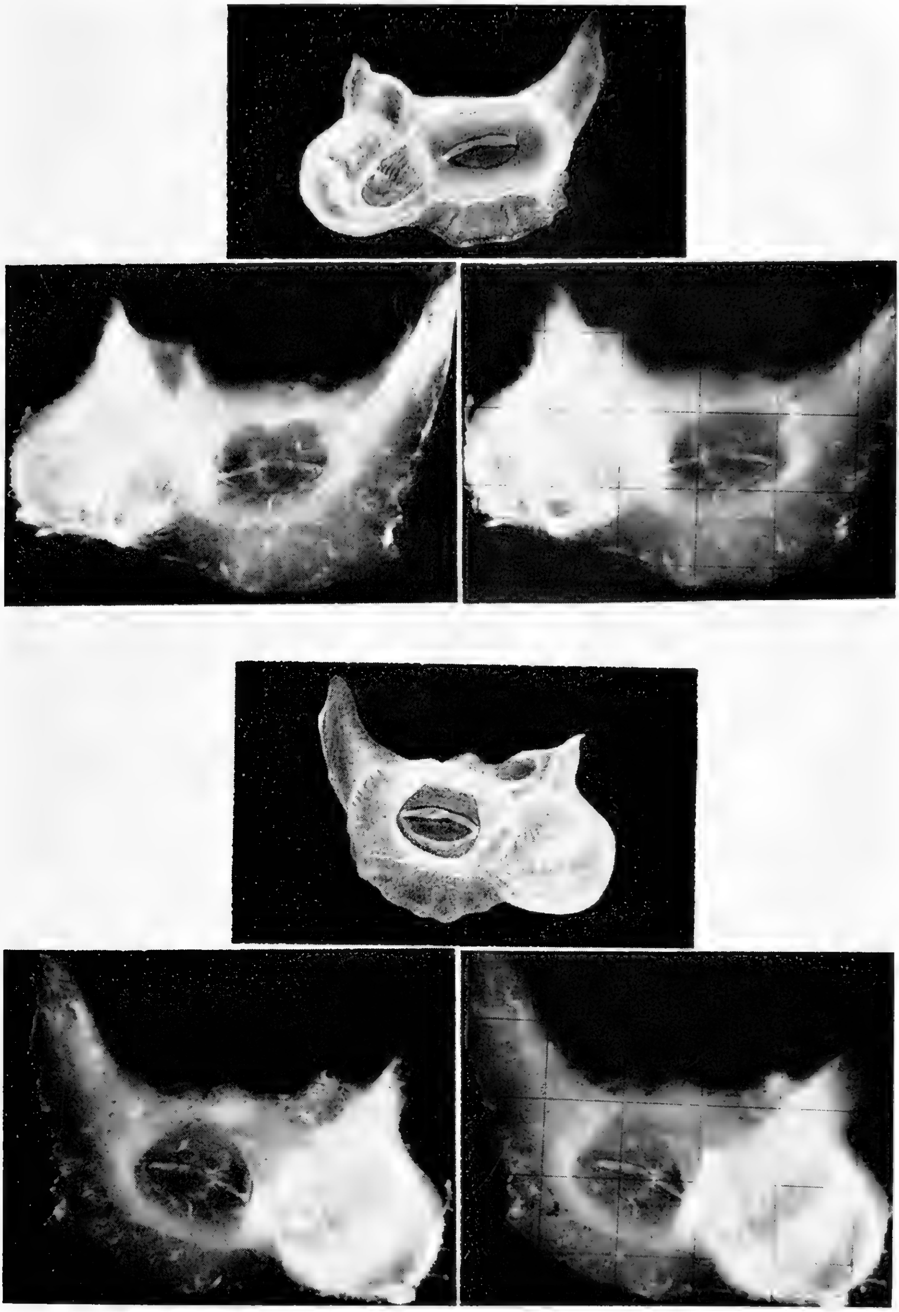

Plate XXI. The cochlear duct of *Sphenodon punctatum* (Sphenodontidae).

PLATE XXII

Summary plate comparing the lateral aspect of the cochlear duct in lizard families

Drawings of the lateral view of the left cochlear ducts from representatives of different families of lizards and an example of a snake, a turtle, and *Sphenodon.*

The cochlear ducts are not drawn to the same scale.

The cochlear ducts are arranged according to my present concept of the possible relationships between different lizard families as determined in part by the anatomical similarities in cochlear duct anatomy (see Discussion for further details).

I. Iguanidae Agamidae
II. Chamaeleonidae
V. Lacertidae Teiidae
VI. Gekkonidae Pygopodidae
VII. a. Scincidae b. Feyliniidae
c. Xantusiidae d. Cordylidae

III. a. Anguidae b. Anniellidae
c. Xenosauridae d. Helodermatidae
IV. Varanidae
VIII. Dibamidae IX. Amphisbaenidae
Snake—Colubridae Turtle–Testudinidae
Sphenodon

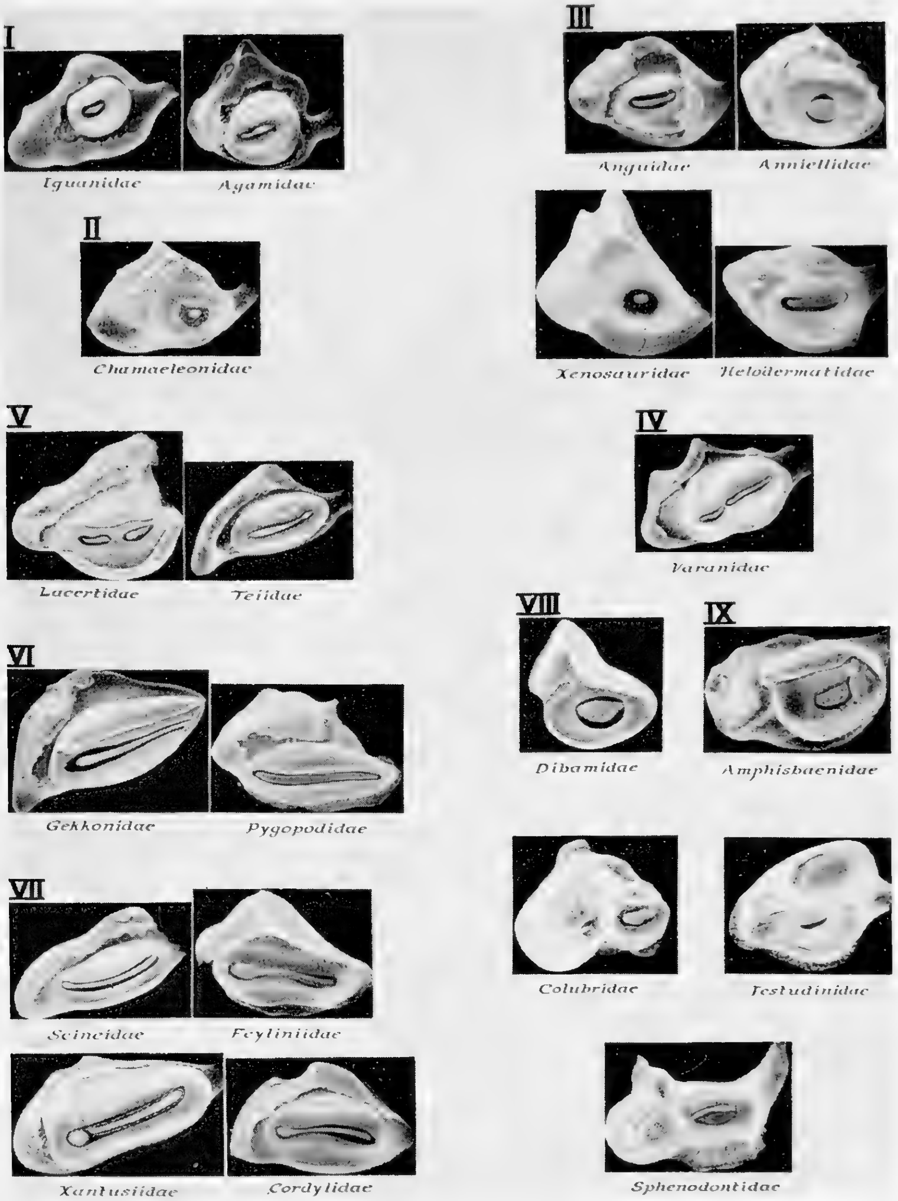

Plate XXII. Summary plate comparing the lateral aspect of the cochlear duct in lizard families.

PLATE XXIII

Summary plate comparing the medial aspect of the cochlear duct in lizard families

Drawings of the medial view of the left cochlear ducts from representatives of different families of lizards and an example of a snake, a turtle, and *Sphenodon*.

The cochlear ducts are not drawn to the same scale.

For explanation of arrangement see plate XXII.

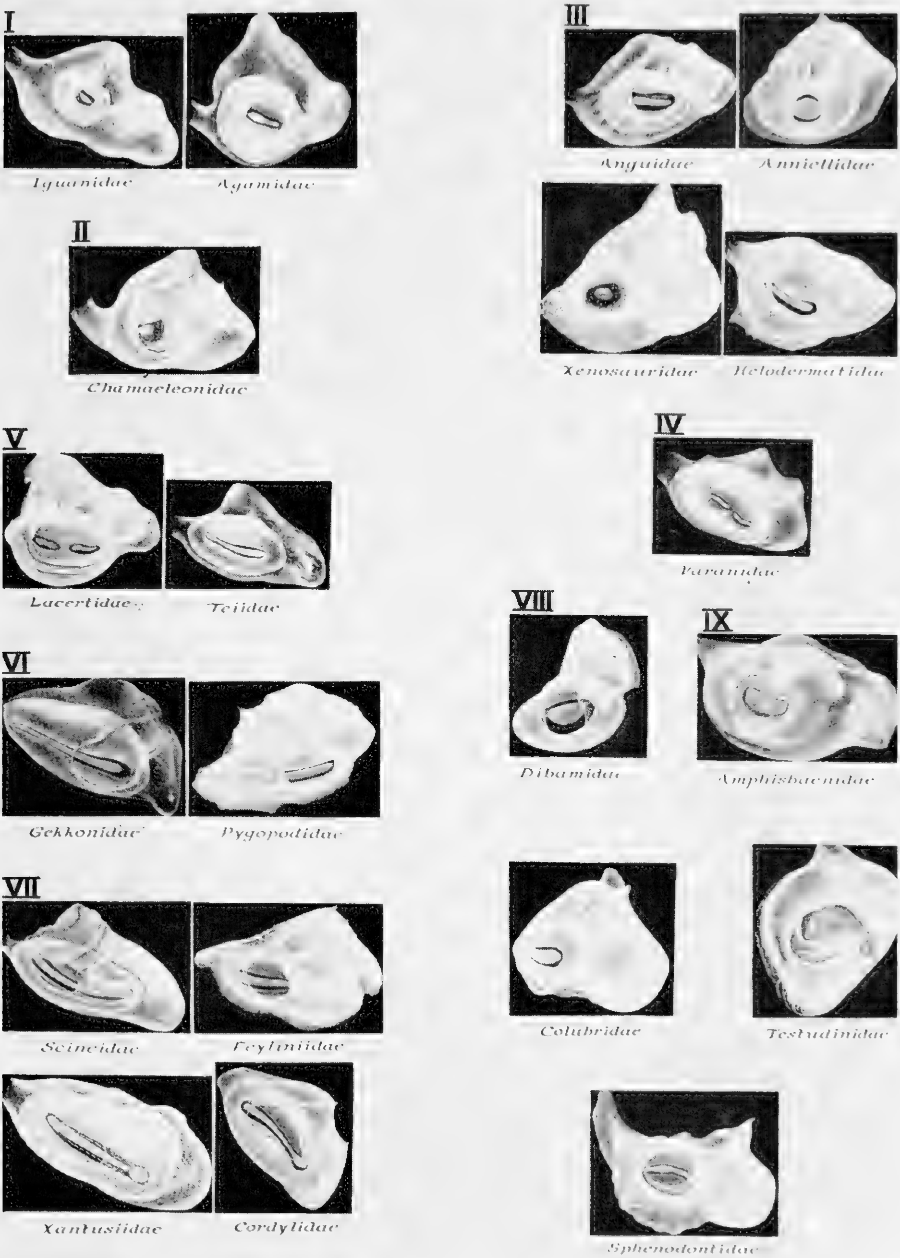

Plate XXIII. Summary plate comparing the medial aspect of the cochlear duct in lizard families.

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 12, pp. 361–414; 24 figs.; 5 tables May 12, 1966

GEOLOGY OF THE ISLAS REVILLAGIGEDO, MEXICO, 2. GEOLOGY AND PETROGRAPHY OF ISLA SAN BENEDICTO[1,2]

By

Adrian F. Richards

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Abstract: Isla San Benedicto is located where the Clarion fracture zone crosses a range of submarine volcanoes extending south towards Clipperton Island and including Isla Socorro. Field work conducted from 1952 to 1957 shows that San Benedicto is situated at the intersection of four local submarine ridges thought to mark fissures; the one extending north is the longest. Compared to the other three islands in the Revillagigedo archipelago, the insular shelf of San Benedicto is poorly developed and very narrow; shelf-break occurs at 55 to 75 fathoms. Principal landforms are large eroded trachytic domes, older in age than late Pleistocene, and two pyroclastic volcanoes of recent origin. The first geological map of the island shows that by volume the most abundant rock above sea level is sodic trachyte. Flows of trachybasalt and trachyandesite (mugearite) occur in a low stratigraphic position on the island and trachybasalt has been dredged from the narrow ridge extending north of the island. Accessory sodic rhyolite blocks were ejected from Volcán Bárcena during the eruption of August, 1952, to March, 1953. Twelve new chemical and 16 new alkali analyses of San Benedicto rocks indicate a reasonably regular differentiation from trachybasalt (alkali basalt) to sodic rhyolite, and an alkali-lime index of 52.6. Tholeiitic basalts, high alumina basalts, and rocks bearing feldspathoids have not been found. The increasing age and the decreasing quantity of silicic lavas and active volcanism from east to west in the Revillagigedos appears related to convection under the East Pacific Rise. The relationship to the Rise appears to account for the similarity of sodic rhyolites found on San Benedicto, Socorro, Easter Island, and elsewhere in the Pacific basin.

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[1] References to numbers 1, 3, and 4 of this series are cited in the bibliography in the present paper.

[2] Contribution from the Scripps Institution of Oceanography, University of California, New Series.

[3] Present address, Departments of Geology and Civil Engineering, University of Illinois, Urbana, Illinois 61803.

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INTRODUCTION

Isla San Benedicto is the third largest and most northeasterly of the four Islas Revillagigedo. It is located about 870 nautical miles south-southeast of San Diego, California (fig. 1); 220 miles south of Cabo San Lucas, the south tip of Baja California; and in the same latitude as Colima, Parícutin, Popocatépetl, and other volcanoes of the trans-Mexico volcanic axis.

On August 1, 1952, San Benedicto literally burst from obscurity to become known as the location of the first new volcano in the east Pacific Ocean whose birth was observed by human eyes. The birth and development of Volcán Bárcena, as the new volcano was named, is described in detail elsewhere (Richards, 1959—hereafter called part 1). Studies of this volcano led to an investigation of the terrestrial and submarine geology of the Revillagigedo archipelago by the University of California's Scripps Institution of Oceanography, in part with the cooperation of the Instituto de Geofísica, Universidad Nacional de México, and with the assistance of investigators from other institutions and organizations in the United States and Mexico.

San Benedicto was discovered by the Spanish explorer Ruy López de Villalobos in 1542. According to Herrera (Burney, 1803, p. 226–232), López de Villalobos named the island Santo Tomé. Other historians claim he called it Anublada or Nublada, meaning cloudy. A discussion of the early names applied to the island is given by Richards and Brattstrom (1959). The island never has been inhabited.

The first landing and geological study of San Benedicto was made on December 25, 1862, by members of the Longinos Banda expedition. Banda (1862, p. 183–184) reported that the island was volcanic, but not of recent origin, and that the rocks included basalt, trachyte, porphry, and pumice. There were brief visits to this island by expeditions of the California Academy of Sciences in 1905 (Slevin, 1931) and 1925 (Hanna, 1926), but if specimens were collected they are not known to be extant (L. G. Hertlein, personal communication).

Robert S. Dietz conducted the first investigation of the new volcano on two U.S. Air Force flights to the island in September, 1952, (Dietz, 1953). Howel Williams prepared a geological sketch map of San Benedicto during the time the plane circled the island on the second flight. In addition to papers listed in Richards and Brattstrom (1959) that briefly describe aspects of the eruption of Volcán Bárcena, more recent reports have appeared by Maldonado-Koerdell (1958b), Mooser (1958), Richards (1960), and Brattstrom (1963).

Field work consisted of a short visit by private ship in 1952 and by research ships of the Scripps Institution in 1953, 1955 (two cruises), and 1957. Ten photographic and observation flights were made to the island between early September, 1952, and late January, 1956, (part 1; Richards and Brattstrom, 1959); an additional flight was made in 1961. North of Cráter Herrera (fig. 2)

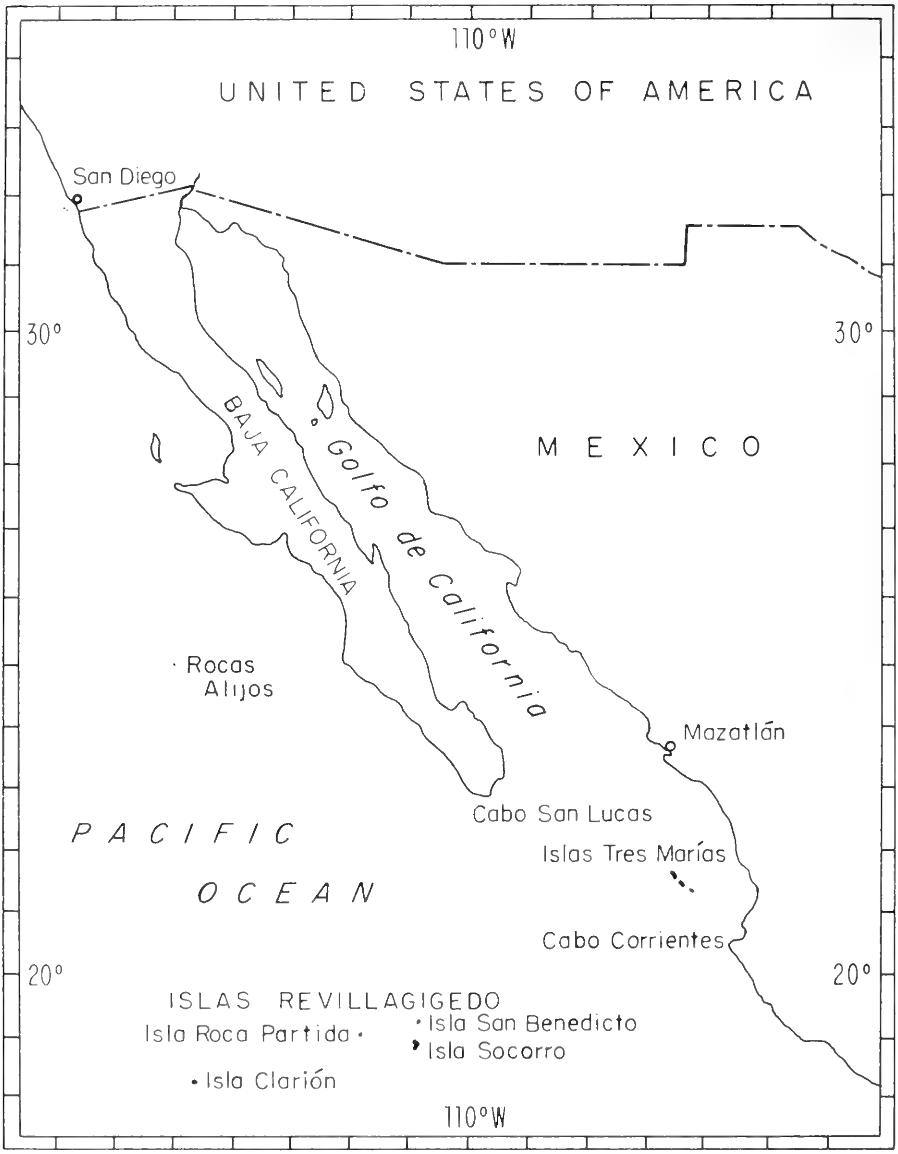

FIGURE 1. Location of the Islas Revillagigedo.

the geology was largely investigated by observing and sampling the near-vertical cliffs, and was appreciably assisted by examination of stereo-oblique air photographs taken at close range during an encirclement of the island by an airplane flying at an altitude of 600 feet. Elsewhere, investigations were conducted on

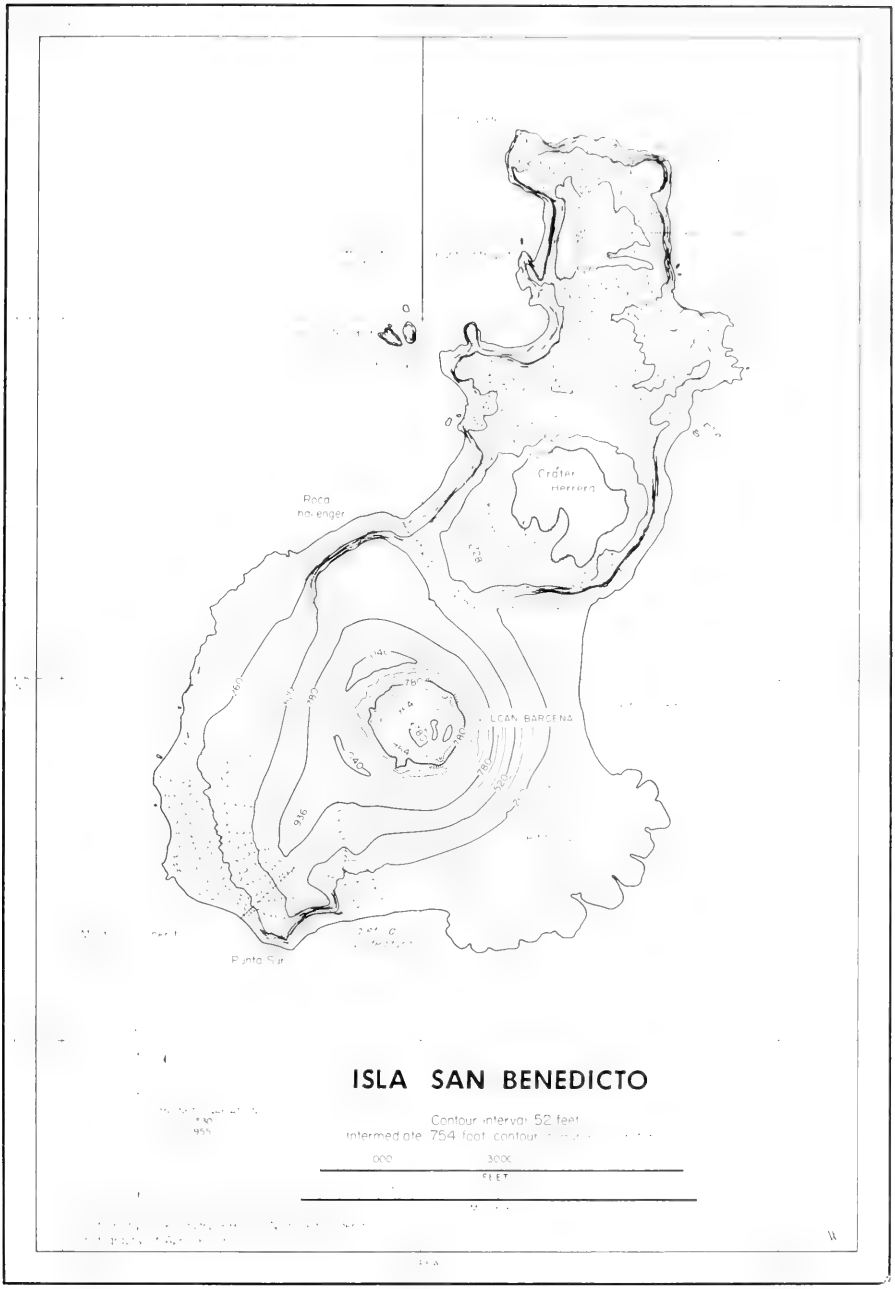

Figure 2. Topographic map of Isla San Benedicto.

foot with the aid of numerous photographs taken from airplanes, ships, and on land. Bathymetric studies in the vicinity of San Benedicto were made using techniques stated in the appendix; soundings in this region prior to 1952 were almost nonexistent.

It is possible to land on San Benedicto with impunity using a row boat only immediately adjacent to the Delta Lávico (usually west of the flow because of the prevailing northerly seas) or on the small pocket beach north of the prominent dikes at Punta Ortolan.

ACKNOWLEDGMENTS

In addition to those persons and organizations acknowledged in part one, Drs. Cordell Durrell and Howel Williams are thanked for petrographic assistance and for helpful discussions on different phases of the investigation. Dr. Williams also contributed a chemical analysis of a piece of floating pumice. Dr. Edward J. Zeller made available the alkali analyses. The two chemical analyses of submarine lava were financed by the California Research Corporation and made available by Drs. Jack Green and N. Allen Riley. Other chemical analyses, some film, and certain travel expenses were financed by Geological Society of America Project Grant 625–53. This paper was revised from part of my doctoral dissertation during the winter of 1960–1961, when I was a National Academy of Sciences—National Research Council Post-doctoral Resident Research Associate at the U.S. Navy Electronics Laboratory working under Dr. E. L. Hamilton. Additional changes to the manuscript were made in January, 1965, at the University of Illinois. I am appreciative to Drs. W. Bryan, Jr., G. Macdonald, and S. R. Nockolds and Ings. F. Mooser and G. P. Salas for reviewing a preliminary copy of this paper and for making helpful suggestions. Opinions and assertions in this paper are my own and are not to be construed as official views of organizations within the Department of Navy.

GEOLOGIC SETTING

Regional.

In the early 19th century Humboldt (1811, p. 221) supposed ". . . that there exists in this part of Mexico (region of Volcán Jorullo), at a great depth in the interior of the earth, a chasm in a direction from east to west—from the Gulf of Mexico to the South Sea." He wondered if the "chasm" extended to the Islas Revillagigedo, which are in the same latitude as the trans-Mexico volcanoes. More recently Menard (1955, p. 1167–1170) proposed that the submergent features of the Clarion fracture zone, extending over 2000 nautical miles west of Isla Clarión, are related to the Islas Revillagigedo and the trans-Mexico volcanic belt. This belt is characterized by late Cenozoic and Recent volcanoes (de Cserna, 1958); recent tectonic interpretations have been made by Maldonado-Koerdell (1958a) and by Mooser and Maldonado-Koerdell (1961). Menard believed that the most probable age of this and other fracture zones off North America was post Mesozoic.

The Clarion fracture zone has been explored in some detail from 121° W. to 109° W. West of 116° W. it is characterized by a narrow, east–west trending ridge located in 18° 10′ N. latitude at the south side of the fracture zone. A trough extends parellel to and is located north of the ridge. Between Clarión and Socorro the ridge is discontinuous. There is some bathymetric evidence indicating that it may continue from about 111° W. (the longitude of Socorro) to about 110° W.; over this distance it is broader and located about 18° N. If this evidence is valid, it is possible that the apparent 10-nautical-mile displacement is related to the range of submarine volcanoes extending over 300 nautical miles south of Socorro toward Clipperton Island (Richards, 1957a, 1957b). Just north of Clipperton this range is represented by the Mathematicians Seamounts (see Menard and Fisher, 1958). Isla San Benedicto is located at the north end of the same range. The Revillagigedo archipelago is located on the west flank of the East Pacific Rise (see Menard, 1958; 1959, p. 207; 1960).

Isla Clarión appears to be genetically related to the Clarion fracture zone and the oldest island in the archipelago for the following reasons: (1) there is an east–west elongation of the deep submarine isobaths around the island, (2) the oldest rocks on land were erupted from an east–west fissure extending along the south side of Clarión (Bryan, 1959), and (3) Clarión has, compared to the other islands, more advanced terrestrial erosion, (4) a greater insular shelf width, (5) better development of fringing coral reefs, and (6) no historic record of volcanic activity.

The relative age of Isla Roca Partida is uncertain (Richards, 1964). If a west to east progression of volcanism occurred in the Islas Revillagigedo similar to the Hawaiian, Caroline, and Society islands (Richards and Dietz, 1956, p. 165), then Roca Partida is probably younger than Clarión but older than San Benedicto and Socorro, which probably are about the same age.

There is no historic record of volcanic activity on San Benedicto before the eruption of Bárcena in 1952. Socorro is the only island in the archipelago with known past activity, reported eruptions having occurred in 1848 (Revere, 1849, see reprint, 1947, p. 234–235), 1896 (Yarza, 1948, p. 163), and 1951 (Crowe and Crowe, 1955, p. 252). Sapper (1917a, p. 299) cites a manuscript by Noak stating that floating pumice, presumably from a submarine volcano, was reported in the vicinity of the Revillagigedos, 19° N. and 110° 12′ W.; unfortunately, a date was not given by Noak. A misprint of the longitude is given in another paper by Sapper (1917b, p. 75), which is repeated by Neumann van Padang (1938, p. 95). There is no bathymetric evidence for a submarine volcano in this location and it is likely that the observed pumice had a terrestrial origin, conceivably from the Montículo Cinerítico volcano on San Benedicto? Large amounts of drift pumice similarly resulted from the eruption of Volcán Bárcena (Richards, 1958a). Detected earthquakes reported by the United States Coast and Geodetic Survey are rare in the vicinity of the Islas Revillagigedo. In the period 1952 through 1959, 7 earthquakes were reported, 5 of which appear to have had epicenters near Isla San Benedicto and Isla Socorro.

Local.

Orientation of four submarine ridges at San Benedicto suggests the probable presence of a major fissure striking about N. 15° to 20° W. and two minor fissures striking about N. 37° E. and N. 41° W. (fig. 3). A 3-mile strike-slip displacement of the major ridge (N. 15° to 20° W.) by the one extending southwest of the island may have occurred, but the evidence is inconclusive. The fissures intersect at Isla San Benedicto, which represents the location of the maximum outpouring of lava. In figure 3, the dashed lines represent the inferred continuation of fissures for which there is no bathymetric evidence.

Where the topography is not complicated by ridges, the insular slope between 100 and 500 fathoms is about 20 °. An abrupt change of declivity, the shelf-break, is located between insular slope and shelf. Off south San Benedicto shelf-break occurs at 55 to 60 fathoms near the Delta Lávico. Off north San Benedicto a shelf-break of about 70 to 75 fathoms was recorded on a line of soundings north-northeast of Punta Observer. Elsewhere, shelf-break is poorly defined on echograms. According to the concept of Dietz and Menard (1951, p. 2011), shelf-break is abrasional in origin and related to sea level about 5 fathoms or less above the break. This implies that the shelf was cut during a lower sea level, presumably during the Pleistocene. An alternative explanation, that the island has submerged this much, is unlikely. The gradually decreasing depth of shelf-break from north to south suggests tilt of the insular mass, probably caused by ascending magma under the south part of the island. The insular shelf is absent southwest of Montículo Cinerítico, which apparently extends across it. In the vicinity of Cráter Herrera the shelf is about 3800 feet wide. The shelf is the broadest off Cerro López de Villalobos, where it extends 3300 to 9000 feet beyond the shoreline. In this region it has a seaward slope of 3° to 8°.

CARTOGRAPHY

The first map of Isla San Benedicto probably was drawn by Captain Colnett, R. N., (1798) in 1793. A sketch survey made by the officers and men under Commander George Dewey of the U.S.S. *Narragansett* in 1874 was the first map to show the island in any detail. This sketch was in use on U.S. Navy Hydrographic Office chart no. 1688 as recently as the edition of 1951.

San Benedicto was photographed from the air in April and May, 1953, by the U.S. Navy Photographic Squadron Sixty-one at the request of the Office of Naval Research for the Scripps Institution of Oceanography. Jack Caudry,

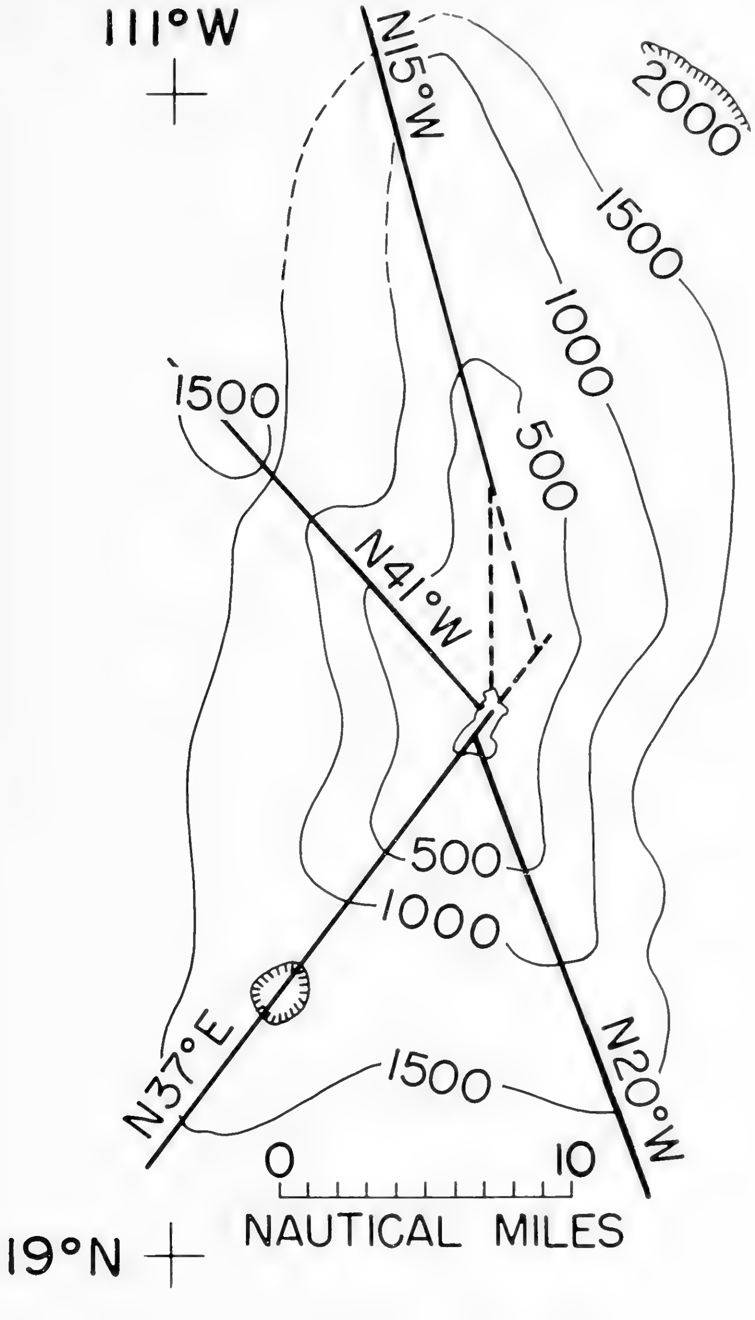

Figure 3. Map showing the inferred submarine fissure pattern in the vicinity of San Benedicto.

PHC, USN, prepared an excellent topographic map from these photographs during the summer of 1954. He drew form lines by stereocomparagraph and multiplex methods from the aerial photographs taken on April 16, 1953. Technical assumptions made by me when the contour interval, geographic coordinates, and scale were established are discussed in the appendix.

This new map (fig. 4 and fig. 2) shows that San Benedicto is about 2.8 miles long, 1.6 miles wide at Volcán Bárcena, and has an area of 2.32 square statute miles. Geographic names shown on this map previously were reported and discussed by Richards and Brattstrom (1959).

GEOLOGY

San Benedicto is divided into four regions for descriptive purposes: the long submarine ridge extending north of the island; a region of eroded domes, lava flows, and tuffs extending from Cráter Herrera to the north end of the island and including the Rocas Trinidad sea stacks; Roca Challenger and Cráter Herrera domes; and the tephra (collective term for all rock materials fragmented by a volcanic eruption that have not consolidated) cones of Bárcena and Montículo Cinerítico and their associated lava flows. The west side of the island is not easily accessible and is less well known compared to the east side, particularly north of Cráter Herrera.

NORTH RIDGE.

It seems appropriate to call the long, narrow submarine ridge extending almost due north of Isla San Benedicto (fig. 5) "North Ridge" because of its lineation. Bathymetry of the north part of this ridge is only approximately defined in figure 5 because of the difficulty in obtaining accurate bearings on the island. The extreme north end is abruptly terminated about 23 nautical miles north-northwest of San Benedicto by a moat. The narrowness of the ridge is indicated by a 5.5-mile width between 1000-fathom isobaths 10 miles north of the island and a 4-mile width 15 miles north. Less than 7 miles north of San Benedicto the ridge changes direction from north to north-northwest.

A number of shoal areas, not all of which are shown in figure 5 because of the scale, are located on North Ridge. Possibly these areas may represent parasitic cones or domes? It is equally possible that the "cones" will be found to coalese and become north–south ridges when North Ridge is surveyed in greater detail. The shoal areas have an average slope of 13° to 24° in the upper 150 to 200 fathoms, generally steeper than the 15° flank slope normal to the ridge axis 10 miles north of the island.

Olivine-bearing alkali basalt lava and scoria was dredged from a depth of about 350 fathoms near the summit of North Ridge at a distance of 8 nautical miles from the island in March, 1957. It is likely that the bulk of North Ridge is composed of tephra and lava having about this composition.

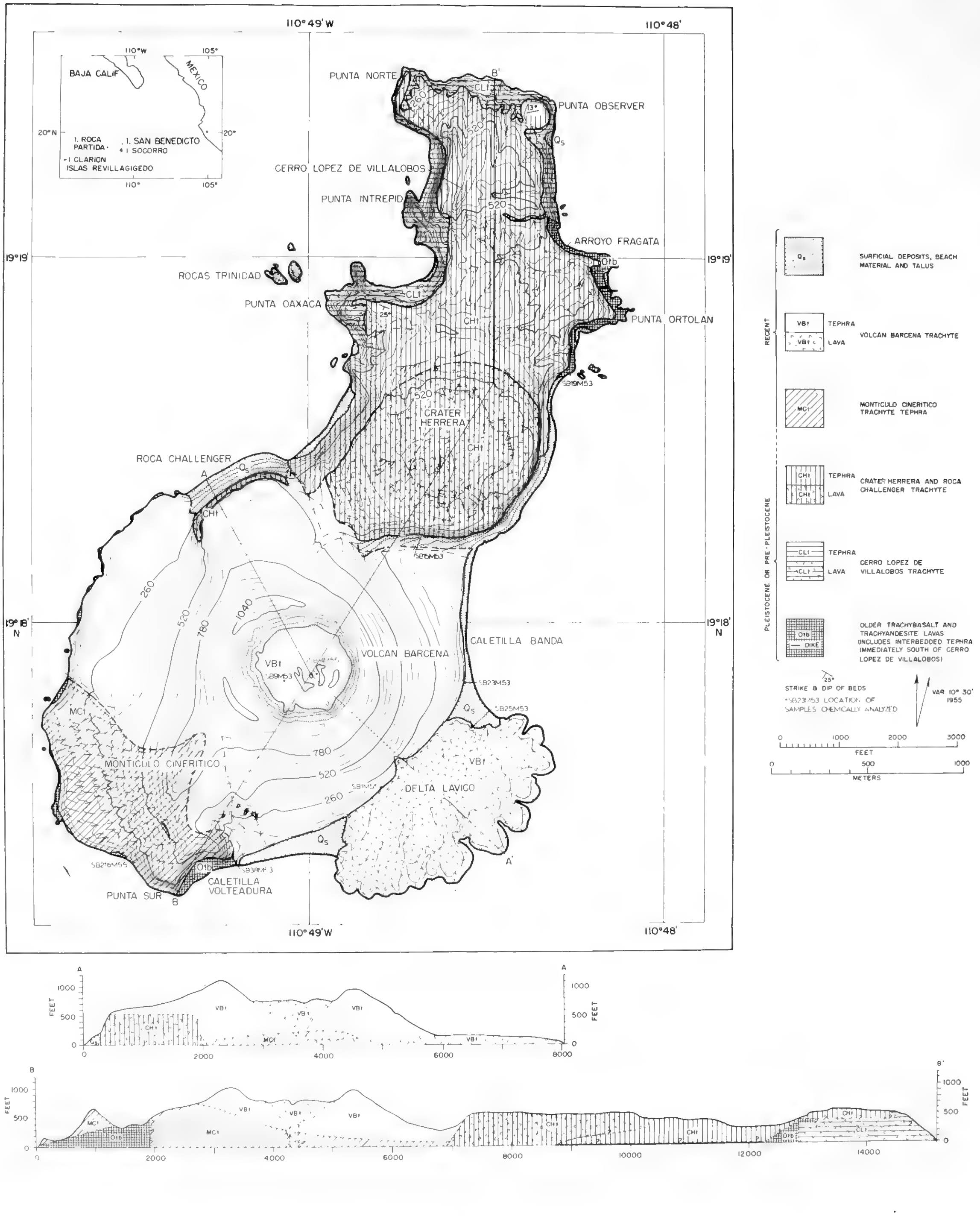

Figure 4. Geologic Map of Isla San Benedicto.

Figure 5. Map of the submarine topography in the vicinity of Isla San Benedicto.

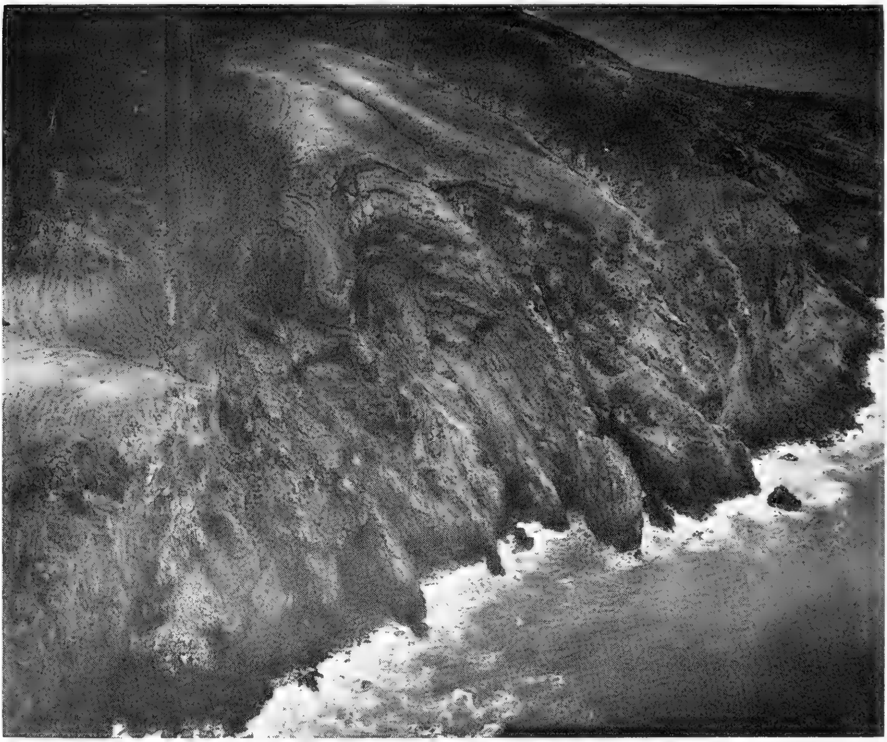

Figure 6. Oblique air photograph of the north side of San Benedicto showing tuffaceous strata dipping north. Punta Observer just to left of photograph, Rocas Trinidad top center. U.S. Navy official photo, November 15, 1952.

North end of Isla San Benedicto.

North of Cráter Herrera the island consists of mafic flows occurring near sea level; overlying trachytic tuffs, tephra, and lava; and the complex of Cerro López de Villalobos. Bárcena tephra covers most of the outcrops, except those in the arroyos, and the geology is best observed in the sea-cliffs (fig. 6).

Flows of trachybasalt extend from under the north end of Cráter Herrera to Cerro López de Villalobos. Most of Punta Ortolan is composed of these flows and tuffs. South of the point the flows are thin and are found at the base of the east sea-cliff. The least silicic lava thus far found on San Benedicto, trachybasalt, occurs as a conspicuous small flow of dense, dark gray lava with abundant reddish-brown olivine megaphenocrysts just north of the minor headland with off-lying rocks located about 1200 feet south of Punta Ortolan. The flows and tuffs comprising Punta Ortolan are capped with a flow of trachyandesite and are cut by vertical dikes both north and south of the point. North of the point these dikes are composed of trachyandesite and appear to intersect the horizontal

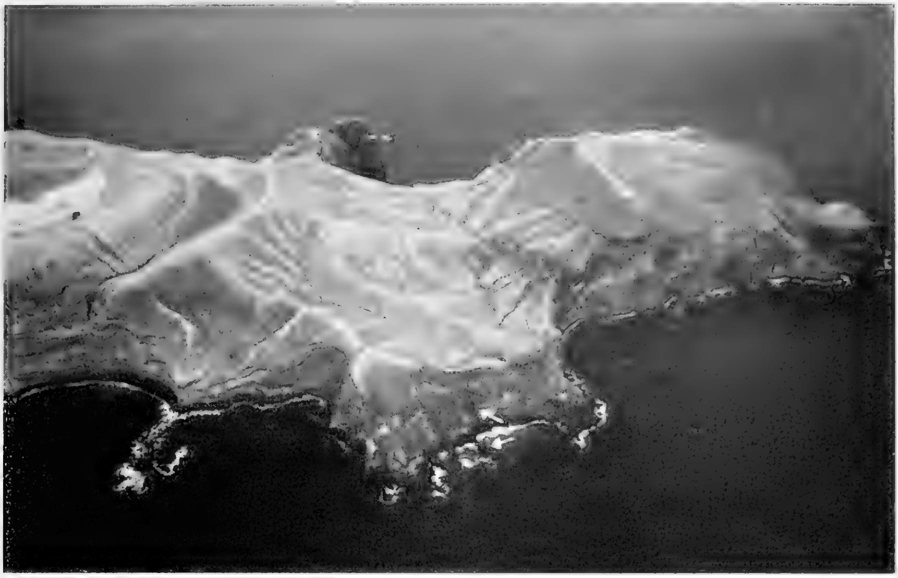

Figure 7. Oblique air photograph of the northeast end of San Benedicto. Punta Ortolan, vertical dikes (shown by arrows), and landing place to the right of arrows; Punta Observer extreme right. U.S. Navy official photo, May 27, 1955.

trachyandesite flow; they do not extend into the flow of trachyte directly above it. Commencing with the small promontory north of Punta Ortolan, interbedded tuffs and flows of trachybasalt and trachyandesite dipping about 30° south-southwest abut against the massive lava of the Cerro. They do not appear to be exposed on the west side of the island.

Thick deposits of horizontally-bedded trachytic tephra, tuff, and lava extending from under the dome of Cráter Herrera to the north end of the island cover the more basic flows. South of the Cerro, these deposits and overlying Bárcena tephra are dissected by the Arroyo Fragata drainage system. The prominent ridge paralleling Cráter Herrera to the north appears from the east cliff exposure to be composed of these tuffs, although trachytic lava crops out on the south side midway between shores.

Cerro López de Villalobos geology is relatively more complicated. The Cerro is veneered on the north side with trachyte and sodic andesite (?) tuffs and lavas that dip about 30° to the north (fig. 7). On the southeast side, as previously mentioned, mafic lavas and tuffs dip to the south-southwest. On the southwest side about 1000 feet south of Punta Intrepid, horizontally-bedded tuffaceous strata turn up where they abut against the massive lava of the Cerro. Punta Observer is composed of massive trachytic lava. Presumably the unsampled lava exposed in the east cliff of the Cerro is part of the same structure? Columnar

FIGURE 8. Photograph of Roca Challenger viewed from the east before the eruption of Volcán Bárcena. Cráter Herrera to right. D. H. Bates photo, February, 1952.

jointing is fairly well developed south of Punta Observer. A flow of trachyandesite having a slight dip to the east conspicuously crops out on the south flank of the Cerro at an altitude of about 260 feet. It does not appear to extend very far to the north. This flow and the massive trachytic lava farther north are overlain by nearly-horizontal trachytic tuffs and lavas.

Northwest of Cráter Herrera a lithic basaltic tuff is found at the foot of the arroyo immediately south of Punta Oaxaca. Elsewhere in this region the horizontal strata predominantly are trachytic tuffs. The massive lava of Punta Oaxaca is trachyte and the lithic trachytic tuffs overlying it dip about 25° to the south-southwest.

The relation of the remnants of the presumably trachytic domes of Punta Oaxaca, Rocas Trinidad, the sunken rock west of the Rocas Trinidad, and one or more domes of Cerro López de Villalobos is obscure. The extent of the insular shelf off the north end of the island suggests that long ago there may have been a number of volcanoes in this region.

CRÁTER HERRERA AND ROCA CHALLENGER.

The domes of Roca Challenger and Cráter Herrera are similar in appearance, structure, and composition. Both are steep-sided, nearly cylindrical in plan, rise over 500 feet above sea level, and have a rocky talus at their base. It is uncertain whether they interconnect beneath the pyroclastics that connect the two domes (see fig. 8). Roca Challenger has an approximate diameter of 2000 feet and an estimated volume of 700 to 1300 million cubic feet above sea level (estimate aided with pre-Bárcena photographs). Cráter Herrera has an average diameter of 3000 feet and an estimated volume above sea level of 1500 to 3500 million cubic feet. More exact volumetric figures cannot be obtained because

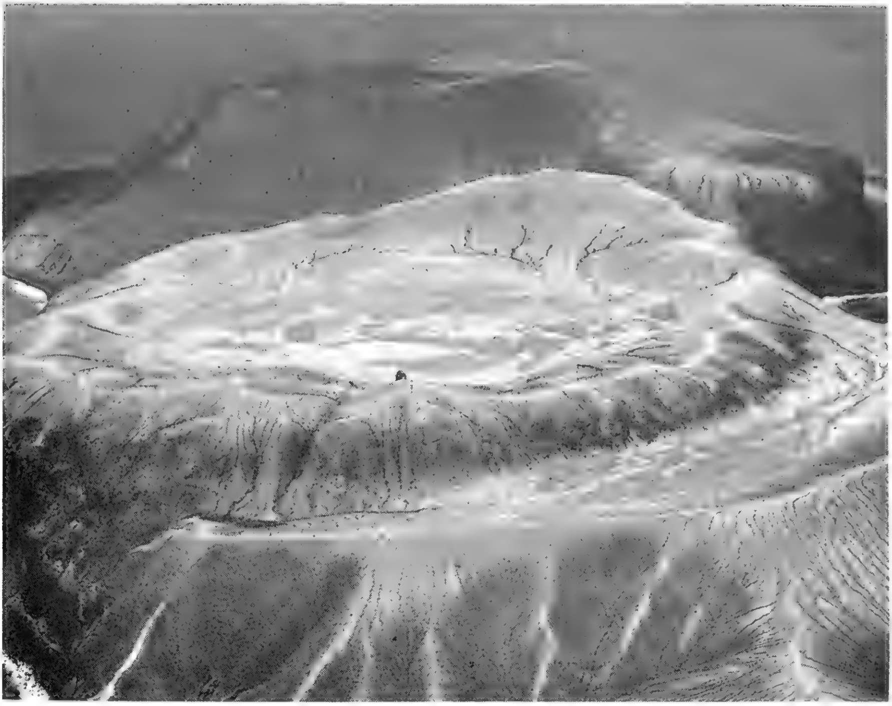

Figure 9. Oblique air photograph of Cráter Herrera showing summit crater, resistant outcrop on north rim (foreground), and Volcán Bárcena and Roca Challenger in background. Water is ponded in the north part of the crater. U.S. Navy official photo, September 21, 1953.

the position of contacts beneath the domes, except for a few places, are unknown.

The top of Roca Challenger was very slightly convex and littered with scattered angular blocks before the eruption of Bárcena (fig. 8). The top of Cráter Herrera still is basin-shaped, . . ."the most perfect crater many of us had seen" (Hanna, 1926, p. 63), and dips to the northeast (fig. 9). Near the center of the depression there is a small summit crater that is breached to the northwest. A semi-detached outcrop of lava looking like an eroded spine is located at the north end of the basin; it represents a more resistant portion of the steep north rim. Attitude of Cráter Herrera trachyte lava above the tuffaceous trachytic strata on the northeast side suggests that at least Herrera dome was formed within the crater of a pyroclastic cone, now almost entirely eroded away, rather than being the remnant of an extremely large viscous extrusion. Trachytic lava of both domes is porphyritic, dense, and probably was emplaced by exogenous growth by effusion from a summit crater. Such a crater has not been observed on Roca Challenger, however. Vertical columnar jointing is well developed on most of the cliffs.

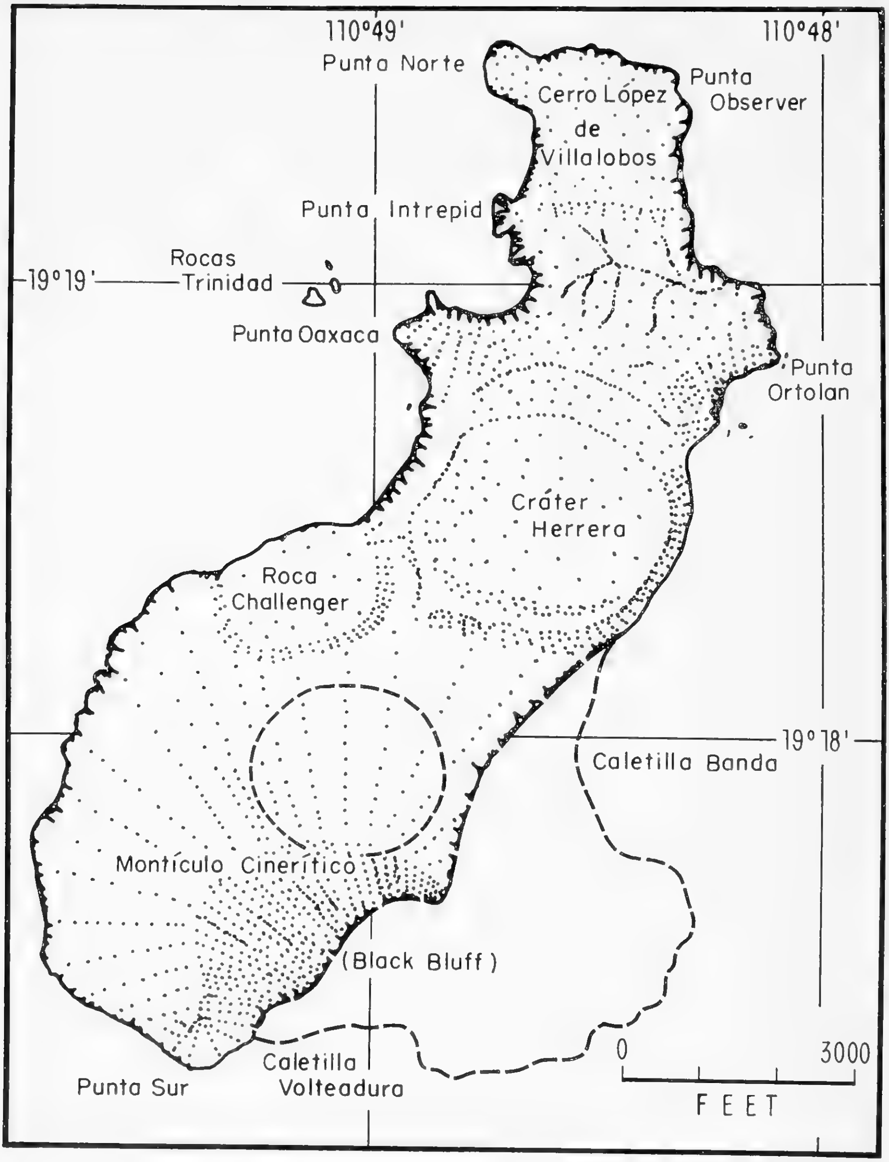

Figure 10. Sketch map showing the shoreline of Isla San Benedicto before the eruption of Volcán Bárcena in 1952.

Montículo Cinerítico.

Only the south and part of the west side of the remnant of a large, pluvially-dissected volcano called the Montículo Cinerítico (Ash Heap) escaped being buried by Bárcena tephra (fig. 10). The following description was possible only

Figure 11. Photograph of the Montículo Cinerítico tephra cone viewed from the east before the eruption of Volcán Bárcena. The vent is exposed showing vent agglomerate and a dome of trachytic lava partly filling the crater. D. H. Bates photo, February, 1952.

by a study of photographs taken in 1905 and 1925 by the California Academy of Sciences and in 1952 by Mr. D. H. Bates.

At the time Bárcena erupted, the east side of Volcán Cinerítico had been eroded away by waves exposing the vent, vent agglomerate, crater lava, and pyroclastic cone (fig. 11). Field inspection of the cone west of Punta Sur indicated that it is composed to trachytic ash, tuff, and beds of loose angular fragments of trachytic pumice. Only a very small portion of the crater lava escaped burial by Bárcena tephra; it crops out on the south flank of Bárcena (fig. 12).

The pre-Bárcena summit of Montículo Cinerítico had an altitude of 975 feet, according to U.S. Navy Hydrographic Office charts, and was the highest point on the island. The original diameter of the base of the volcano is estimated to be slightly greater than one mile and the crater rim probably had a diameter of about 3000 feet.

One or more trachyandesite lava flows having a thickness of 50 to 100 feet above sea level stratigraphically underlie Montículo Cinerítico pyroclastics and form the prominent sea-cliff on the southwest side of the island (fig. 13). Basalt or trachyandesite flows crop out in the southeast-facing, near vertical cliff of Montículo Cinerítico, slightly west and above the exposure of Montículo Cinerítico crater lava; and at the base of the southeast cliffs between Volteadura Beach and Punta Sur (fig. 12). These flows appear to be the eroded remains of an ancient volcano underlying the Montículo Cinerítico; they may be genetically related to the flows of similar composition located north of Cráter Herrera?

FIGURE 12. Photograph of the southeast face of Montículo Cinerítico showing outcrops of basalt and trachyandesite underlying Montículo Cinerítico tephra and partly covered by Bárcena tephra. A. F. Richards photo, March, 1953.

VOLCÁN BÁRCENA.

The birth and development of Bárcena and the subsequent effects of terrestrial and marine erosion of the volcano and Isla San Benedicto have been recorded in detail (part 1; Richards, 1965) and need not be repeated here.

Bárcena tephra cone initially had a maximum altitude of about 1120 feet, an exterior slope of 33°, and a 7° crater-rim slope to the east. The tephra is trachytic, having nearly the same chemical and mineralogical composition as the Montículo Cinerítico pyroclastics.

Two domes of trachytic lava are superposed, one above the other, in Bárcena crater (fig. 14). Both have central summit craters. Growth probably was largely by exogenous effusion, although it is not known for certain (part 1, p. 116). Later lava extrusion through the base of the cone resulted in magma withdrawal, subsidence of the domes, and fragmentation of their surface; the chilled margin of the outer, larger dome was left with relatively high relief. Subsequent rain erosion of the interior crater wall and redeposition on the floor of the crater is filling in low areas of the basined domes.

Bárcena first erupted on August 1, 1952. Initial activity was violent and cone growth was rapid. By August 12 the tephra cone was nearly fully formed

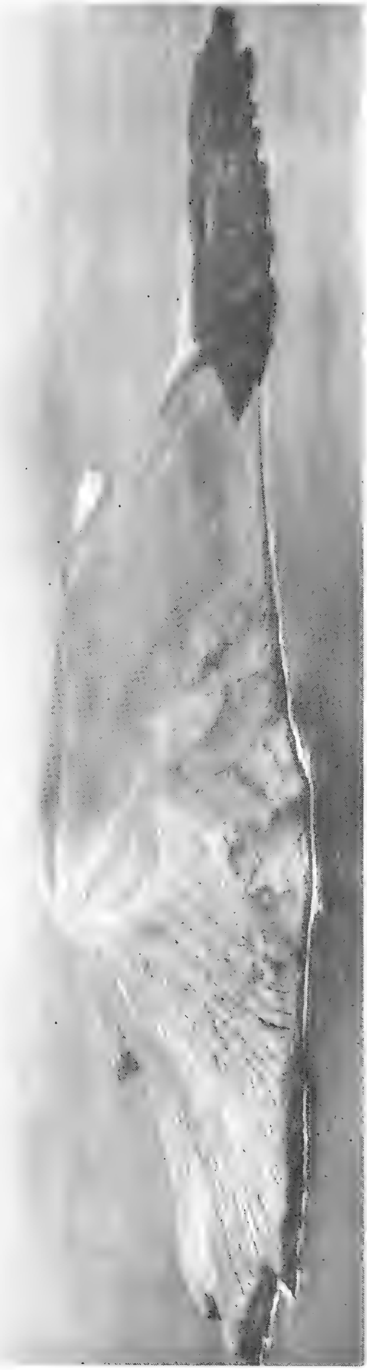

Figure 13. Oblique air photograph of the south side of San Benedicto showing the remnant of Montículo Cinerítico, Volcán Bárcena, and the Delta Lávico. U.S. Navy official photo, May 27, 1956.

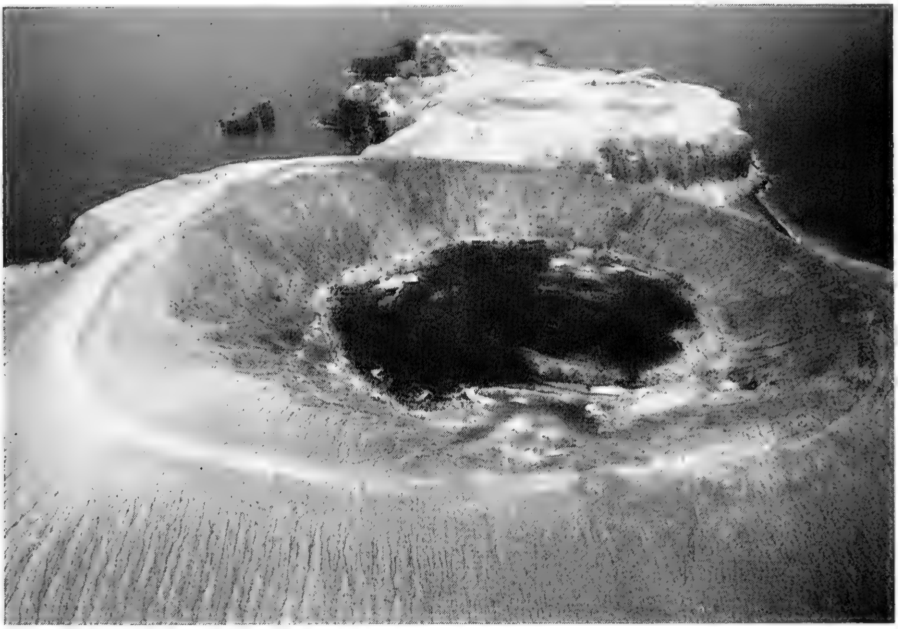

FIGURE 14. Oblique air photograph of Bárcena crater showing encroachment of redeposited crater-wall material on the surface of the domes. Cráter Herrera and Cerro López de Villalobos in background. U. S. Navy official photo, May 27, 1955.

by fallout and by deposition from tephra avalanches (*nuées ardentes*). Cone formation ceased by mid-September. The domes were emplaced in November and early December. Lava began flowing out to sea from a basal fissure in the cone on December 8, continued until the end of February, 1953, and formed a large delta of lava—the Delta Lávico (fig. 15). Visible activity stopped at the end of February, except for quiet solfataric steaming from the lava flows.

In May, 1955, a bathymetric survey near the Delta Lávico was made to determine the submarine extent and underwater slope of a viscous flow of trachyte. The survey consisted of a pattern of 8 sounding lines approximately normal to the front of the flow and 3 to 4 lines, depending on the region, parallel to the margin. Soundings taken in March and November, 1953, were added to the map shown in figure 16, which originally was plotted to a scale of 1:5100.

A marked increase in declivity near the Delta Lávico is shown on echograms from sounding lines south of the flow. Lines southeast of the flow show less pronounced rises. Lines east and northeast did not show a change of slope as the margin of the flow was approached. It is inferred that the abrupt change of slope represents the submarine margin of the flow and the east and northeast lines did not reach the flow margin. The distance from the emergent edge of

Table 1. *Seaward slopes of the Delta Lávico.*

Terrestrial
December 10, 1952: 14°
March 9, 1953: 28° to 40°

Submarine

Sounding lines normal to flow	*Location off delta*	*Margin depth in feet*	*Distance of margin from shore in feet*	*Slope, to nearest half degree*
2	SSW	210	420	26.5
3	S	240	480	26.5
4	SSE	300*	660	24.5
5	SE	150*	405	20.5

* Approximate depth at change of declivity.

the delta to the submarine limit (fig. 16) averages 490 feet on the four lines that crossed the submarine portion of the flow (table 1). In December, 1952, the yacht *Observer* anchored in 120 to 126 feet of water 2700 feet from shore southeast of Bárcena (about 510 feet seaward of a line tangent to the edge of the flow tongues). The depth at this point still is about 120 feet, which is an additional indication that lava did not flow this far.

Submarine and terrestrial slopes determined from figure 16 and from visual observation, respectively, are listed in table 1. The pre-Delta Lávico submarine surface had an approximate slope of 3° to 7° to the southeast.

The bend seaward of the submarine isobaths southeast of the Delta Lávico probably is caused by a pre-Bárcena structure. Although the insular slope directly below the 300-foot shelf-break is about 33° (sonic soundings slope corrected from data by Raitt in Hamilton, 1956, fig. 12), the same as Bárcena cone, the similarity is coincidental; the 2700-foot distance from the seaward edge of the Delta Lávico and the presence of a shelf-break are evidence that the slope is not genetically related to Bárcena.

An area of irregular topography is located southwest of the Delta Lávico. The close proximity of two small peaks, rising within 60 feet of the surface, to Montículo Cinerítico and the hummocky topography in this area is suggestive that it may be related to the summit of an old volcano.

GEOLOGIC HISTORY

Rending of the sea floor by one or more fissures and the subsequent effusive outpouring of lava accompanied by explosive activity above a depth of about 1560 fathoms (equivalent to the critical pressure of sea water) gradually built a volcanic edifice rising more than 1800 fathoms or 11,000 feet above the ocean floor. Presumably this activity occurred in the late Cenozoic, although direct evidence is lacking.

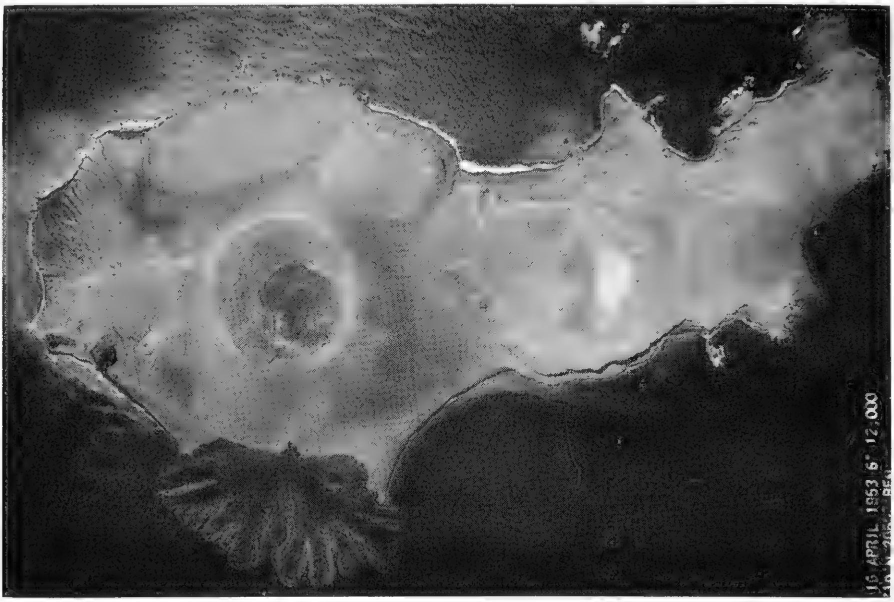

Figure 15. Vertical air photograph of Isla San Benedicto taken from a 12,000 foot altitude before wave erosion attacked the Delta Lávico. U.S. Navy official photo, April 16, 1953.

The sequence of events resulting in the eruption of the mafic rocks of San Benedicto and their partial erosion by waves, rain, and wind, is obscure. There is some evidence for the existence of one or more large volcanoes in the general vicinity of Cerro López de Villalobos associated with the eruption of trachybasalts, trachyandesites, and a plug or plugs or trachyte. Conical geomorphic forms that are believed to be parasitic volcanoes are located below sea level north and south of the present island. They may have formed during Pleistocene lower stands of the sea or it is equally possible that they were submarine volcanoes at the time of their formation.

The size of Cráter Herrera and the thick deposits of pyroclastics underlying the dome to the north suggests that the tephra cone of Volcán Herrera was very large at the time that it was formed. Roca Challenger dome appears to have been closely associated with Volcán Herrera. The appearance of nearly all sides of Cráter Herrera and Roca Challenger indicates an extended period of wave erosion followed the cessation of Herrera activity; erosion completely wore away all sides of the cone except to the north and immediately adjacent to the southwest side of Cráter Herrera.

The extent of the insular shelf implies a pre- late-Pleistocene age for Volcán Herrera and those volcanoes formed before Herrera.

Montículo Cinerítico shows every sign of being relatively young. As speculated

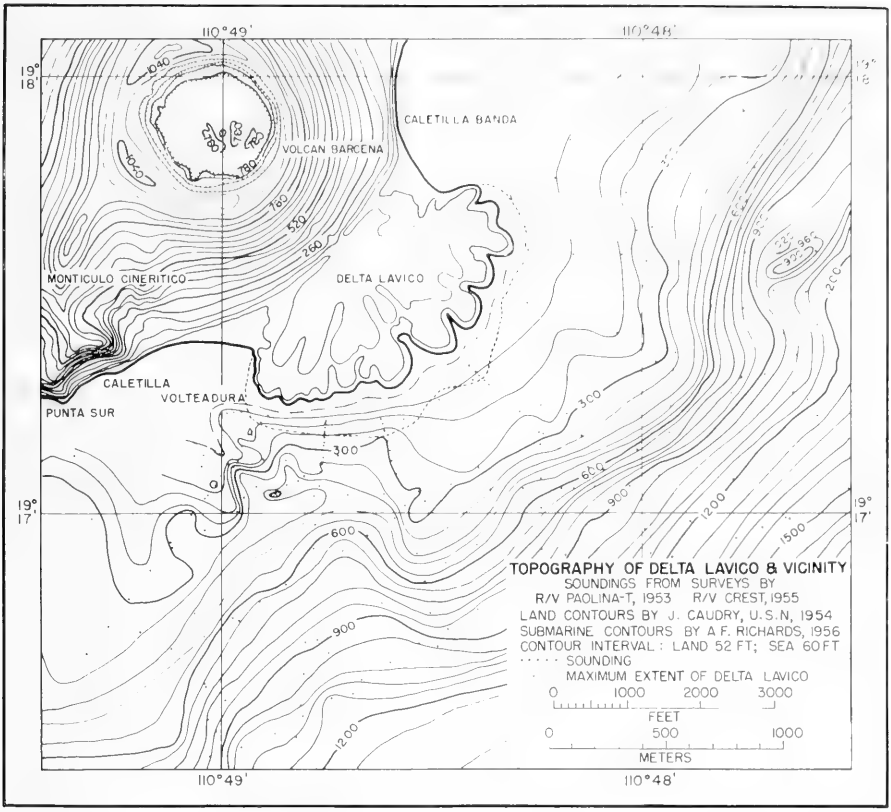

Figure 16. Map of the submarine topography in the vicinity of the Delta Lávico. Also shown is the probable maximum submarine extent of the lava flow.

previously, it may have erupted within the last few hundred years. Wave erosion had nearly carved the volcano in half by the time Volcán Bárcena was born in 1952.

Absence of fringing coral reefs around the island suggests that the eruption of Montículo Cinerítico and the subsequent erosion of its pumiceous cone liberated sufficient abrasive material into the surf zone to effectively inhibit the colonization of reef-forming corals at Isla San Benedicto.

PETROGRAHY

Seventy-five samples of San Benedicto lavas and pumices were examined in hand specimens, thin section, and by oil-immersion methods. Plagioclase composition was estimated from extinction angles (Winchell, 1951, p. 262, 283) and indices of refraction determined by immersion methods using data from Chayes (1952) and Crump and Ketner (1953, p. 31) given in Wahlstrom

(1955, p. 118). Where alkali feldspar composition is given it was estimated from optic axial angles and immersion in oil of n = 1.530 using graphs by Tuttle (1952) and modifications of these graphs by MacKenzie and Smith (1956). There is a marked difference in augite-aergirine composition determined by optic axial angles and extinction measurements in the rocks studied (see Tröger, 1952, p. 64, and *cf.* Winchell, 1951, p. 414). Consequently, molecular proportions are not assigned and the estimated optic axial angle and Z∧c extinction are stated. Olivine composition was obtained from estimated optic axial angles (Poldervaart, 1950, p. 1073). Rock color in hand specimens was determined from the rock color chart published by the Geological Society of America.

Most of the rocks examined in thin section are too fine-grained for modal analysis. Rocks for which chemical data are available are named in accordance with the chemical classification proposed by Rittmann (1952, 1960) for the *Catalogue of the Active Volcanoes of the World.* Where modes were determinable, nomenclature by Williams and others (1954) has been used, and is preferred where discrepancies exist between the two classifications.

Petrographic descriptions in this paper are generalized according to rock type, except for Bárcena tephra and lava which are described separately. Descriptions more directly related to specific locations on Isla San Benedicto are given elsewhere (Richards, 1957a).

TRACHYBASALTS (ALKALI BASALTS).

The most mafic rock found on San Benedicto is a trachybasalt from northeast of Cráter Herrera. It is medium dark gray, vesicular, and porphyritic in hand specimen. In thin section, the lava consists of about 20 per cent phenocrysts of corroded, euhedral to anhedral calcic labradorite or bytownite ($An_{68\text{ to }76}$) that are up to 6 mm. in diameter and rimmed with andesine; rare, pale tanish-green, subhedral clear olivine; and more common embayed olivine ($Fo_{75\text{ to }80}$) showing alteration to iddingsite and opaques (20%); plagioclase microlites (40%), which appeared to be calcic andesine; and small, elongated, pale buff grains of augite (10%) having a +2V of about 40° and a Z∧c of 45°. Modal alkali feldspar was absent. The opaques are granular, although partly altered, yellowish red-brown, earthy microphenocrysts occur up to 0.3 mm. in size. Accessory apatite is rare. An alkalic content sufficiently high to warrant an alkali or trachy prefix was indicated by minute, elongated grains of a greenish-brown sodic amphibole (?) strongly pleochroic in shades of pale to dark grass green. A chemical analysis of this rock is given in table 4, no. 3.

Trachybasalts elsewhere are similar in composition, but usually contain only a few per cent of olivine, a little glass, and an occasional sanidine megaphenocryst. Olivines having the highest fosterite content occurred in submarine basalts from north of the island; a chemical analysis of a submarine basalt is given in table 4, nos. 1 and 2. In one basalt from under the Montículo Cinerítico, a prismatic, subhedral augite microphenocryst was zoned and showed a $Z' \wedge c$ extinction of 47° in the core and about 58° in the rim, denoting a probable sodic enrichment of the melt. Most augites present in San Benedicto basalts and andesites have a +2V of about 50° and a $Z \wedge c$ of about 50°, with slightly higher extinction angles occurring in groundmass augites.

TRACHYANDESITES (MUGEARITES).

In hand specimen, San Benedicto trachyandesites (mugearites) range in color from dark brownish black to medium gray. They are usually vesicular and porphyritic, containing megaphenocrysts of plagioclase to 5 mm. in diameter, magnetite up to 8 mm., occasional alkali feldspar, and rare olivine to 1 mm. in diameter. Plagioclase phenocrysts in thin section, which show twinning according to the albite, carlsbad, and pericline laws, are composed of euhedral to subhedral corroded labradorite (An_{68}) that often show marginal resorption, and possess narrow, clear rims of oligoclase-andesine (about An_{30}). Olivines (about Fo_{75}) usually occur as microphenocrysts showing slight resorption and a little alteration; they are not common. Pale buff, subhedral augites (+2V 55° to 60° and $Z \wedge c$ 50°) also occur as microphenocrysts.

An intergranular texture is most common. Oligoclase-andesine microphenocrysts and microlites comprise about 50 per cent of the rocks. Granular augite also occurs in the groundmass along with finely-divided opaques, some of which show alteration to an earthy, reddish oxide that may be goethite? Accessory acicular or granular apatite and interstitial glass are rare. The fine-grained dike north of Punta Ortolan shows a trachytic groundmass in which was found about 10 per cent modal alkali feldspar and a very small lath-shaped sodic amphibole (?). This mineral had low birefringence, moderate relief, a small extinction angle, and exhibited weak pleochroism in shades of yellow brown, pale reddish brown, and olive or greenish brown; it may be arfvedsonite or barkevikite?

One chemical analysis (table 4, no. 5) and two alkali analyses (table 5, columns A and B) of San Benedicto andesites show sufficient alkali to indicate that these andesites should be classified as trachyandesites or mugearites (Nockolds, 1954, p. 1018; Muir and Tilley, 1961); they all are of the oceanic type (see Macdonald, 1960).

SODIC TRACHYTES.

San Benedicto trachytes in hand specimen range in color from medium gray to olive and brownish gray. Flows are usually vesicular while domes are not. Practically all trachytic pumices and lavas contain phenocrysts of blocky alkali feldspar and a small amount of sodic plagioclase up to 5 mm. in diameter, augite to 2 mm. long, and occasionally olivine. Cráter Herrera trachyte is typical of the group. A sample from the south cliff that was chemically analyzed (table 4, no. 9) contains megaphenocrysts of alkali feldspar (about 15%) and olivine (rare) set in a glassy trachytic groundmass of alkali feldspar microlites (70%), augite and aegirine-augite (about 7%), a few per cent each of opaques and interstitial quartz, and a little sodic amphibole and apatite. Phenocrysts of alkali feldspar are euhedral to subhedral and corroded, with common grid and very fine albite twinning. Remnants of the corroded interior and the rim have lower refractive indices than the central portion of a few phenocrysts, which indicates that apparently both the core and rim are more potassic than the central part. The transition from interior to central part of the crystals is abrupt and from the central part to the rim gradational. Sanidine (2V about 30°) and anorthoclase (2V 50–55°) are both present in separate phenocrysts. Olivines are iron-rich (greenish color), anhedral, and deeply embayed. Prismatic, subhedral, light-green augite (+2V 60°, $Z\Lambda c$ 50°) microphenocrysts show marginal alteration to a sodic amphibole having a very small extinction angle and strong pleochroism ($\alpha' =$ yellow brown and $\gamma' =$ very dark brown, almost black). The pleochroism suggests enigmatite (Bowen, 1937). This mineral also occurs in patches in the groundmass along with relatively abundant blunt-ended, rod-shaped aegirine-augite ($Z\Lambda c$ about 80°) possessing deep grass-green to brown pleochroism, and finely divided opaques that are probably magnetite. Alkali analyses of Cráter Herrera trachytes are listed in table 5, columns E and F.

Other trachytes may contain alkali feldspar phenocrysts having cross-hatch twinning (see MacKenzie, 1956), which probably is anorthoclase (2Z about 50°). Olivines (Fo_{55}) may have resorbed borders showing alteration to magnetite with a dark reddish-brown mineral (iddingsite?) at the margin. Tiny grains of a mineral having weak pleochroism in shades of yellowish pink and lemon also may be present in the groundmass. Alkali analyses of different trachytes are given in table 5, columns D–P.

Sodic rhyolites.

Although two analyzed pumices contain slightly more than 10 per cent normative quartz and are called sodic rhyolite, the only unequivocal rhyolites from San Benedicto are accessory blocks found lying on or near Bárcena cone. These blocks are up to a foot or more in diameter and apparently were blown out of the volcano during the last stages of the tephra eruption because they have not been found buried in the cone tephra. The blocks are subangular, mottled greenish gray and white in color, dense, and often show conspicuous flow structure. Phenocrysts of alkali feldspar, up to 3 mm. long, and rarely a green pyroxene, less than 2 mm. long, occur in hand specimen. In thin section, 5 to 10 percent of the rock consists of phenocrysts of subhedral sanidine having large cores with narrow rims of higher relief. Less common phenocryts of aegirine-augite (+2V about 70°) comprise about 10 per cent of the rock; they are 0.5 to 2 mm. long and show weak pleochroism in pale green, buff, and dark olive-green colors. The trachytic groundmass consists of about 50 per cent of microphenocrysts and microlites of alkali feldspar; 10 per cent of tiny laths and irregular patches of yellow-green to grass-green aegirine-augite (+2V 80°, Z∧c 85°); 2 per cent of riebeckite (?) having a small extinction angle and strongly pleochroic in shades of green, blue, and violet; and 3 per cent of a mineral exhibiting strong pleochroism in very dark brown—nearly opaque, pale yellow-brown, and reddish-brown colors, which may be enigmatite or cossyrite. Three to four per cent of opaques, some of which appear pseudomorphous after olivine, a very little accessory zircon, and about 5 per cent glass also were found in the groundmass. A quantitative determination of the interstitial quartz by X-ray diffraction was made by Dr. Robert Rex, who reported that one sample contained 8.7 ± 0.5 per cent quartz. Ten per cent was estimated in the thin section. This percentage indicates that the rocks are quartz trachytes according to Williams and others (1954, p. 98). Quartz in the norm (table 4, no. 12) however, is twice the amount in the mode and suggests that excess silica that might have crystallized as quartz may be contained in groundmass glass. A high temperature, primary origin of the free quartz is shown by an $0^{18}/0^{16}$ ratio of 7.6 (sample SB1M55; R. Rex, personal communication). The rock is called a sodic rhyolite following Rittmann's classification, and because of the large amount of normative quartz. A chemical analysis is given in table 4, no. 12. An alkali analysis of another sample listed in table 5, column P, shows a Na_2O content higher by 1.4 per cent. These analyses show that the sodic rhyolite contains significantly higher Al_2O_3 and lower TiO_2 compared to pantellerites from Pantelleria (Washington, 1914, p. 17; Zies, 1960); consequently, they are not called pantellerite.

VOLCÁN BÁRCENA.

Tephra. Examination of glass and phenocrysts in a specimen of black trachytic pumice from Bárcena cone and white pumices from Montículo Cinerítico shows a similar mineralogical composition (table 2). Bárcena pumice is less silicic, however, a fact indicated by the higher refractive index of Bárcena glass and by a chemical analysis (table 4). In Bárcena pumice, sanidine ($Or_{60}(Ab + An)_{40}$) is clear and subhedral; albite (An_4) is euhedral, cloudy, twinned according to the albite law, and possesses an intermediate 2V; and grass-green aegirine-augite ($N_y = 1.724$) is rod-shaped with lengths 3 to 8 times the width. An alkali analysis of another sample of Bárcena pumice is given in table 5, column 1. A chemical analysis of light-colored pumiceous ash is listed in column 8 of table 4; compare the alkali analysis of the same sample in table 5, column 4.

A large range is present in the refractive index of natural glass in several other Bárcena pumice samples (table 3). Glass of individual coarse ash particles has a constant refractive index. Variation appears to be present only between the glass of different ash particles, indicating a heterogeneous composition of the ashy tephra. Bárcena tephra may include both essential ash from Bárcena and

TABLE 2. *Refractive indices of phenocrysts and glass in San Benedicto pumices.*

Sample	*Location*	*Glass refractive index (±0.002)*	*Sanidine refractive indices (±0.002)*	*Albite refractive indices (±0.002)*	*Aegirine-augite refractive indices (±0.006)*
SB21M55	Montículo Cinerítico	1.503	N_x1.521		N_x1.727
			N_y1.527		N_y1.736
			N_z1.528		N_z1.756
SB21bM55	Montículo Cinerítico	1.503	1.521	N_x1.532	1.726
			1.527	N_y1.536	1.734
			1.528	N_z1.541	1.761
SB24M53	Bárcena	1.516	1.522	1.530	1.713
			1.527	1.534	1.724
			1.528	1.538	1.743

accessory ash from Montículo Cinerítico.

Bárcena lava ejected from the crater is a medium gray or black porphyritic trachyte. Some fragments are composed of over 50 per cent glass and have a subconchoidal fracture. Phenocrysts of sanidine, calcic oligoclase (about An$_{25}$), and a very little titaniferous augite are commonly set in a glassy groundmass of alkali feldspar, augite (+2V 60°, Z∧c 50°), granular opaques, and a very little accessory zircon. Needles of apatite are enclosed in alkali feldspar. A little olivine may be present. An alkali analysis is given in table 5, column J.

Lava. Six lava samples from the crater and eight from the Delta Lávico show essentially the same mineralogy. Petrographically all are oligoclase-augite andesites (mugearite) with one exception, which had sufficient modal alkali feldspar to be called a trachyte. A typical sample in hand specimen is vesicular, grayish black, and slightly porphyritic with occasional phenocrysts of blocky, lath-shaped alkali feldspar about 1 mm. long, augite up to 2 mm. long, olivine to 2 mm. long, and plagioclase, commonly 1 to 3 mm. in length—rarely to 13 mm. long.

In thin section, the groundmass texture is usually trachytic or felty. Sanidine phenocrysts are anhedral and corroded. Labradorite phenocrysts are euhedral to anhedral in lath and tabular shapes and are both corroded and clear. They are zoned from about An$_{65}$ in the core to An$_{28-30}$ in a narrow rim. Twinning is common. Calcic oligoclase also is found as microphenocrysts

TABLE 3. *Variation of glass refractive index in Bárcena pumices.*

Composite sample	*Glass refractive index*	*Color of pumice*	
SB23M53	1.506	white	
	1.510	gray	most common
	1.512	buff	
	1.523	black	

Table 4. *Chemical analyses.**

	1	*1b*	*2*	*2b*		*3*	
SiO_2	41.18	44.06	44.01	45.17	(21.10)	47.25	(22.09)
TiO_2	2.48	2.66	2.50	2.57	(1.54)	2.05	(1.23)
Al_2O_3	19.45	20.80	20.24	20.78	(10.98)	17.22	(9.11)
Fe_2O_3	6.05	6.47	3.89	3.99	(2.79)	5.05	(3.53)
FeO	4.06	4.34	4.85	4.98	(3.87)	5.26	(4.09)
MnO	0.08	0.09	0.09	0.09	(0.07)	0.14	(0.11)
MgO	4.48	4.79	4.02	4.13	(2.49)	6.10	(3.68)
CaO	9.66	10.34	11.30	11.60	(8.28)	9.72	(6.95)
Na_2O	3.39	3.63	3.39	3.48	(2.58)	3.34	(2.48)
K_2O	0.86	0.92	1.11	1.14	(0.95)	1.15	(0.95)
P_2O_5	1.73	1.85	1.81	1.86	(0.81)	0.32	(0.14)
H_2O^+	3.75	–	1.54	–		1.38	(0.15)
H_2O^- 110°C.	3.18	–	1.03	–		0.29	
CO_2	0.05	0.05	0.20	0.21	(0.06)	0.23	(0.06)
Cl	n.d.	n.d.	n.d.	n.d.		0.10	
F	n.d.	n.d.	n.d.	n.d.		n.d.	
	100.40	100.00	99.98	100.00		99.60	
–0 for Cl & F						0.02	
						99.58	

* Cation weight percentage in parenthesis follows the oxide weight percentage column for those analyses used in the variation diagrams.

Table 4. *Continued.*

	4		*5*		*6*		*7*	
SiO_2	48.28	(22.57)	54.94	(25.68)	60.78	(28.41)	61.33	(28.67)
TiO_2	2.64	(1.58)	1.58	(0.95)	0.73	(0.44)	0.76	(0.46)
Al_2O_3	19.09	(10.10)	17.07	(9.03)	16.11	(8.53)	16.82	(8.90)
Fe_2O_3	3.09	(2.16)	1.64	(1.15)	0.73	(0.51)	1.70	(1.19)
FeO	7.33	(5.70)	7.83	(6.09)	6.33	(4.92)	5.30	(4.12)
MnO	0.06	(0.05)	0.20	(0.15)	0.17	(0.13)	0.12	(0.09)
MgO	5.30	(3.20)	2.45	(1.48)	0.89	(0.54)	0.91	0.55
CaO	9.17	(6.55)	5.67	(4.05)	3.77	(2.69)	3.31	2.37)
Na_2O	3.29	(2.44)	5.56	(4.13)	6.12	(4.54)	6.25	(4.64)
K_2O	0.92	(0.76)	2.30	(1.91)	3.20	(2.66)	3.18	(2.64)
P_2O_5	0.84	(0.37)	0.04	(0.02)	0.10	(0.04)	0.21	(0.09
H_2O^+	0.00	(0.00)	0.60	(0.07)	0.43	(0.05)	0.44	0.05)
H_2O^- 110°C.	0.00		0.11		0.04		0.01	
CO_2	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
Cl	n.d.		0.07		0.07		0.07	
F	n.d.		n.d.		n.d.		n.d.	
	100.01		100.06		99.47		100.41	
–0 for Cl &F			0.02		0.02		0.02	
			100.04		99.45		100.39	

TABLE 4. *Continued.*

	8a	*8b*		*9*		*10a*	*10b*	
SiO_2	61.66	64.60	(30.20)	64.19	(30.01)	62.49	67.45	(31.53)
TiO_2	0.47	0.49	(0.29)	0.38	(0.23)	0.28	0.30	(0.18)
Al_2O_3	15.27	16.00	(8.47)	16.42	(8.69)	14.36	15.51	(8.21)
Fe_2O_3	0.36	0.38	(0.25)	3.27	(2.29)	1.42	1.53	(1.07)
FeO	4.84	5.08	(3.95)	1.56	(1.21)	3.36	3.63	(2.82)
MnO	0.12	0.13	(0.10)	0.07	(0.05)	0.14	0.15	(0.12)
MgO	0.43	0.45	(0.27)	0.25	(0.15)	0.38	0.40	(0.24)
CaO	1.97	2.06	(1.47)	1.82	(1.30)	0.82	0.89	(0.64)
Na_2O	7.30	6.34	(4.70)	6.70	(4.97)	7.58	6.07	(4.50)
K_2O	4.25	4.46	(3.70)	4.53	(3.76)	3.61	3.90	(3.24)
P_2O_5	0.01	0.01	(0.00)	0.03	(0.01)	0.04	0.04	(0.02)
H_2O^+	2.12	–		0.42	(0.05)	2.13	–	
H_2O 110°C.	0.33	–		0.13		1.47*	–	
CO_2	0.00	0.00	(0.00)	0.00	(0.00)	nil	nil	(nil)
Cl	1.43	–		0.23		2.23	–	
F	n.d.	n.d.		n.d.		0.12	0.12	
	100.56	100.00		100.00		100.42	100.00	
–0 for Cl & F	0.31			0.05		0.55		
	100.25			99.95		99.87		

* 105° C.

TABLE 4. *Continued.*

	11a	*11b*		*12*	
SiO_2	64.91	68.44	(31.99)	69.90	(32.68)
TiO_2	0.26	0.27	(0.16)	0.17	(0.10)
Al_2O_3	13.83	14.59	(7.72)	13.96	(7.39)
Fe_2O_3	1.25	1.30	(0.91)	1.32	(0.92)
FeO	2.56	2.70	(2.10)	2.06	(1.60)
MnO	0.07	0.07	(0.05)	0.04	(0.03)
MgO	0.05	0.05	(0.03)	0.04	(0.02)
CaO	1.08	1.14	(0.81)	0.62	(0.44)
Na_2O	7.14	6.42	(4.76)	5.71	(4.24)
K_2O	4.72	4.98	(4.13)	4.65	(3.86)
P_2O_5	0.04	0.04	(0.02)	0.00	(0.00)
H_2O^+	2.20	–		0.58	(0.06)
H_2O^- 110°C.	0.52	–		0.05	
CO_2	0.00	0.00	(0.00)	0.00	(0.00)
Cl	1.21	–		0.29	
F	n.d.	n.d.		n.d.	
	99.84	100.00		99.39	
–0 for Cl & F	0.26			0.06	
	99.58			99.33	

Table 4. *Continued.*

C.I.P.W. Norms

(weight per cent)

	2b	*3*	*4*	*5*	*6*	*7*	*8b*	*9*	*10b*	*11b*	*12*
q	–	–	–	–	1.98	3.18	3.66	7.26	12.90	11.40	18.90
or	6.67	6.67	5.56	13.34	18.90	18.90	26.13	25.02	22.80	29.47	27.80
ab	28.30	28.30	27.77	46.63	51.87	52.40	53.45	55.54	51.35	47.16	46.63
an	37.81	29.75	34.47	15.57	7.51	8.62	2.22	3.06	3.61	–	–
ne	0.57	–	–	–	–	–	–	–			
hl	–	0.35	–	0.23	0.23	0.23	–	0.77	–	–	0.94
ac	–	–	–	–	–	–	–	–	–	3.70	
ns	–	–	–	–	–	–	–	–	–	0.61	–
wo	2.67	6.61	2.32	5.34	4.41	2.90	3.36	2.44	–	2.32	1.28
en	–	9.00	9.70	1.15	2.20	2.30	1.30	0.60	1.00	0.10	0.10
fs	–	1.32	5.02	2.04	10.30	7.26	8.45	–	5.15	4.62	2.51
fo	7.14	4.62	2.45	3.50	–	–	–	–			
fa	1.22	0.82	1.32	6.94	–	–	–	–	–	–	–
mt	5.80	7.66	4.41	2.32	0.93	2.55	0.70	4.18	2.09	–	1.86
il	4.86	3.95	5.02	3.04	1.37	1.37	0.91	0.76	0.61	0.61	0.30
hm	–	–	–	–	–	–	–	0.48	–	–	
ap	4.37	0.67	2.02	–	0.34	0.34	–	–			–
fr	–	–	–	–	–	–	–	–	0.47	–	–
cc	0.50	0.60	–	–	–	–	–	–	–	–	–
	99.91	100.32	100.06	100.10	100.04	100.05	100.18	100.11	99.98	99.99	100.32

Table 4. *Continued.*

1a. Trachybasalt. Analysis near the exterior (sigre 3). Dredged eight miles north of San Benedicto in 350 fathoms. H. B. Wiik, analyst.

1b. Trachybasalt. Analysis 1a computed water-free.

2a. Trachybasalt. Analysis near the center (sigre 3). Same specimen as 1a. H. B. Wiik, analyst.

2b. Trachybasalt. Analysis 2a computed water-free.

3\. Trachybasalt (SB19M53). Lava from cove northeast of Cráter Herrera. H. B. Wiik, analyst.

4\. Trachybasalt. Xenolith in Bárcena crater lava (SB4M55). H. B. Wiik, analyst.

5\. Trachyandesite or mugearite (SB38M53). Pre-Montículo Cinerítico lava. H. B. Wiik, analyst.

6\. Sodic trachyte (SB9M53). Bárcena crater lava. H. B. Wiik, analyst.

7\. Sodic trachyte (SB25M53). Delta Lávico lava. H. B. Wiik, analyst.

8a. Sodic trachyte. Volcán Bárcena pumiceous ash (SB23M53). H. B. Wiik, analyst.

8b. Sodic trachyte. Analysis 6a computed water-free with enough Na_2O combined with Cl to give NaCl, which is excluded.

9\. Sodic trachyte (SB15M53). Cráter Herrera lava. H. B. Wiik, analyst.

10a. Sodic rhyolite (sample 216). Drift pumice collected 104 miles north of Isla San Benedicto. W. H. Herdsman, analyst. (Analysis includes nil Ba and Sr.)

10b. Sodic rhyolite. Analysis 10a computed water-free with enough Na_2O combined with Cl to give NaCl, which is excluded.

11a. Sodic trachyte (rhyolite) (SB21bM55). Montículo Cinerítico pumice. H. B. Wiik, analyst.

11b. Sodic rhyolite. Analysis 11a computed water-free with enough Na_2O combined with Cl to give NaCl, which is excluded.

12. Sodic rhyolite (SB1M55). Accessory block ejecta from Volcán Bárcena. H. B. Wiik, analyst.

TABLE 5. *Alkali analyses.*[1]

	A	*B*	*C*	*D*	*E*	*F*	*G*
Na_2O	5.63	5.72 av.	6.48	6.63 av.	6.18	6.98	6.89
K_2O	2.14	2.47 av.	4.78	4.88 av.	3.83	4.58	4.57
CaO	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Net relative alpha counts/hour	26	20	28	33.5	32.5	30.5	32

	H	*(8a)*[2]	*I*	*J*	*K*	*(6)*[2]	*L*
Na_2O	7.35	(7.30)	7.68	3.51	4.83	(6.12)	6.92
K_2O	4.19	(4.25)	4.50	5.30	2.40	(3.20)	3.24
CaO	n.d.	(1.97)	1.06	1.70	n.d.	(3.77)	1.64
Net relative alpha counts/hour	37 av.		n.d.	36	21.5		n.d.

	M	*N*	*O*	*P*
Na_2O	6.75	7.23 av.	6.81	7.07
K_2O	3.47	3.27 av.	3.30	4.74
CaO	n.d.	1.56	n.d.	n.d.
Net relative alpha counts/hour	20	14	25 av.	63

A. Trachyandesite, Punta Ortolan, dike on northeast side, SB17N53.
B. Trachyandesite, pre-Montículo Cinerítico lava, flow at west end of Volteadura Beach, SB11N53 (same as SB38M53, analysis 5 in table 4).
C. Trachyte, Cerro López de Villalobos lava, north end, SB21N53.
D. Trachyte, Montículo Cinerítico lava, east side, T947.
E. Trachyte, Cráter Herrera, north top, SB15N53.
F. Trachyte, Cráter Herrera, south side, SB16M53.
G. Trachyte, Roca Challenger, north side, SB13M53.
H. Trachyte, Volcán Bárcena pumiceous ash, SB23M53.
I. Trachyte, Bárcena pumice, SB21M53.
J. Trachyte, Bárcena glassy ejecta, SB22M53.
K. Trachyte, Bárcena crater lava, SB9M53.
L. Trachyte, Bárcena crater lava (more vitric than SB9M53), SB8M53.
M. Trachyte, Delta Lávico lava, first flow, SB3D52.
N. Trachyte, Delta Lávico lava, north end of flow, SB26M53.
O. Trachyte, Delta Lávico lava, from mouth of vent, last flow, SB3N53.
P. Sodic rhyolite, Bárcena accessory block ejecta, SB19N53.

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[1] Analytical methods and procedure for obtaining alpha counts are described by Adams (1954, p. 90-92). The CaO analyses were made using a wet chemical method.

[2] Value from chemical analysis (table 4) listed for comparison.

in a groundmass of laths and microlites of oligoclase (An_{25}). Pale tan to green augite (+2V 55°, Z∧c 50°), while rare as megaphenocrysts, occurs as subhedral laths and prisms commonly 0.5 mm. long. They are sometimes zoned, apparently with a slightly higher sodic content (greener color) in the rim. Aegirine-bearing augite (Z∧c 60°) in the groundmass is present as tiny laths or granules. Phenocrysts of olivine (about Fo_{70}) are rare. Olivine microphenocrysts in the groundmass, about 0.2 mm. in diameter are subhedral with embayed interiors and marginal resorption, some marginal alteration to opaques is present, but iddingsite was not observed. Magnetite occurs as microphenocrysts up to 0.3 mm.; it also occurs finely divided in the groundmass causing the lava to appear black in hand specimen. Glass, with an average index of refraction of 1.527, is usually present as a minor constituent of the groundmass, but may on occasion comprise one-third or more of the groundmass giving the rock a hyalopilitic texture. Apatite is rare and commonly occurs as tiny needles in alkali feldspar phenocrysts. A little interstitial quartz and a blue sodic amphibole are present in one sample from the Delta Lávico.

A specimen of the youngest lava of the delta was collected from the mouth of the vent. Sanidine is present in the thin section but plagioclase was not observed. The alkali content of this trachyte (table 5, column O) is similar to the other crater and delta lavas. A second sample, which was collected nearby, is the usual oligoclase andesite. Alkali presumably is occult in the glass but it must also be occult elsewhere when there is little glass.

Bárcena lavas are classed as sodic trachytes according to their chemical composition.

Chemical analyses of crater and delta lavas are given in table 4, nos. 6 and 7. A series of alkali analyses of crater and delta lavas is given in table 5, columns K to O.

Olivine-bearing basalt occurs as rare xenoliths, up to about 6 inches in diameter, in Bárcena lavas. In one very vesicular sample having an intergranular texture, plagioclase was zoned from about An_{85} to An_{30}. Other constituents included non-pleochroic, greenish-tan augite (+2V 50°, Z∧c 60°), anhedral olivine and a little euhedral apatite. The one sample analyzed strangely contained no water (table 4, no. 4). Although this lava is classified a basalt according to Rittmann's system, in all probability, compared to the analyses of the trachybasalts, it should be considered an alkali basalt or trachybasalt.

PETROCHEMISTRY

Twelve new chemical analyses are listed in table 4. Cation weight percentages in parentheses follow the oxide percentage column; they were obtained using conversion factors computed by Green (1955, p. 304). Analyses 8 and 11 of pumice and ash show apparent water and salt contamination, probably derived from surf spray before the samples were collected. The pumice analyzed in column 10a had floated in the ocean for several weeks before it was collected. The analysis of this pumice shows excessive absorbed water, Na_2O, and Cl. All three analyses have been computed water-free with enough Na_2O assigned to Cl to yield halite, which was excluded because igneous rocks commonly contain less than 0.05 per cent chlorine (Kuroda and Sandell, 1953, p. 884). However, Zies' (1960) recent analyses showing relatively large amount of insoluble Cl in pantellerites are suggestive that this assumption may be questionable. In column 10a a correction was not made for fluorine. While the analyzed amount is high, it is within the range of values in eruptive rocks reported by Shepherd (1940, p. 119).

In the listing of C.I.P.W. norms (table 5), summation of the calcium, magnesium, and iron metasilicates is given in preference to a breakdown into normative diopside and hypersthene because these minerals do not appear in the mode and their use might be confusing. A norm is not given for the altered exterior of the dredged trachybasalt (analysis 1a), nor is the analysis shown in the variation diagrams.

The trachybasalt dredged from North Ridge (table 4, nos. 1 and 2) keys out to be a "nephelite basanite" in Rittmann's (1952) classification. This name is not adopted because of the absence of modal feldspathoids and virtual absence of normative nepheline. The trachybasalt shows impoverishment of silica, calcium, and potassium, enrichment of magnesium and sodium, and oxidation of the ferrous iron resulting from submarine weathering. Mellis (1960) and Matthews (1962) described similar alteration in mafic rocks dredged from the Atlantic, except that an increase in silica was found by Mellis and both writers report enrichment rather than impoverishment of potassium. Correns (1937) likewise reports enrichment of potassium in a basalt dredged from the Atlantic and impoverishment of SiO_2, FeO, CaO, MgO, and Na_2O.

The trachybasalts, although unusually high in Al_2O_3 for oceanic rocks, are not high-alumina basalts because of their Na_2O and K_2O content. They are similar to alumina-rich alkali basalts occurring in Japan, Hawaii, and elsewhere that have been described and discussed by Kuno (1960).

Alkali analyses, four of which include CaO, and alpha activity of 16 samples (table 5) were obtained for me by Dr. Edward J. Zeller, previously with the University of Wisconsin. Three alkali analyses are duplicated by chemical analyses. Variability between different analyses of the same sample is within the range of values reported by Fairbairn and others (1951) and Stevens and others (1960) except for alkali analysis K, which appears to be in error. The relation between alpha activity and uranium content has been discussed by Adams (1954).

PETROLOGY AND RELATION TO THE EAST PACIFIC RISE

Isla San Benedicto represents only a very small proportion of the total volume of the volcanic structure, the bulk of which is below sea level. When considering magmatic differentiation of the insular and offshore rocks, it must be kept in mind that these rocks represent only the top of the volcanic pile; presumably they are also the latest and most silicic differentiates.

A Harker variation diagram of the analyzed San Benedicto rocks is shown in figure 17. It is not further mentioned for reasons similar to those ably expounded by Chayes (1964b). Ionic variation diagrams of these rocks (figs. 18 and 19) show the relationship between (Fe^{+2} + Fe^{+3}), (Na + K), and Mg, and between the alkalis and calcium. Also shown in these diagrams is the ionic variation of the similar Hawaiian alkali basalt-trachyte suite after Nockolds and Allen (1954, fig. 17). There is only a small departure of points from smooth curves and the trend of differentiation at San Benedicto from trachybasalt or alkali basalt to sodic rhyolite is indicated by arrows. Fractionation of felsic minerals with alkali enrichment and improverishment of iron and Mg is dominant over fractionation of ferromagnesian minerals with attendant iron enrichment. The most mafic rocks show a rapid impoverishment in Ca and enrichment in alkali as differentiation proceeds. At the felsic end of the curves a slight enrichment of K is apparent, more so for San Benedicto than for Hawaiian rocks. Green and Poldervaart (1958, p. 95) believe that in the production of sodic versus potassic rocks the effects of locally operative processes predominate over the generally operative fractionation process, which tends to produce rocks with a Na/K ratio of unity. Ionic variation in Si, Al, and Na (fig. 20) shows that initial differentiation was an enrichment of Si and impoverishment in Al. The rapid increase in Na curiously occurs over the silica interval (53 to 57 weight per cent SiO_2) believed to constitute a compositional "gap" by Barth (1939, p. 65–66) for rocks from the Hawaiian islands, which recently has been discussed by Chayes (1963a, 1963b), Harris (1963), Macdonald (1963), Bryan (1964), and others. Figure 20 also shows the close relationship of variation in San Benedicto rocks compared to the average alkali trachyte and peralkaline rhyolite of Nockolds and Allen (1954). Rocks from Socorro and Easter Island show a similar relationship, except that a higher degree of variation in Si occurs and there is a second phase of enrichment in Na (fig. 21, A and B).

The alkali-lime index (Peacock, 1931) for San Benedicto rocks is 52.6 or alkali-calcic; for Hawaiian rocks it is about 54 (Macdonald, 1949, p. 1570).

Nockolds and Allen (1953, p. 106) believe that the mafic end of the smooth curves in their ionic variation diagrams represented the parental magma; the scatter of points beyond the smooth curves were interpretated as accumulative rocks. There are no points beyond the smooth curves shown for San Benedicto rocks (figs. 18 and 19). The parent magma at San Benedicto appears to be a more-or-less normal alkali basalt. The oceanic character of the suite of basalts is shown by the high TiO_2 content (Chayes, 1964a). This magma is not tholeiitic fig. 23), based on the rocks thus far analyzed compared to the similar Hawaiian alkali suite presented by Kuno and others (1957). In later papers by Macdonald

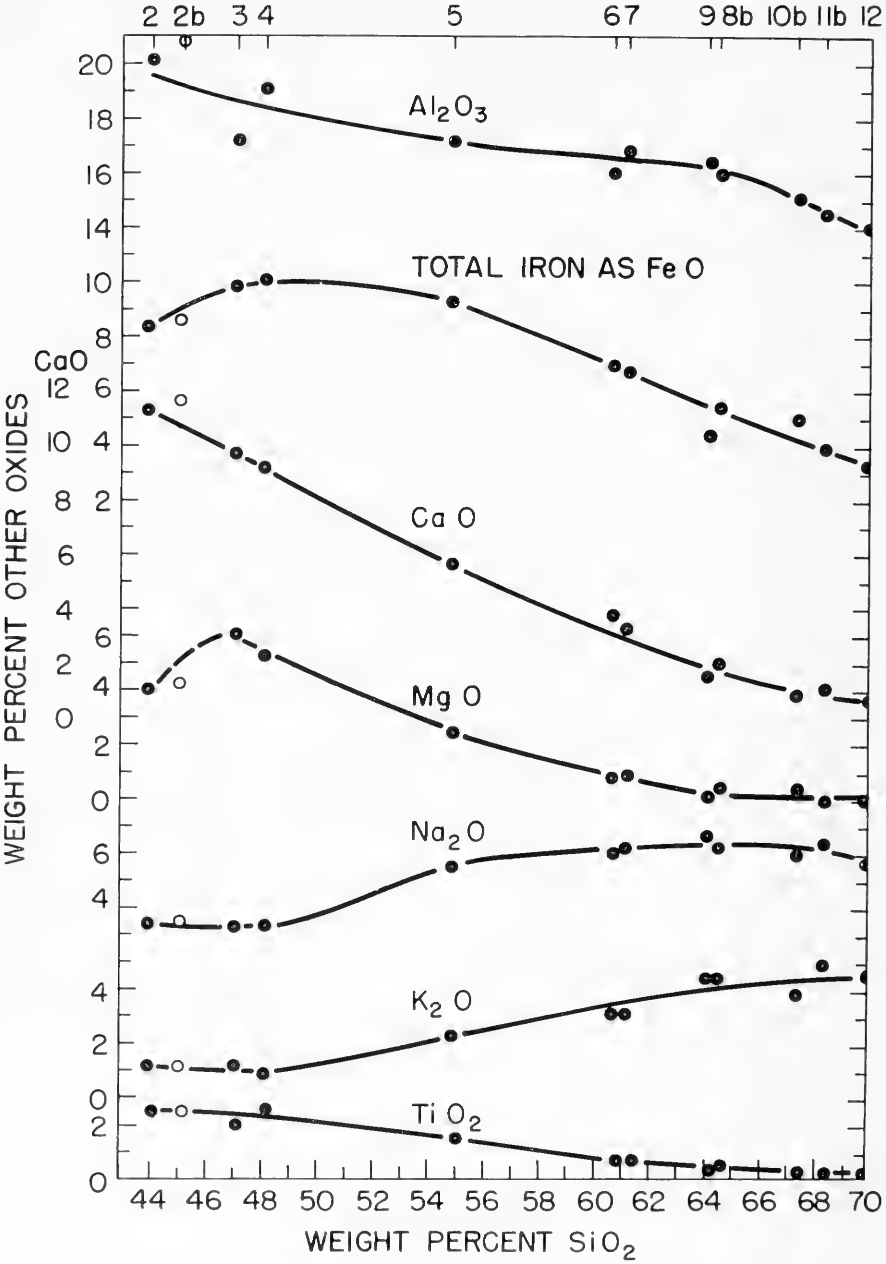


FIGURE 17. Harker variation diagram of San Benedicto rocks. The water-free sample 2b, represented by the open circles, is shown for information only.

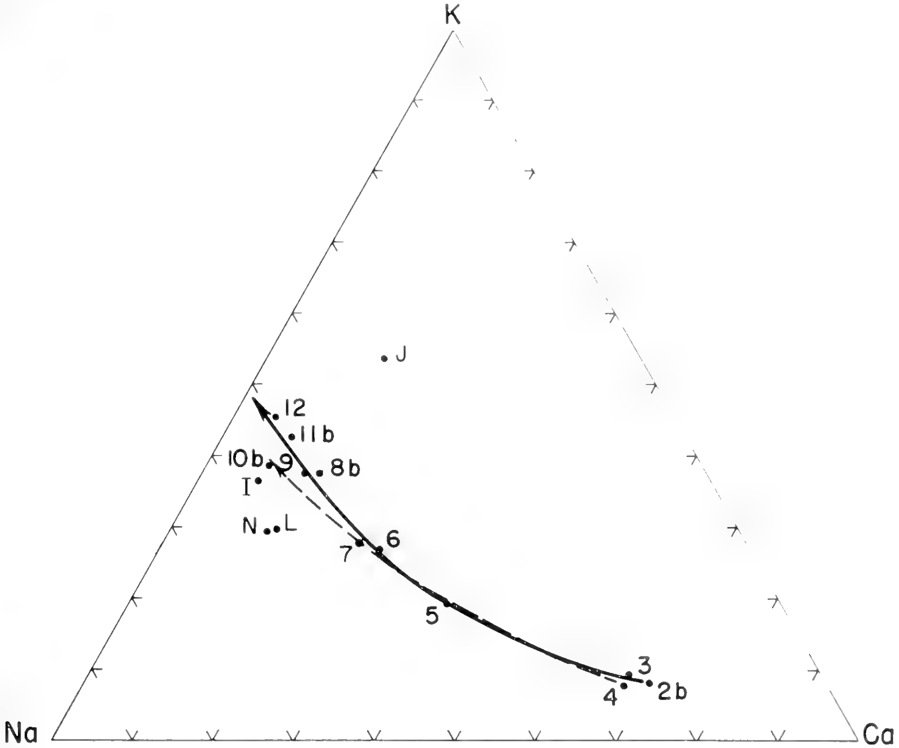


Figure 18. Ionic variation diagram of San Benedicto rocks. Variation of K – Na – Ca. Dashed line denotes variation of the Hawaiian alkali basalt-trachyte suite (Nockolds and Allen, 1954, fig. 17).

and Katsura (1962, fig. 2; 1964, fig. 1), an alkali-silica diagram illustrates the difference between tholeiitic and alkali fields. While the boundary shown in figure 22 (which was drawn in 1960) is slightly different, compared to the position of the boundary given by Macdonald and Katsura, the relationship remains unchanged.

The final stage of differentiation, from sodic trachyte to sodic rhyolite, is similar to that observed on other oceanic islands. Lavas containing at least 10 per cent modal or 15 per cent normative quartz with SiO_2 contents of about 70 per cent or more occur on the following (intrapacific) islands within the basin: San Benedicto (this paper) and Socorro (Bryan, 1959), Islas Revillagigedo; Marutea du Sud, Tuamotu Islands (Lacroix, 1927, 1939); Easter Island (Lacroix, 1936, 1939; Bandy, 1937); Oahu, Hawaii (Macdonald and Katsura, 1962; 1964); Tutuila, Samoa (Daly, 1924; Macdonald, 1944); and Hiva Oa, Marquesas (Barth, 1931). These high-silica rocks generally appear closer in composition to the average alkali or peralkali rhyolites of Nockolds (1954) than

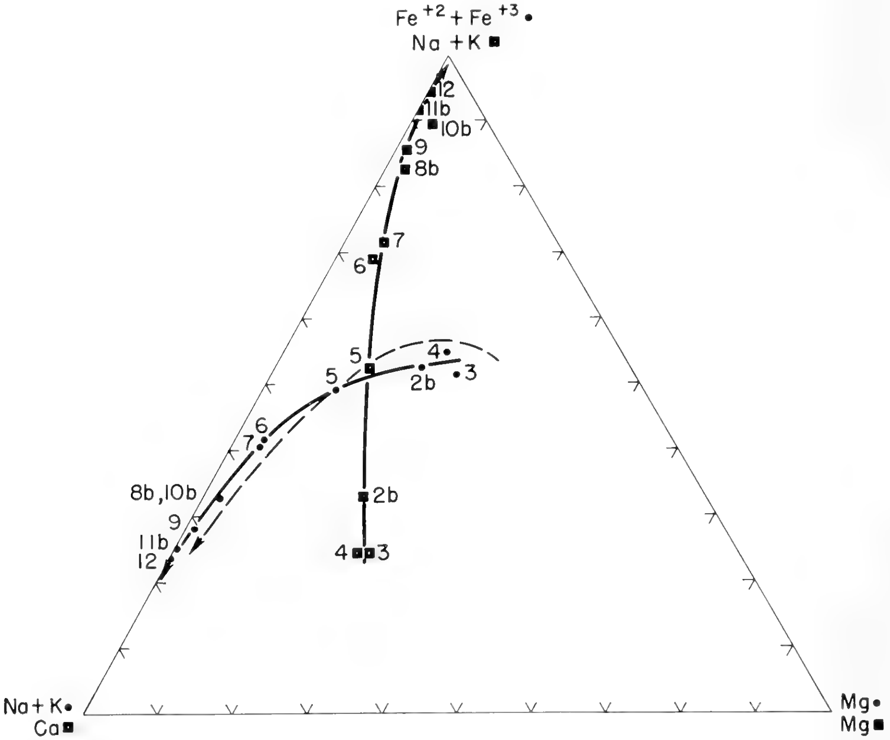


FIGURE 19. Ionic variation diagram of San Benedicto rocks. Dots show variation of total Fe – Na + K – Mg, and squares show variation of Na + K – Ca – Mg. Dashed line denotes variation of the Hawaiian alkali basalt-trachyte suite (Nockolds and Allen, 1954, fig. 17).

to his alkali or peralkali trachytes (fig. 22). All appear to be normal silicic derivitives from alkali basaltic magmas (Daly, 1925, 1934; Bandy, 1937; Tilley, 1950; Richards, 1957a; Bryan, 1959; Kuno, 1959).

It is postulated that the occurrence of the extreme silicic differentiation products (sodic rhyolite) on San Benedicto is related to the rising convective currents located under the crest of the East Pacific Rise. A discussion of the relationship of high heat flow, thin crust above the Moho, and other evidence pointing to mantle convection under the Rise has been summarized by Hess (1962) and Menard (1964).

It follows from the concept of the spreading sea floor (Hess, 1959; Dietz, 1961; Wilson, 1963a; and others) that rhyolites are not found on Roca Partida or Clarión because these islands were formed by primitive (mafic) volcanic activity occurring at an early stage in the convective process that created the East Pacific Rise. Such a process may have been similar to that proposed by Hess (1954, fig. 10, hypothesis B).

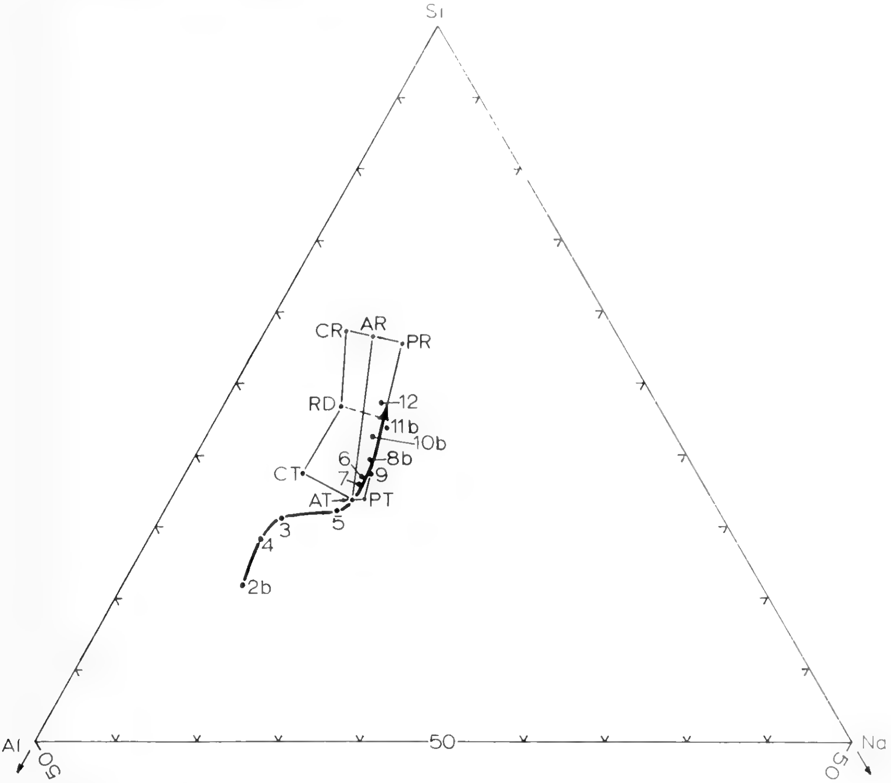


FIGURE 20. Ionic variation diagram of San Benedicto rocks showing variation of Si – Al – Na (SAN diagram). Also shown are the average: calc-alkali rhyolite and rhyolite obsidian (AR), peralkaline rhyolite and rhyolite obsidian (PR), rhyodacite and rhyodacite obsidian (RD), and the corresponding calc-alkali trachyte (CT), alkali trachyte (AT), and peralkaline trachyte (PT) that are given by Nockolds and Allen (1954). Lines connecting average values were drawn by me for illustrative purposes.

After Clarión was built above sea level by successive outpourings of relatively mafic lava, it gradually was carried along by translatory convective movement to its present position about 380 nautical miles west of the median of the crest. Wilson (1963a, 1963b, 1964) has presented evidence that "of eleven straight chains of young islands in the Pacific, ten get older away from the east Pacific rise." San Benedicto and Socorro presumably have moved less far, and increasing time somehow has enabled a higher degree of differentiation to occur, which ultimately led to the late eruption of rhyolites on these islands. Present volcanic activity attests to the fact that the process is continuing. The relationship within the suite of chemically analyzed lavas on each of the four islands is shown in figure 24.

Observed differentiation of Bárcena magma was slight. It consisted of a decrease in Si and K and an increase in most of the other elements from pumiceous ash (analysis 8b) to crater (analysis 6) and delta (analysis 7) lavas (figs. 17–20). Na remained relatively constant. The minor differences between the crater and delta lavas may not be significant.

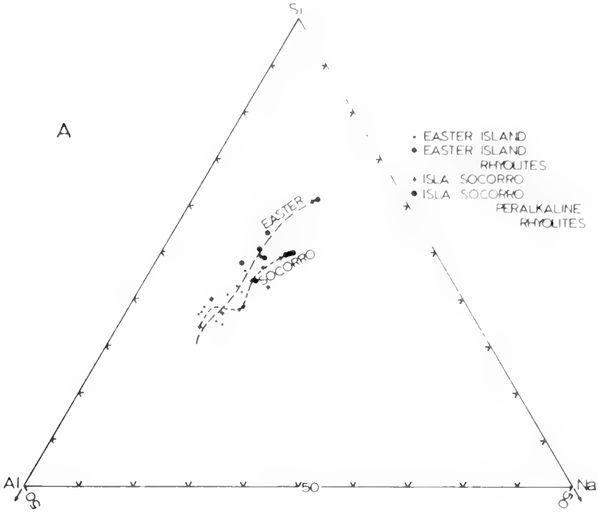
At the beginning of the eruption the gas-rich, silicic top of the magma reservoir was erupted as ash, probably following Verhoogen's (1951) postulation. After the gas pressure had diminished, lava was later erupted from a lower level in the magma chamber. It was less silicic, somewhat richer in ferromagnesian minerals than the upper part that erupted first, and showed a fivefold reduction in water of crystallinity. The presence of olivine-bearing trachybasalt xenoliths in trachyte indicates the existence of these rocks at lower levels and thus indirectly supports the conclusion that differentiation probably resulted from the normal fractional crystallization of an alkali basalt magma.

While the silicic differentiates do not appear to be related to a tholeiitic magma, such as was suggested by Macdonald and Katsura (1964, p. 106) to account for the rhyodacite on Oahu, it is recognized that the alkali series *may be* derived from a tholeiitic magma following the line of evidence presented by Engel and Engel (1964) and Kushiro (1964). As mentioned previously, however, there appears to be no evidence for tholeiitic volcanics on San Benedicto. More convincing are the arguments (Yoder and Tilley, 1962) that tholeiitic and alkali-basalt magmas are derived from a single parent. The derivation is pressure (depth) dependent, and alkali-type basaltic liquids were considered to be produced at higher temperatures than tholeiitic liquids (p. 520). If this relation is valid at depth in the vicinity of San Benedicto, it is unlikely that tholeiitic rocks underly the volcanic pile.

Oceanic Rhyolites from Islands on the East Pacific Rise

Peterson and Goldberg (1962) reported on the relative abundances and types of feldspar in pelagic sediments of the South Pacific. Their work showed that volcanism along the crest of the East Pacific Rise produced silicic lavas, which were characterized by an abundance of locally-derived alkali feldspars, and that the proportion of more mafic lavas, containing plagioclase feldspars, increased with increasing distance away from the Rise crest. They also found a distinctly higher quartz/feldspar ratio in the coarse-size fraction of sediments collected near the crest. The relation of the Revillagigedo volcanics to the Rise had not been recognized prior to the publication of this important study.

The occasion of giving an invited paper on the petrochemistry of the East Pacific Rise at Kiel University in early 1963 provided an opportunity to reexamine the relationship in the Archipiélago de Colón (Galápagos). This group of islands trend approximately normal to the trend of the East Pacific Rise, although the situation is complicated by the presence of the Cocos Ridge, extending northeast, and the Carnegie Ridge extending east of the archipelago



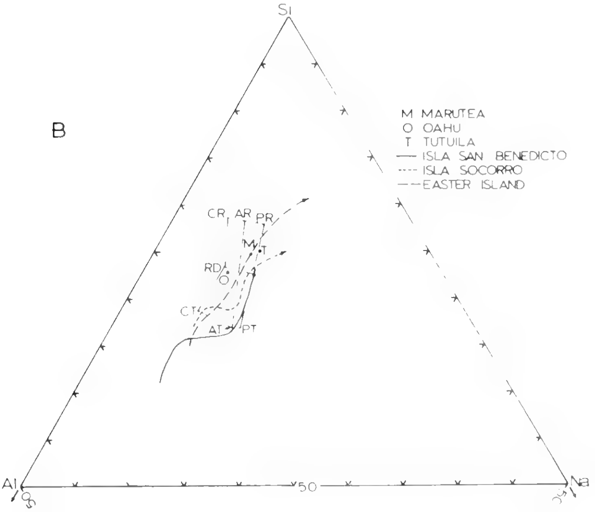


FIGURE 21. Ionic variation diagrams for oceanic rhyolites from intrapacific islands. A. SAN diagram for Easter Island (data from Lacroix, 1939, analyses 4–10, 12–19) and Isla Socorro (data from Bryan, 1959, p. 88–90). B. SAN diagram of rhyolite from Marutea (Lacroix, 1927, p. 45), rhyodacite from Oahu (Macdonald and Katsura, 1962, p. 192), and quartz trachyte from Tutuila (Daly, 1924, p. 107). Other symbols are explained in the caption to figure 20.

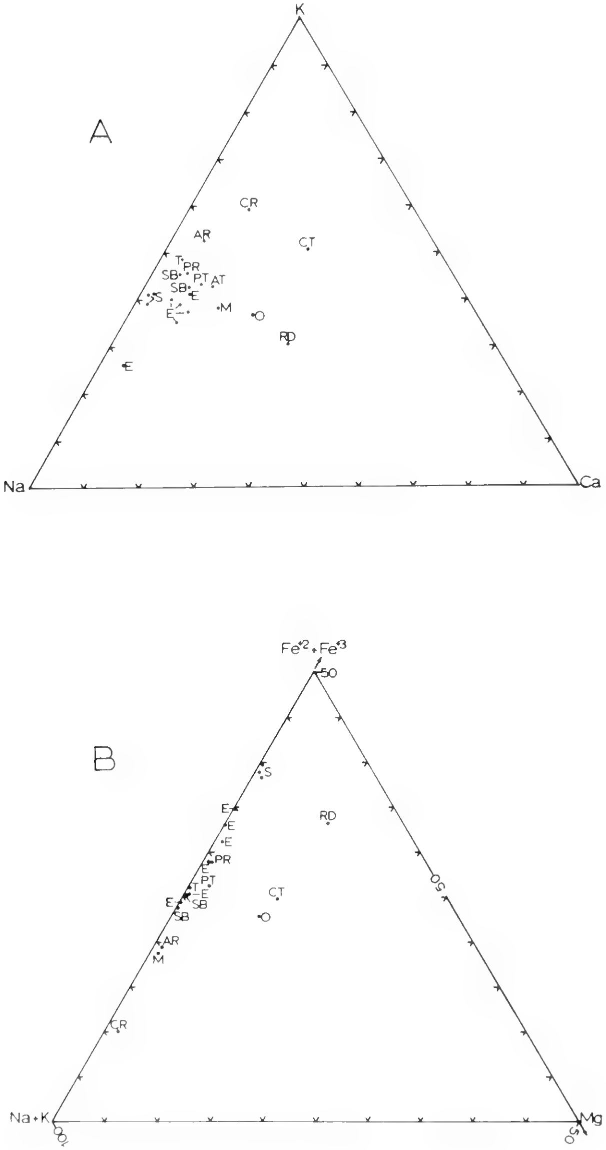


Figure 22. Ionic variation diagrams for oceanic rhyolites from intrapacific islands. A. Variation of K – Na – Ca. B. Variation of $Fe^{+2} + Fe^{+3}$ – Na + K – Mg (FAM diagram). In the diagrams E represents Easter Island, M the Marquesas Islands, O Oahu Island, S Isla Socorro, and SB Isla San Benedictò; other letters are explained in the caption to figure 20.

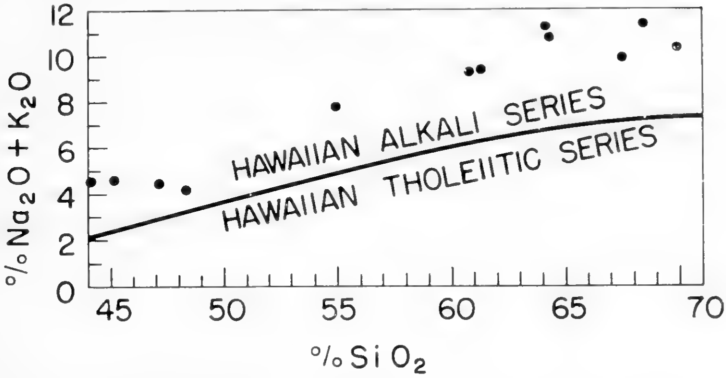


FIGURE 23. Alkali related to silica in San Benedicto rocks. The line divides the Hawaiian alkali rocks from the Hawaiian tholeiitic rocks (after Kuno and others, 1957). The position of this line also is nearly identical to a line separating the Circum-Japan alkali series and the Izu-Hakone tholeiite series reported by Kuno (1959).

(Shumway, 1954, 1957). In a recent summary of historic volcanic activity in this island group (Richards, 1962), it was shown that the most active volcanoes were confined to the extreme west end of the archipelago, which is nearest to the crest of the Rise. While insufficient evidence is available to state whether there exists an areal relationship of silicic and mafic rocks to the Rise, the islands at the eastern end of the archipelago definitely appear older than those at the western end, an observation previously stated by Chubb (1933, p. 21–22).

It probably is not a coincidence that the sodic rhyolites from Easter, Socorro, and San Benedicto are similar (figs. 21 and 22). The most silicic rhyolites found anywhere on intrapacific islands occur on Easter, which lies on the crest of the East Pacific Rise. Sodic rhyolites found on San Benedicto and Socorro, which are located west of the outer limit of the crest, are not as highly differentiated with respect to silica.

On other intrapacific islands, rhyodacite has been reported from Oahu (Macdonald and Katsura, 1962, p. 192; 1964, p. 106–107), sodic rhyolite from Hiva Oa, Marquesas Islands (Barth[4], 1931, p. 525–526), and sodic rhyolite (quartz trachyte) from Tutuila, Samoa Islands (Daly, 1924, p. 106–107; Macdonald, 1944, p. 1344–1347). None of these islands appear to be associated with a rise. All are related to fissures or fracture zones from which vast outpourings of lava have built the submarine foundations of each archipelago. Variation in selected cations is shown in figure 21.

The sodic rhyolite pumice collected from what evidently was a deposit of

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[4] Barth refers to a paper, "Petrology of the Marquesas Islands," in press by H. S. Washington. The manuscript was never published and it and the analysis of this rhyolite by Keyes appear to be lost (Yoder and Tilley, 1962, p. 405; F. Chayes, 1965, personal communication).

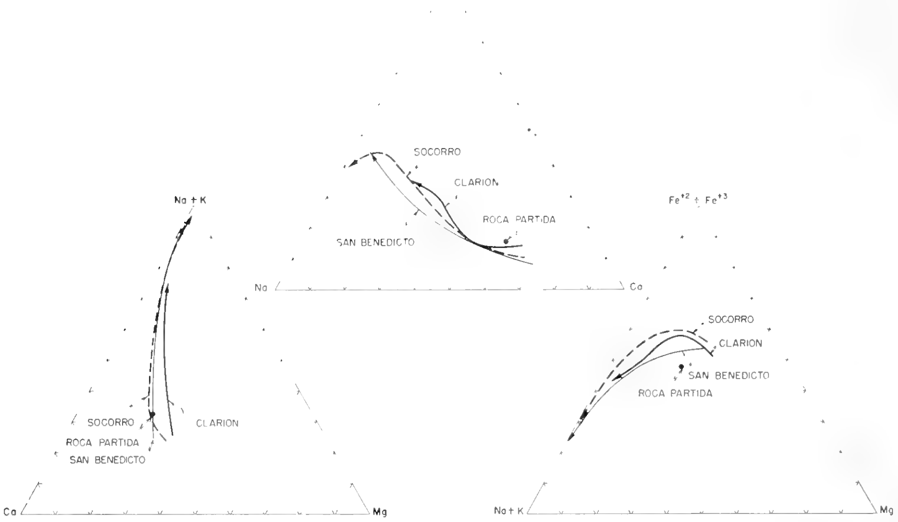

FIGURE 24. Ionic variation diagram for the volcanic rocks of the four Islas Revillagigedo. The arrow length represents the range of values reported. Chemical data for Isla Socorro and Isla Clarión are from Bryan (1959); for Isla Roca Partida they are from Richards (1964).

beach rock on Marutea, Tuamotu Archipelago (Lacroix, 1927, p. 44–45), probably did not originate from a volcano in the Tuamotus, where other sodic rhyolites are unknown. The similarity of the analysis of the Marutea pumice compared to the sodic rhyolites from Easter suggests that it may have drifted to Marutea in the South Equatorial Current following an eruption on Easter. An oceanic drift previously was proposed by Lacroix, who did not suggest a place of origin.

With respect to Easter, it is strange that silicic differentiates have not been reported from Sala-y-Gomez, which is located near Easter Island (Fisher and Norris, 1960) and appears to be composed of lavas of the alkali basalt suite.

It is concluded that while magmatic differentiates as silicic as sodic rhyolite occur on a few islands at or near the crest of the East Pacific Rise, there is no evidence to date indicating that other sodic rhyolites in the Pacific basin are intimately associated with rises.

SUMMARY AND CONCLUSIONS

Isla San Benedicto is located at the north end of a range of submarine volcanoes (and Isla Socorro) that comprise the Mathematician Seamounts. A more satisfactory name for this feature of north–south trending basins and ridges (Richards, unpublished) would be the San Benedicto-Clipperton Ridge.

This ridge is cut by the Clarion Fracture Zone, and its landward continuation of the trans-Mexico volcanic axis, in the latitude of San Benedicto and Socorro. A pattern of local ridges mark the presence of fissures from which have erupted the sequence of alkali basalt to sodic rhyolite that form the island and the submarine ridge that trends north of San Benedicto.

The insular shelf of San Benedicto is poorly developed; shelf-break occurs about 55–60 fathoms at the south end and 70–75 fathoms at the north end of the island. Ascending magma under the south end of the island is believed to satisfactorily account for the tilt of the shelf.

Volcanism progressed from north to south in the immediate vicinity of San Benedicto; the oldest rocks are at the north end. This volcanism probably occurred during the Pleistocene or at least during the late Cenozoic; the island is older than late Pleistocene.

The first geological map of San Benedicto shows the relations of the eroded volcanics at the north end of the island, the large trachytic domes in the center, and the two newest pyroclastic volcanoes, Montículo Cinerítico and Bárcena, at the south end. The latter volcano originated between August, 1952, and March, 1953.

Petrographic investigations and chemical studies based on 12 new analyses show a differentiation sequence:

Trachybasalt (alkali basalt) → trachyandesite (mugearite) → sodic trachyte → sodic rhyolite.

Tholeiites and high alumina basalts have not been found and are believed not to exist in the vicinity of San Benedicto. The trachyandesite appears marginal in composition between hawaiite (Macdonald, 1960) and mugearite. Evidence is presented that while the sodic rhyolites are unusual, they are considered to be normal extreme differentiates in the sequence. The described sodic rhyolites do not appear to be pantellerites.

With increasing distance from the crest of the East Pacific Rise, the geologic age of the Revillagigedo islands increase and there is a progression towards more mafic volcanics to the west. The sodic rhyolites of San Benedicto and Socorro are not found on Isla Clarión or Isla Roca Partida. Active volcanism is confined to San Benedicto and Socorro, which are nearest to the crest of the Rise.

A similar relationship is reported for the Archipiélago de Colón (Galápagos Islands); however, the active volcanoes are at the west end of the archipelago and the age of the islands increases to the east.

Elsewhere in the east Pacific possible relationships between petrographic provinces and oceanic rises generally are not clear because of the paucity of samples and the conflicting nomenclature. In the years since Macdonald's (1949) classic paper summarized volcanic rocks found on central and some east Pacific islands, igneous rocks have been collected and described from a number of east Pacific islands and submarine volcanoes by Bryan (1959), Budinger and Enbysk (1958), Carsola and Dietz (1952), Chesterman (1963), Engel and Engel (1963, 1964), Fisher and Norris (1960), Johnson (1953), Krause (1961, 1964), Obermuller (1959), and Richards (1957a, 1957b, 1958b, 1964). Little more can be said than that all of the described rocks appear to represent reasonably normal oceanic volcanics as defined by Macdonald (1960) and discussed by Chayes (1964a). Very recently, however, an increasing number of tholeiitic basalts have been dredged from the sea floor. It is likely that this trend will continue, as shown by Moore's (1965) description of dredged tholeiites from the vicinity of Hawaii.

APPENDIX

TOPOGRAPHIC MAP OF SAN BENEDICTO.

The following assumptions were made by me when contour interval, coordinates, and scale were established in the preparation of figures 2 and 4.

The maximum altitude of Bárcena was determined by four different methods: (1) a 1250-foot altitude was obtained from nearly identical altimeter readings made on three flights in 1952 and 1953. (2) On the May 25, 1955, flight a radio altimeter measurement indicated 1120 feet for the maximum altitude. (3) A figure of about 1130 feet was obtained by parallax measurements (Tewinkel, 1952, p. 324–328) from photographs taken in May, 1953. (4) The external slope of Bárcena is 33°. Assuming that the map scale is correct, a 1100-foot maximum altitude is indicated by trigonometry. Altimetry measurements are frequently unreliable because of differences in barometric pressure owing to the lapse of time between readings made for calibration and at the point to be determined. The latter three methods are more accurate and they indicate an approximate maximum altitude of about 1120 feet.

Twenty-one form lines are shown on the original "topographic map" made by Jack Caudry, PHC, USN. The resulting contour interval is 52 feet, based on a maximum altitude of 1090 feet for the 21st form line. Form line or contour accuracy is very good south of Cráter Herrera and fair to good north of Cráter Herrera (Jack Caudry, personal communication). Some cliffs should be steeper than indicated, particularly Roca Challenger and Cráter Herrera.

The map scale was determined photogrammetically using the relation that the natural scale is equal to the flying altitude divided by the focal length of the camera lens. This figure was verified by extrapolation from the measured lengths of Banda and Volteadura beaches made in November, 1953, by Donald Wise and James Bobcock.

True north was obtained in May, 1955, from the R/V *Crest* by gyrocompass bearings made between the Delta Lávico, Bárcena, Punta Ortolan, and Punta Observer. The reproducibility of the measurements is about one degree.

Coordinates are based on Punta Sur, which was determined by the U.S.S.

Narragansett Survey in 1874 (Dewey, 1874) to be located at 19° 17′ 15″ north latitude and 110° 49′ 25″ west longitude (U.S. Navy Hydrographic Office chart no. 1687, 9th ed., May, 1925). This position is approximate because in the late ninteenth century longitude was based on chronometer time obtained in the last port of call and it was not possible to establish precise positions from shipboard.

Bathymetry.

In the preparation of figure 5, soundings originally were plotted to a chart scale of 1:21,000; the chart, with 50-fathom contours, was pantographed to a scale of 1:49,500 before it was redrawn showing 100-fathom contours.

Soundings were taken with a Navy type NMC-1 echo sounder, calibrated for a nominal sound velocity in sea water of 4800 feet per second. They have not been corrected for velocity variation due to effects of temperature, salinity, and pressure. True depths would be about 2 per cent greater.

Control of ship position near San Benedicto was based on horizontal sextant angles, pelorus bearings from a gyrocompass repeater, and radar ranges. North of the island, where sextant angles tangent to the east and west sides were less than 5° to 7°, positions were obtained from pelorus bearings, radar ranges, and dead reckoning.

Terminology of topographic features in general conforms with definitions proposed by the International Committee on the Nomenclature of Ocean Bottom Features (Wiseman and Ovey, 1953).

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 13, pp. 415–452; 12 figs. May 12, 1966

SPECIATION AND SYSTEMATICS OF THE GEKKONID LIZARD GENUS *PHYLLODACTYLUS* OF THE ISLANDS OF THE GULF OF CALIFORNIA

By

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ABSTRACT: The possible factors affecting the rate of speciation of *Phyllodactylus* of the Gulf of California are discussed. Six new species and five new subspecies of *Phyllodactylus* are described from the islands. An analysis of variation within and between the populations of *Phyllodactylus* inhabiting the islands is presented.

INTRODUCTION

The California Gulf islands have, during the past 60 years, received considerable attention from biologists and geologists. Many collections of plants and animals have been taken from the islands, yet certain groups of vertebrates have been neglected. Among these have been the nocturnal lizards of the genus *Phyllodactylus*. The first record of *Phyllodactylus* from the islands was by Van Denburgh (1922). From 1922 to 1960, 113 specimens of *Phyllodactylus* had been taken from the approximately 30 islands of the Gulf, a number too few to be very helpful in understanding the insular relationships of this difficult group of lizards.

Between 1960 and 1965 several expeditions visited the Gulf islands and as a consequence about 400 specimens of *Phyllodactylus* are now available for study. Among the expeditions which have been responsible for this noteworthy addition to the available samples of this interesting gekkonid group must be

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mentioned the Belvedere Scientific Fund expedition of the California Academy of Sciences in 1962, the "Sea of Cortez" expedition of the California Academy of Sciences and San Diego Natural History Museum, 1964, and the "Biology of the Insular Lizards of the Gulf of California" expedition, of which the author was a member, in 1964. Further, a few specimens of *Phyllodactylus* have been collected by individuals who have on their own visited one or more of the Gulf islands in recent years; the numbers of specimens taken have not been large.

Davis and Dixon, in 1961, and Dixon in a series of papers between 1960 and 1964 (1960a, 1960b, 1962, 1964a, 1964b) reported on those populations of *Phyllodactylus* inhabiting the mainland of Mexico and Peninsular Baja California. In the present report I am concerned primarily with the dispersal and speciation of the insular populations of *Phyllodactylus xanti.* However, two other species, *P. unctus* and *P. tuberculosus*, are currently recognized as inhabitants of the Gulf islands; their insular relationships will be reported on briefly in the text of this paper. With this report I conclude my studies of those populations of *Phyllodactylus* found north of the Isthmus of Panama.

Acknowledgments

I wish to thank the following persons and institutions for making available to me specimens of *Phyllodactylus* from the islands of the Gulf of California: C. M. Bogert, American Museum of Natural History (AMNH); J. M. Savage, University of Southern California–Allen Hancock Foundation (AHF–USC); the late Norman Hartweg, University of Michigan Museum of Zoology (UMMZ); R. F. Inger, Chicago Natural History Museum (CNHM); L. M. Klauber, San Diego Natural History Museum (LMK-SDMNH); A. E. Leviton, California Academy of Sciences (CAS); G. S. Myers, Division of Systematic Biology, Stanford University (SU); K. L. Norris, University of California at Los Angeles (UCLA); A. J. Sloan, San Diego Museum of Natural History (SDMNH); E. E. Williams, Museum of Comparative Zoology, Harvard University (MCZ).

I also wish to thank the following scientists and students of the 1964 "Biology of Insular Lizards" expedition to the islands of the Gulf of California for their able help in securing specimens: C. C. Carpenter, R. F. Clarke, T. P. Maslin, D. W. Tinkle, C. J. McCoy, L. J. Bussjaeger, W. C. McGrew, O. Cuellar, and S. W. Taft. I am especially grateful to S. W. Taft, D. W. Tinkle, and O. Cuellar for their many hours they spent with me toiling among the northern islands of the Gulf in pursuit of these elusive lizards.

This research project was supported in part by a cooperative grant to the author from the National Science Foundation (G. B. 2362).

Historical Considerations

Genetic and physical factors obviously have had a marked effect on the dispersion and speciation of reptiles among the islands of the Gulf of California.

The same species may occur on neighboring islands, or have a disjunct distribution occurring on islands that are not adjacent to one another, or different species of the same genus may occur on neighboring islands. For example, *Sauromalus hispidus* is found on two islands of a northern chain of islands which lie in a north–south direction. These islands, beginning at the northern end are: Angel de la Guarda, Partida (N.), Raza, Salsipuedes, San Lorenzo (N.), and San Lorenzo (S.). *Sauromalus hispidus* is found on Angel de la Guarda and adjacent islets, and on San Lorenzo (N.) and (S.) but it is not known to occur on any of the three intervening islands. On the other hand distinct species of *Phyllodactylus* occur on most of the islands mentioned.

An analysis of the populations of *Phyllodactylus* that have been sampled from 25 of the approximately 30 islands of the Gulf suggests three stages of speciation: 1) fairly recent separation from a parental stock, there being little or no evidence that these recently isolated populations differ genetically (as inferred from their morphologies) from the parental population; 2) a long period of isolation from a parental stock giving rise to readily distinguishable populations (species level); and 3) an intermediate condition of the first two stages (subspecies level).

Geographical isolation has played a leading role in providing an opportunity for diversification of populations of *Phyllodactylus* to take place. Reasonably well understood are the genetic mechanisms involved in speciation. Not so well known, however, are the unique characteristics of the Gulf islands in providing a singular geographical environment in which speciation can take place rapidly.

Description of the Islands

According to King (1959), the coastal ranges of Baja California belong to the Nevadan Orogeny of the Cretaceous Era. King indicates that the probable formation of the Gulf of California was during a strike-slip movement of the San Andreas fault, and subsequent faults related to the San Andreas system may have displaced the main mountain mass some distance to the northwest from the original fracture zone. This type of faulting, a rise to the west and a drop to the east along the fault line, easily could have created the present inundation of land underlying the Gulf of California. More recently Allison (1964) discussed the geology of areas bordering the Gulf of California and mentioned additional hypotheses concerning the origin of the Gulf.

King (*op. cit.*) indicates that there were several subsequent compressions of rocks in the coastal ranges during the Tertiary period. The two general climax periods of orogeny occurred near the middle of the Miocene and early in the Pleistocene.

There are indications that while there were great areas still inundated following the mid-Miocene deformation, the mid-Pleistocene deformation brought about a widespread emergence. This may account for the fossil shell beds atop

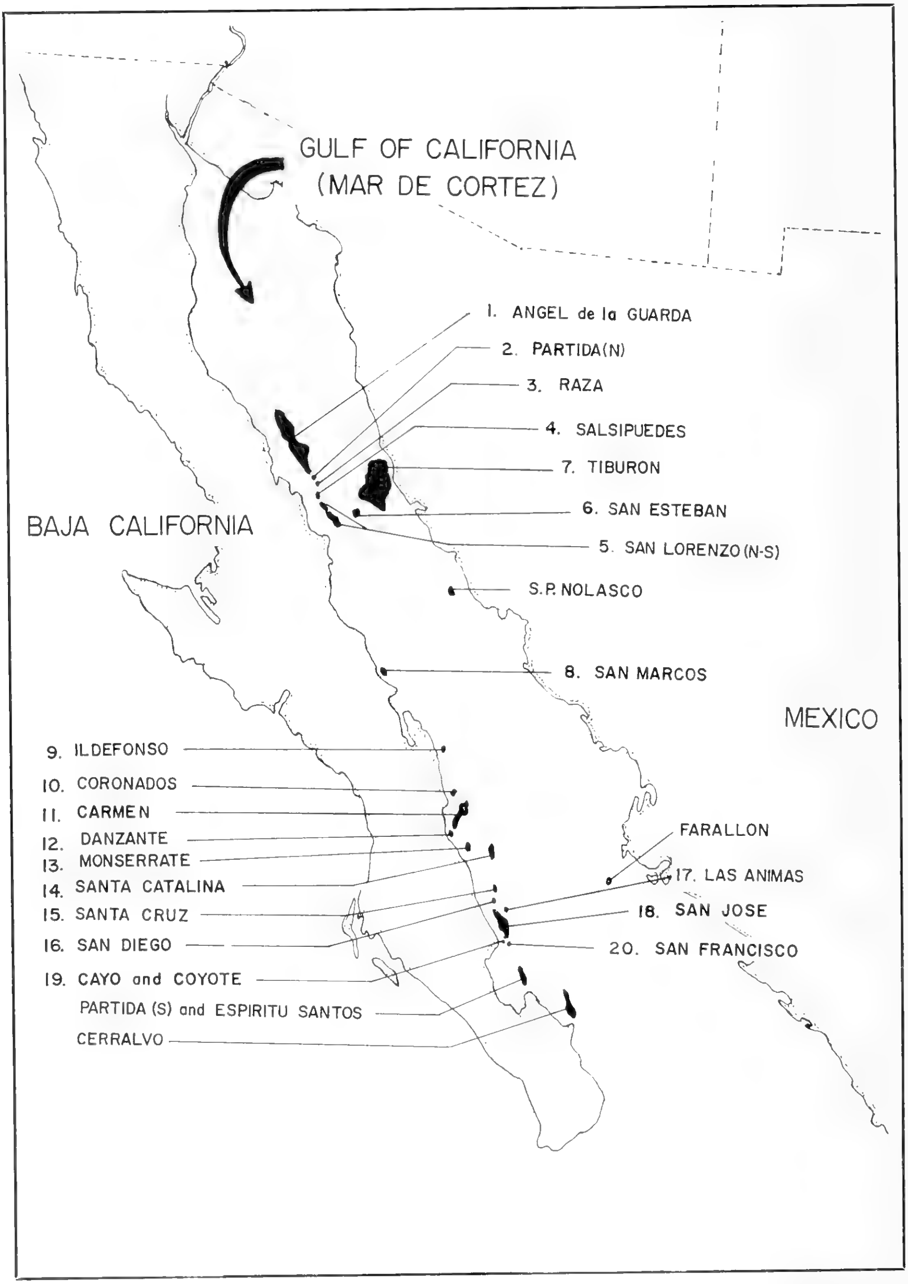


FIGURE 1. A map of the Gulf of California indicating the islands where *Phyllodactylus* have been taken. The numbers present before some of the islands correspond with the sequence of numbers found in figures 3 through 12.

some of the islands in the Gulf. These islands lying close to the peninsula of Baja California have probably been separated from, or united with, the peninsula several times during the late Miocene and early Pleistocene. There are fossil Pleistocene shell beds on nearly all of the islands, indicating a much higher sea level than found at the present time. There are fossil shell beds on the tops of Isla Partida (S.) and Espíritu Santo showing that those islands were once completely submerged. However, some of the islands do not appear to have shell beds; such beds, if present at one time, may have weathered away if the islands have been emerged for a long period of time, or the islands may never have been completely inundated. There is some doubt as to the exact time the Gulf islands were formed or when individual islands were either submerged or exposed. According to geologists W. E. King and J. I. Colbert (personal communication) there have been several periods of emergence and submergence associated with periods of fault activity.

A brief description of the geology, physiography, and vegetation of the islands is given by Lindsay (1962) in his account of the Belvedere Expedition to the Gulf of California. However, a few remarks about the physical distance of each of the northern islands from the Baja California peninsula and from the mainland of Mexico (State of Sonora), and from island to island, seem necessary for the purposes of this report.

Isla San Pedro Martir lies farthest out in the Gulf, about 22 miles south of Isla Tiburon, 32 miles east of peninsular Baja California, and 37 miles west of the Mexican mainland. *Phyllodactylus* has not been taken from this island, nor from Isla Tortuga, which is located about 16 miles NE. of Isla San Marcos, 22 miles E. of Baja California, and 81 miles W. of Sonora.

Phyllodactylus has been taken from all the remaining islands of the northern portion of the Gulf. Isla Tiburon lies 2 miles west of the Sonoran mainland. Isla San Esteban lies 8 miles west of Tiburon and 10 miles east of Isla San Lorenzo. Isla Salsipuedes lies 1 mile NW. of San Lorenzo and five miles south of Isla Raza. Isla Partida (N.) is located 8 miles SSE. of Angel de la Guarda and 7 miles NNW. of Isla Raza. The latter islands form a long chain in northern terminus lying 8 miles east of Baja California, the southern end 11 miles east of the peninsula. The island chain is surrounded by depths of water greater than 600 feet, while depth of the water between San Esteban and Tiburon and the Sonoran mainland is less than 600 feet. All of the remaining islands lie on the continental shelf of Baja California or of mainland Mexico with the exception of San Pedro Martir and Isla Tortuga. All of the southern Gulf islands lie within 14 miles of the peninsula of Baja California, and most lie within 4 miles.

Distance from island to peninsula or mainland or from island to island does not appear to be an important factor in determining the possible routes of dispersal in the Gulf of California. However, the combination of distance, depth of water, and present relationship of insular populations with those of the main-

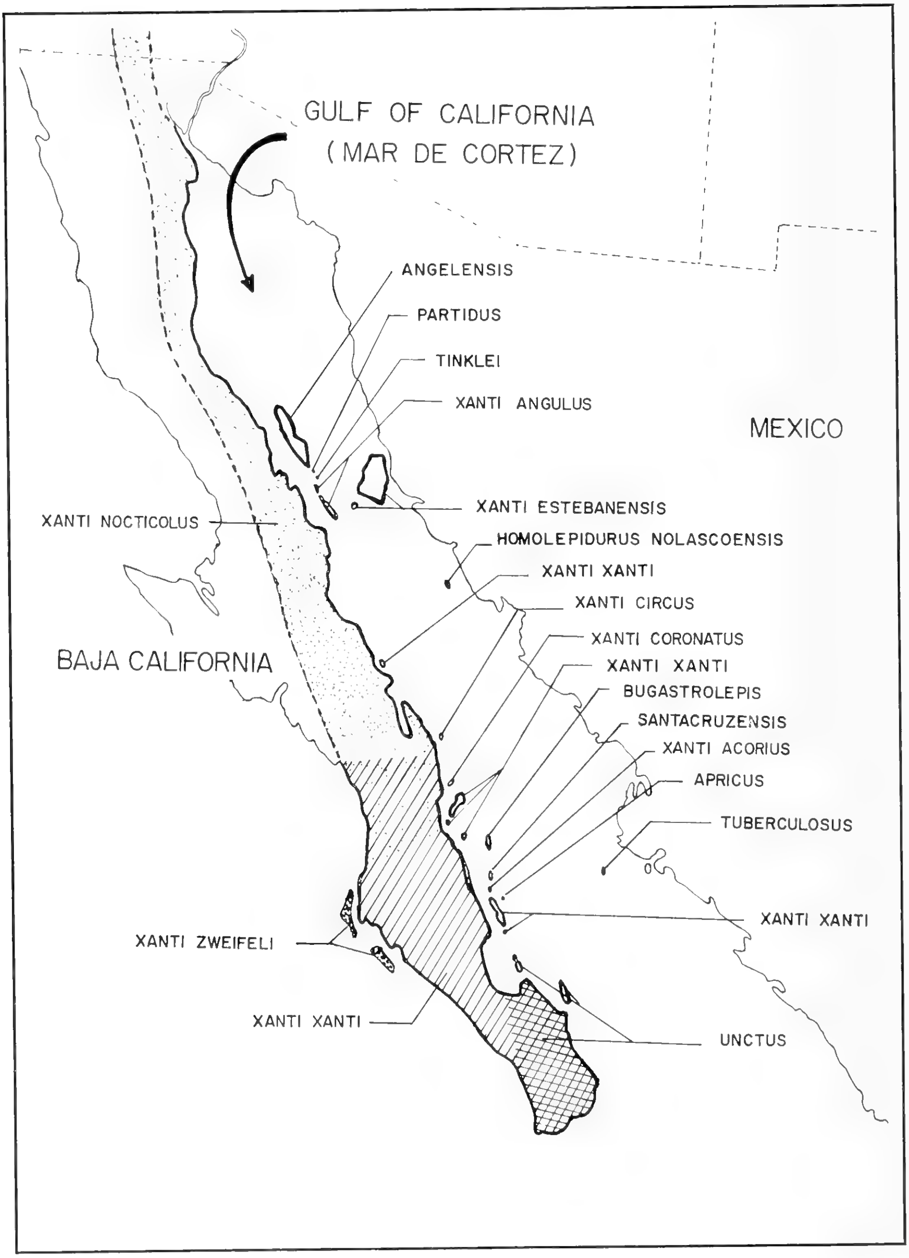


FIGURE 2. A distribution map of the species and subspecies of *Phyllodactylus* inhabiting Baja California and the islands of the Gulf of California.

land and/or peninsula does give some insight into the comparative recency that islands may have been connected with the mainland, with the peninsula, or to one another.

SPECIATION IN GULF ISLAND *PHYLLODACTYLUS*

The rate of speciation is affected by both genetic and geographical factors. Morphological characteristics of the various insular populations may be used as an index of genetic similarity between populations. The rate of speciation between island populations and between island and mainland or peninsular populations may be surmised. The rate of differentiation that one insular population may reveal over another is also suggested, but not the possible reasons why one population evolves faster or slower than another.

The following may serve as an example of the above: Islas Cerralvo, Partida (S.), Espíritu Santo, and Ballena are 4 to 5 miles from Baja California or from possible connections with other islands and the peninsula. The populations of *P. unctus* found on these islands deviate very little from that on the peninsula. Under the conditions outlined above, this form has shown little tendency toward speciation. However, Isla San Pedro Nolasco lies 9 miles from the Sonoran mainland; the population of *Phyllodactylus* inhabiting the island, though related to a mainland form, is quite distinct, and a rapid rate of evolution is suggested. The name presently applied to the San Pedro Nolasco population is *P. homolepidurus nolascoensis*. Recent additional material from the island indicates a longer period of isolation from the mainland than was originally believed (Dixon, 1964). An analysis of the additional material indicates that the characters that separate *P. h. nolascoensis* from *P. h. homolepidurus* are more uniform and diagnostic in nature. The Isla San Pedro Nolasco population may represent a distinct species, rather than a race of the mainland form.

NORTHERN GULF ISLANDS. The rate of speciation among the leaf-toed geckos of the Gulf of California islands appears to be most rapid in the northern portion of the Gulf. The populations inhabiting Angel de la Guarda, Partida (N.), and Raza appear to be more distinct, with the San Lorenzo–Salsipuedes and San Esteban–Tiburon populations more closely related to *P. xanti nocticolus* of peninsular Baja California. This is unusual inasmuch as Angel de la Guarda is much closer geographically to Baja California than is Isla Tiburon. I cannot explain this insular relationship on the basis of distances from island to island or from island to peninsula beyond calling the reader's attention to those factors. However, the factors mentioned in the historical section surely provide part of the answer.

The similarities of the Tiburon–Esteban population to that of peninsular Baja California may not be as close as the scale characters indicate. If we exclude the latter characters and consider color and color patterns, the relationship is reversed. The ventral color and dorsal color pattern more closely resembles

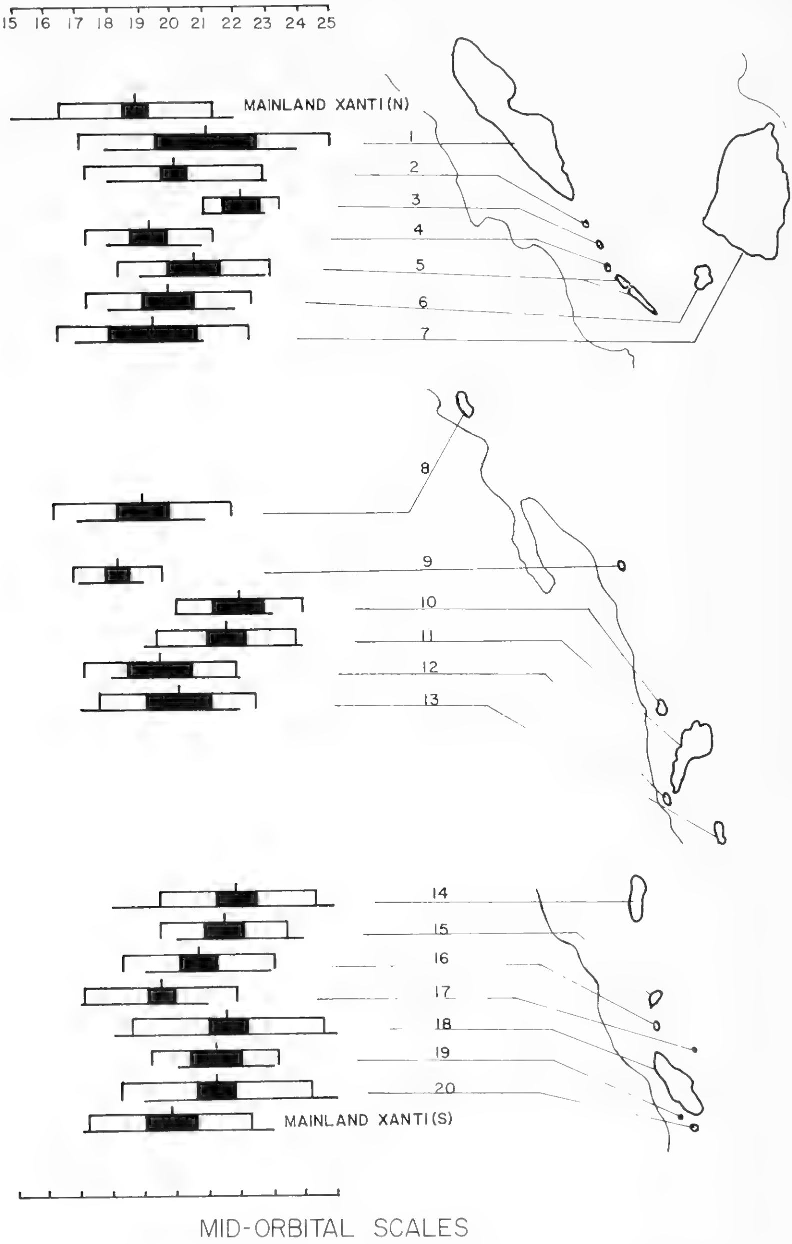


FIGURE 3. Variation in the number of mid-orbital scales of *Phyllodactylus* of the islands of the Gulf of California. Vertical bar represents the mean; open rectangle, twice the standard deviation; black rectangle, twice the standard error; bottom horizontal line, range of variation.

that found in *P. homolepidurus* of the Sonoran mainland. The question arises as to which one of the characters is the more reliable. All specimens of *P. xanti* exhibit more orbital scales than scales across the snout at the level of the third labial, and the reverse is true in all those of *P. homolepidurus*. On the other hand, all individuals of *P. xanti* have a white venter while those of *P. homolepidurus* have yellowish or dusky areas on the lateral margins of the belly. There are more external factors affecting color than those affecting the number of scales. Temperature and humidity frequently cause color changes in *Phyllodactylus*. The color of the *Phyllodactylus* on the eastern side of the Gulf in the vicinity of Tiburon and the Sonoran mainland may be exhibiting a phenotypic response to the environment. The population could also be one that has intergraded with or hybridized with *P. homolepidurus*, and the island population consists wholly of a hybrid population.

However, I believe that the scale characters should exhibit some intermediate condition between the two forms, and this condition has not been found. If the population is responding to phenotypic stimuli, and its true relationship is with *P. xanti* some 32 miles to the west, the resulting zoogeographic pattern of dispersal is confusing.

Isla Partida (N.) is inhabited by a population of *Phyllodactylus* that appears to be related to *P. homolepidurus*. This island is 12 miles east of Baja California and 20 miles west of the Sonoran mainland. This population is unlike its neighboring populations on islands 8 miles to the north (Angel de la Guarda) and 5 miles to the south (Raza), which resemble *P. xanti* in size and in some scale characters.

The islands are probably remnants of mountaintops of an ancient mountain mass once connected to Baja California that became inundated with the formation of the Gulf. A possible answer to the present distribution of *P. xanti* stock would be one of former distribution over the mountain mass prior to inundation. This would explain the relationship of the Tiburon population, but not the one on Partida (N.).

The Partida population may have arrived from Sonora by rafting and hence evolved from *P. homolepidurus* stock. There is the possibility of independent genetic drift of a *P. xanti* stock that just happened to evolve into a population resembling "*homolepidurus*" stock. In any case, the actual mechanics may never be demonstrated. The present fact is that it appears to be of "*homolepidurus*" stock, and I am obligated to treat the population on the basis of its apparent relationship to the Sonoran mainland species.

The populations inhabiting Islas San Esteban and Tiburon are similar in color, color pattern, and in all scale characters except in the number of scales bordering the internasals. The latter character is not statistically distinct and is not considered as a diagnostic feature for differentiation of the two island populations. I consider the two populations identical and of fairly recent origin. They

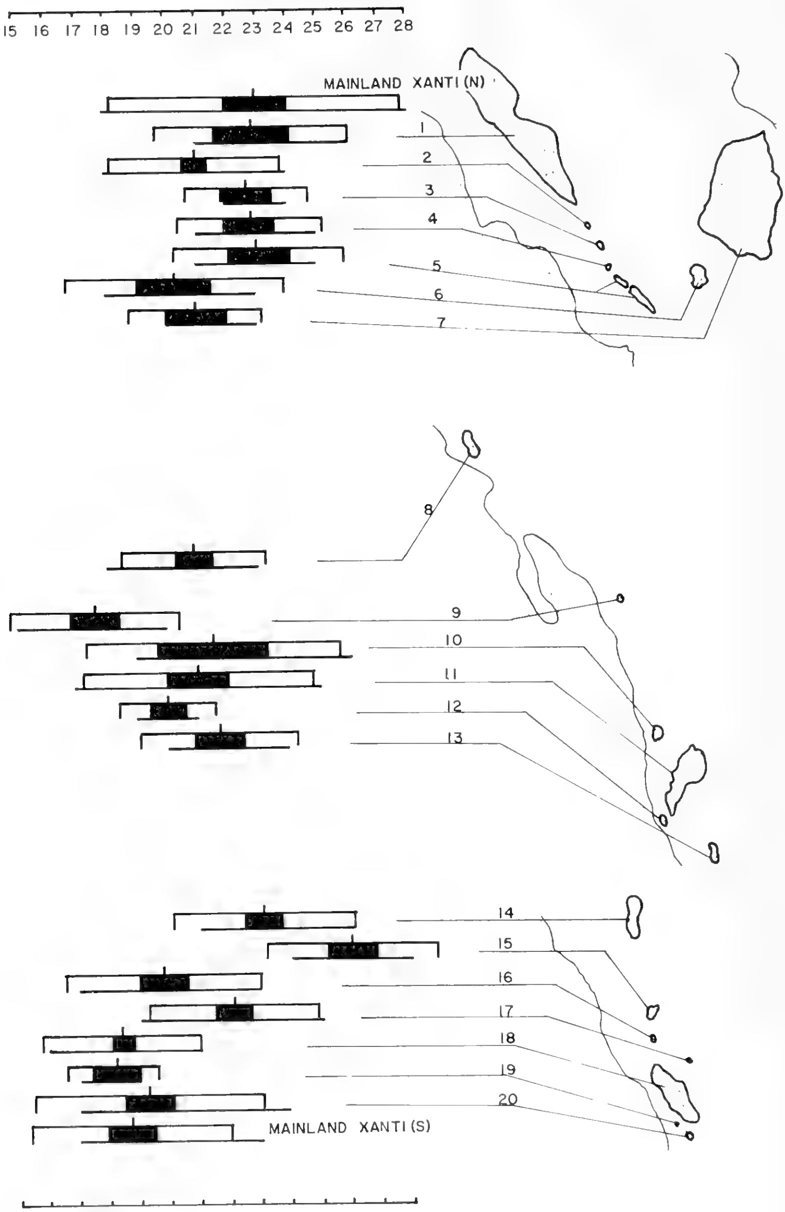


FIGURE 4. Variation in the number of tubercles in a paravertebral row between axilla and groin (see figure 3 for explanation of analysis).

are now sufficiently distinct from *P. xanti nocticolus* to be considered as a subspecies.

The populations occurring in Islas Salsipuedes, San Lorenzo (N.), and San Lorenzo (S.) are in about the same stage of speciation as the San Esteban Tiburon populations. They are relatively close in all characters with the Salsipuedes population, indicating slight divergence in some scale characters from the San Lorenzo populations. However, they are statistically distinct from the San Esteban–Tiburon and the Baja California populations in several scale features. Color and color patterns are similar to those on Baja California rather than to the San Esteban–Tiburon population.

The dispersal route of the parental stock of *P. xanti* seems to be from Baja California to Isla San Esteban and Isla Tiburon via the islands of Salispuedes and San Lorenzo. I base this assumption on the present morphological relationships of the *Phyllodactylus* on these islands.

The Isla Raza population indicates a closer relationship to the Salsipuedes population some 5 miles to the south, than to the Partida population 7 miles to the north. However, the Raza population has evolved much further than the Salsipuedes population. Of 13 essential meristic characters analyzed in this study, the Raza population is statistically distinct from the Salsipuedes population in 6, from the Partida population in 9, and from mainland *P. xanti* in 5. Its relationship with the mainland is not as close as is indicated by its meristic characters for the color and color patterns are quite unlike the mainland *P. xanti* and adjacent islands.

The population inhabiting Isla Angel de la Guarda has apparently reached the advanced stage in speciation. It is statistically distinct from the Partida population in 9 of the 13 meristic characters, and in 8 from the mainland *P. xanti*. The color and color pattern is similar to that of *P. xanti* and quite unlike that of the Partida population.

The rate at which speciation has taken place among the populations inhabiting the northern islands appears to be out of balance. Three islands indicate that their populations have reached the species level while five islands, equally as far from the mainland, as large as some of the others, and with similar vegetation and climate, have differentiated theirs only to the subspecies level. The elements of time and distance may be involved for we do not know how many times in the past the islands may have been connected to the mainland and affected by reinvasion of the parental gene pool. We may surmise that some of the islands were connected to the mainland several times, while others were not, thus slowing the rate of speciation on some islands and increasing it on others. The possibility of any number of environmental changes may have taken place in the Pleistocene that altered gene selection through extrinsic stress upon any number of the islands' populations.

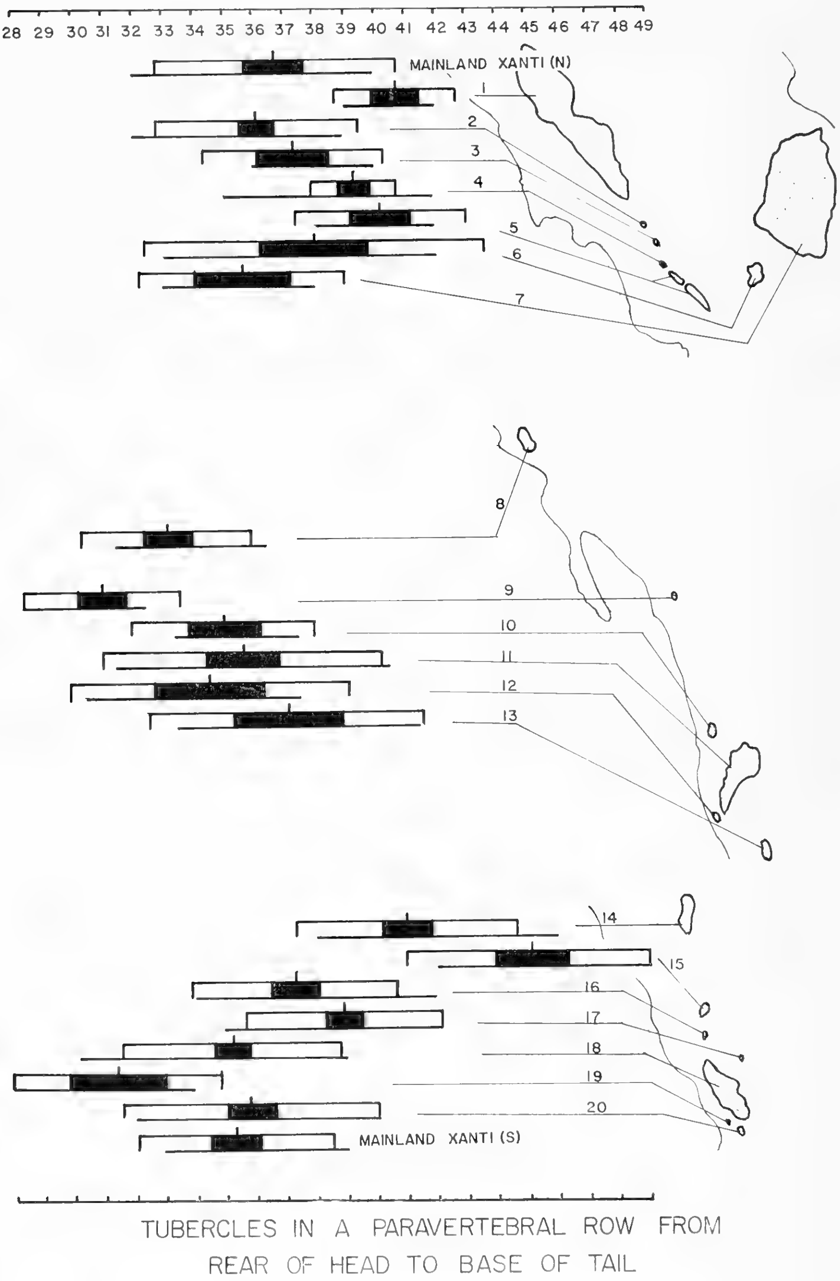


Figure 5. Variation in the number of tubercles in a paravertebral row from rear of head to base of tail (see figure 3 for explanation of analysis).

It is evident that changes of some kind did occur and the various populations were so altered in morphological features as to be unlike the parental stock.

The Central Islands. Isla Tortuga appears to be a recent island, lacking extensive vegetation and numbers of species of terrestrial vertebrates. The island is composed of basaltic lava, and steam fumaroles are still present. *Phyllodactylus* has not been found on this island.

Isla San Marcos is occupied by a population of *Phyllodactylus* that appears to be closely related to the Baja California mainland population of *P. xanti*. There appears to have been some recent gene exchange between the island and mainland populations, as indicated by their present morphology. The population differs from the mainland form in 3 of the 13 meristic characters analyzed, and further analysis of nonmeristic features indicates an early stage of speciation. The island population appears to have been connected to the mainland population in recent times. This may have been by rafting or land connection for the island is only 3 miles from the mainland of Baja California.

Isla Ildefonso lies 7 miles east of the Baja California mainland, and some 54 miles southeast of Isla San Marcos. The *Phyllodactylus* population occupying this island is closely allied to the San Marcos and Baja California mainland populations. The major meristic differences are found in the high number of tubercles in a paravertebral row from head to tail and between axilla and groin. Its apparent rate of speciation is slightly more advanced than that of the San Marcos population.

Two small islets in Bahía Concepcíon have populations of *Phyllodactylus* that indicate a close relationship to Baja California populations. However, there are only two specimens from each of the islets (Mosca and Coyote). Two specimens are not sufficient for an analysis of characters, and I have placed these specimens with *P. xanti xanti* until further specimens are available.

Southern Islands. There are twelve major islands lying relatively close to the southeastern shore of Baja California. Three of these, Cerralvo, Partida (S.), and Espíritu Santo, were discussed previously. Some of the remaining islands have offlying islets that are inhabited by *Phyllodactylus*, and of the 12 major islands 9 have populations of *Phyllodactylus*.

The Isla Coronados population is statistically distinct from *P. xanti nocticolus* in the number of postmentals, scales across the snout at the level of the third labials, and scales across the head in the mid-orbital region. It differs from *P. xanti xanti* in the latter two counts, and in addition, the number of tubercles in a paravertebral row from rear of head to base of tail, and from axilla to groin.

The population differs from the Isla Carmen population, some 7 miles to the south, in the number of scales across the snout at the level of the third labials, scales across the venter, and longitudinal rows of scales of the venter. This population appears to be intermediate in its evolutionary history, and lies somewhere between stages two and three. I do not think that its relationship to the

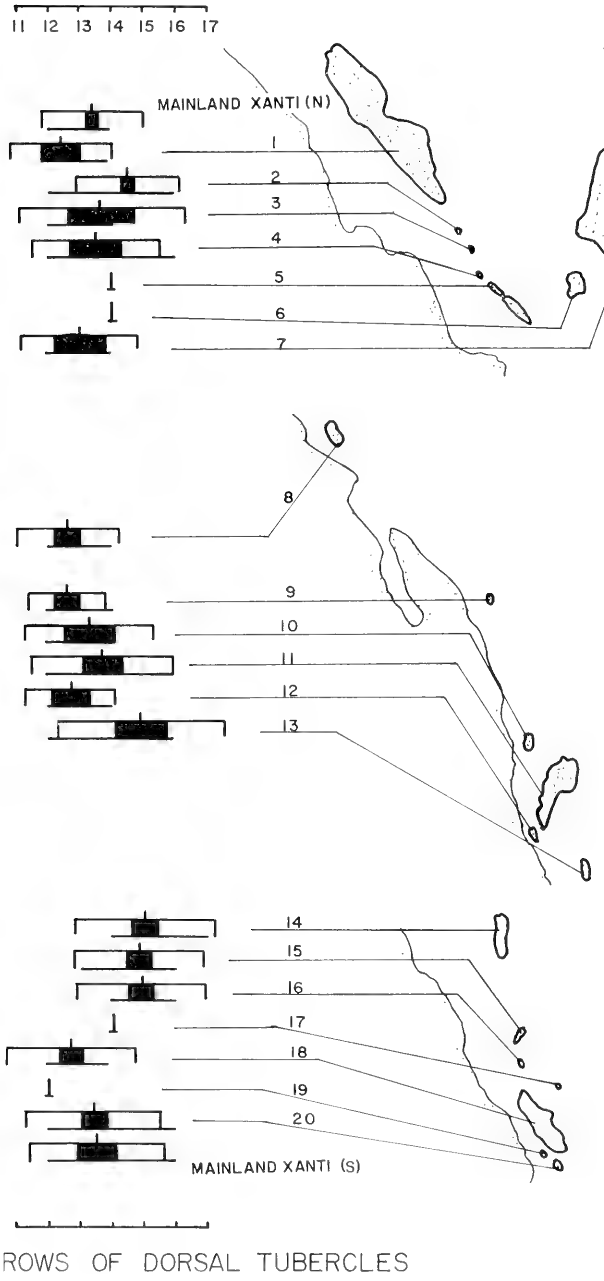


Figure 6. Variation in the number of longitudinal rows of enlarged dorsal tubercles (see figure 3 for explanation of analysis).

mainland population has proceeded much beyond the subspecies stage, yet it shows a certain amount of evolutionary divergence from other island populations.

The Isla Danzante population indicates little divergence from the mainland forms of *P. xanti*. It differs from *P. xanti xanti* in the number of tubercles in a paravertebral row from axilla to groin, and from *P. xanti nocticolus* in the number of scales across the venter. This island lies midway between Isla Carmen and the mainland, and the Isla Carmen population is statistically distinct from the Danzante population in the number of scales between the orbits and across the venter. If we compare the Carmen sample directly to the mainland sample, it deviates in such characters as the number of lamellae beneath the fourth toe, scales between the nostril and eye, between the orbits, scales bordering the postmentals, across the snout, across the venter, longitudinal rows of the venter, and number of tubercles in the paravertebral row from head to tail and between axilla and groin. This would seem to indicate that the Carmen population is quite distinct. However, the Danzante population is intermediate between the Carmen and mainland populations. It appears to me that the Danzante population is a hybrid one, and the mainland and Carmen populations were at one time joined across Danzante. I do not consider the Carmen population as having reached the subspecies level, even though the Carmen population appears distinct from the mainland forms.

The Monserrate population does not differ from the Carmen population in any character, even though it lies 11 miles to the southeast of Isla Carmen. I also find that the two populations are similar in color and color pattern. It is difficult to surmise that these two populations are identical, considering the distance separating the islands. However, until a sibling condition is proven to the satisfaction of all concerned, I find it necessary to retain the two populations as members of the same race.

Isla Catalina is the farthest from the mainland of the southern islands group. Its *Phyllodactylus* population differs from the mainland form in 5 of the 13 characters analyzed; from the Isla Monserrate population in 4 characters; and from the Isla Santa Cruz population in 8 characters. The Catalina population appears to be specifically distinct from the surrounding insular *Phyllodactylus* populations and from the mainland form.

A similar situation exists between the Isla Santa Cruz population and surrounding insular and mainland populations. The populations differs from the Catalina *Phyllodactylus* in 8 characters, and from *Phyllodactylus* inhabiting Isla San Diego in 6 characters.

The San Diego population differs from the Isla San Jose *Phyllodactylus* in 3 characters, and from the mainland form in 3 additional characters. Its relationship appears to be closer to the San Jose population, but differs from the latter form in color and color pattern. The population seems to have reached the subspecies level but has not evolved beyond this point.

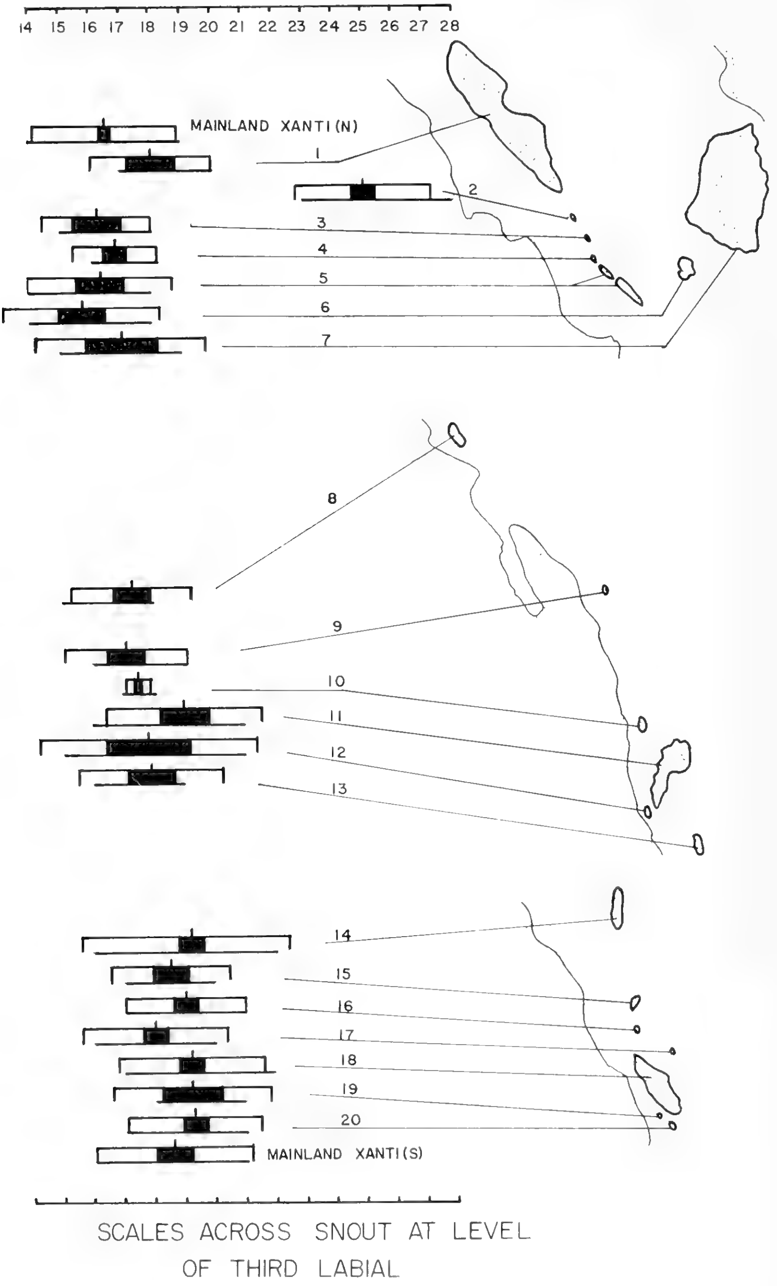


FIGURE 7. Variation in the number of scales across the snout at the level of the third labial (see figure 3 for explanation of analysis).

The *Phyllodactylus* populations inhabiting Islas San Jose and San Francisco appear to be identical in all scale characters, color, and color pattern. The two populations appear to be very close to the mainland form, with a slight deviation in 2 scale characters. Their relationship to the mainland form indicates a recent insular distribution, and I consider the insular populations as members of the mainland race.

Islet Animas, a small granite protusion situated 3 miles east of Isla San Jose, is remarkable in that it has a rather high population density of *Phyllodactylus*. The geckos of this islet deviate from the San Jose population in 8 of 13 scale characters. This amount of divergence from its apparent related stock of San Jose may be due to chance drift. The rate of evolution may have been increased by the relatively small size of the islet and a corresponding increase in gene flow between individual lizards. The islet is only a few hundred yards long and is several thousand times smaller than San Jose. It seems to be specifically distinct from the San Jose and mainland species.

Accounts of the Insular Forms

Six new species and 5 new subspecies are described from the islands of the Gulf of California. All but one of these belong to the *P. xanti* complex of Baja California and the southern California area of the United States. The species inhabiting Isla Partida (N.) is considered as a member of the *P. tuberculosus* group of western Mexico, excluding Baja California. Two Gulf islands, San Pedro Nolasco and Farallon, also have populations of *Phyllodactylus* referable to the *P. tuberculosus* group. Farallon Island harbors a population of *Phyllodactylus* known only from one specimen. It appears to be closely related to *P. tuberculosus* of the mainland, but a study of more specimens will be necessary to assign the population to a species. *Phyllodactylus unctus, P. nolascoensis,* and *P. tuberculosus* have been treated in detail in an earlier paper (Dixon, 1964a) and that information need not be repeated here.

The mainland forms of *P. xanti* have been reported on in the latter paper, but the relationship of *P. xanti* to the insular forms is one of the essential parts of the present study, and much of the comparative analysis is included herein (see figures 3–12).

The variation in scale characters within and between the various insular populations is given in the figures following this account. A written statement concerning variation within this genus and its species is given in Dixon (1964a).

Phyllodactylus xanti xanti Cope.

For an account of the literature, diagnosis, and variation of this subspecies from the mainland of Baja California, see Dixon (1964a). Specimens of this race from Islas San Jose, San Francisco, Coyote, and Cayo differ from the mainland population in having slightly fewer scales across the venter, and fewer lamellae beneath the fourth toe, and in having more interorbital scales. The

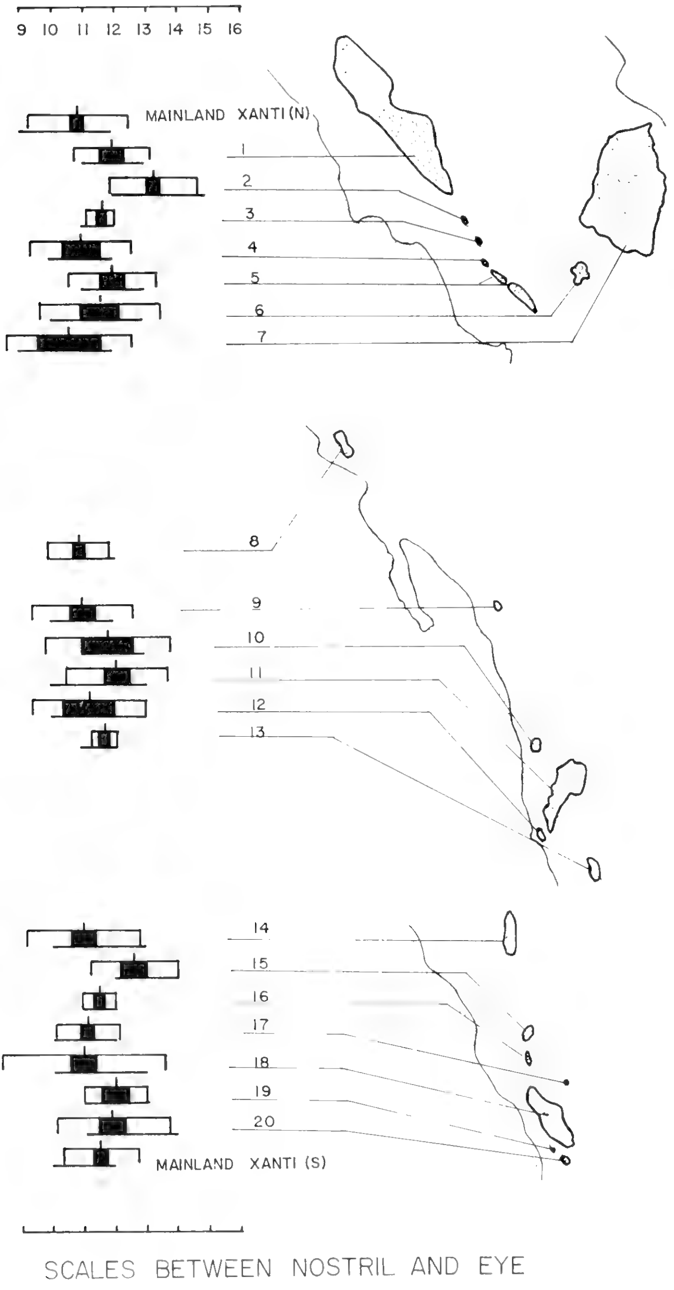


FIGURE 8. Variation in the number of scales between the nostril and eye (see figure 3 for explanation of analysis).

populations from Islets Coyote and Cayo deviate strongly in more features but are intermediate when compared with populations from San Jose and San Francisco.

The populations of *Phyllodactylus* inhabiting Islas Carmen, Danzante, and Monserrate are more closely allied to *P. xanti xanti* than to *P. xanti nocticolus,* the northern Baja California race. The presence of thigh tubercles definitely places these populations with *P. xanti xanti.* However, thigh tubercles are absent on southern island populations of *Phyllodactylus* on Las Animas, and northern populations on Angel, Salsipuedes, and San Lorenzo, but present on all remaining island populations.

Specimens from Isla Danzante are intermediate in all characters between mainland *P. xanti xanti* and the populations occupying Carmen and Monserrate. The Carmen and Monserrate samples appear to be distinct when compared directly to the mainland sample. However, when either population is compared with the Danzante sample there seems to be a cline in all characters.

Range. Islas Danzante, San Marcos, Carmen, Monserrate, San Jose, San Francisco, and islets Cayo and Coyote, Gulf of California.

Specimens examined. (92). Danzante: SDMNH 44608, 50860–62; CAS 52167–68. Carmen: AMNH 65956; CAS 51873, 98506–17; SDMNH 44609. Monserrate: CAS 52307–09; SDMNH 44610, 50804–07; LMK 6832–33; San Jose: CAS 84847–53, 98496–501, 52702–03; SDMNH 50800–02, 50864–67, 44603, 44614–19, 44625–27. San Francisco: CAS 52749–54, 84848, 98502–05; MCZ 31518; SDMNH 44628–29, 50781–90. Cayo: SDMNH 44630, 50796–99. Coyote: SDMNH 50891. San Marcos: CAS 98518–29, SDMNH 50854–55.

Phyllodactylus xanti angulus Dixon, new subspecies.

Holotype. Adult ♂, CAS no. 98477, collected by James R. Dixon and Stanley W. Taft; from a granite boulder, August 19, 1964 Islas Salsipuedes, Baja California.

Paratypes. Salsipuedes: CAS 51231–32, 98479–80; MCZ 82866; SDMNH 44677–78, 50868–69. San Lorenzo: CAS 51295; SDMNH 44238–39, 50856–59, 50833.

Diagnosis. An average snout–vent length of 43.1 mm., differing from *P. xanti xanti* in having a significantly lower number of snout scales, lamellae beneath fourth toe, higher number of tubercles in a paravertebral row; from *P. xanti nocticolus* in having a significantly lower number of transverse belly scales, and higher number of tubercles in a paravertebral row.

Description of holotype. Rostral almost three times as wide as high, its dorsal edge with a slight depression at the mid-point; 2 internasals, triangular, their median edges in narrow contact, bordered posteriorly by 5 granules and the postnasal of each side, nostril surrounded by the rostral, labial, internasal,

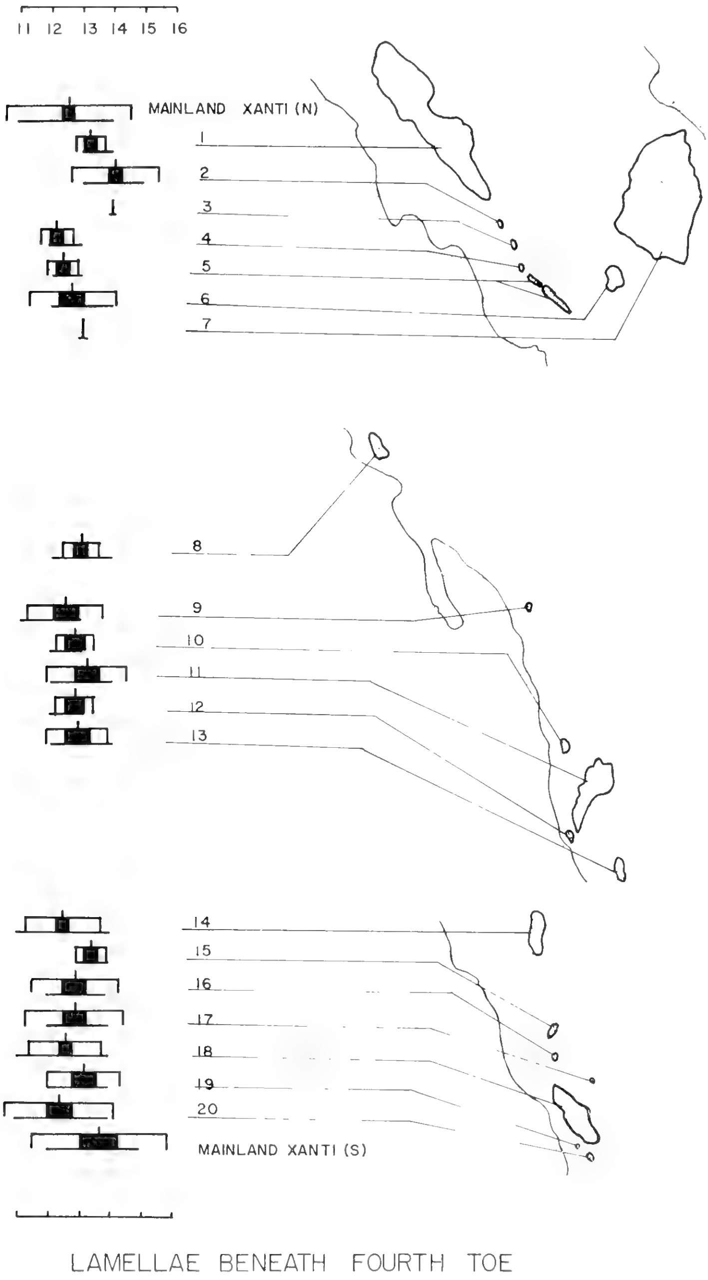


FIGURE 9. Variation in the number of lamellae beneath the fourth toe (see figure 3 for explanation of analysis).

and 2 postnasals. First supralabial in broad contact with ventral edge of nostril; a shallow depression between internasals, a moderate depression in frontal region; 11 scales between eye and nostril, scales in posterior loreal region about 5 to 6 times larger than scales in midorbital region; 17 scales across snout at level of third labials, 15 scales at anterior edge of orbits, 18 interorbital scales; eye large, its diameter contained in length of snout one and one-third times; eyelid with one row of granules and one larger outer row of scales; diameter of ear contained in eye diameter two and one-half times, ear opening not denticulate, scales on anterior and posterior edges rounded, subequal; rear of head granular with many larger intermixed tubercles; 6 supralabials and 6 infralabials to a point below center of eye; mental bell-shaped, as wide as long; bordered posteriorly by postmentals; postmentals wider than long, their median edges in narrow contact, postmentals followed by transverse row of 7 scales, followed by second row of 12 smaller scales; postmentals contact only the first labial of each side.

Dorsum with 14 longitudinal rows of enlarged, keeled tubercles that are somewhat flat; paravertebral row with 39 tubercles from rear of head to base of tail, 23 between axilla and groin; paravertebral rows separated from each other by 4 to 5 rows of granules; 8 rows of tubercles reach to rear of head, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 1 to 2 granules; postanal tubercles number 3 on each side, distinct; venter with 62 longitudinal and 33 transverse rows of scales.

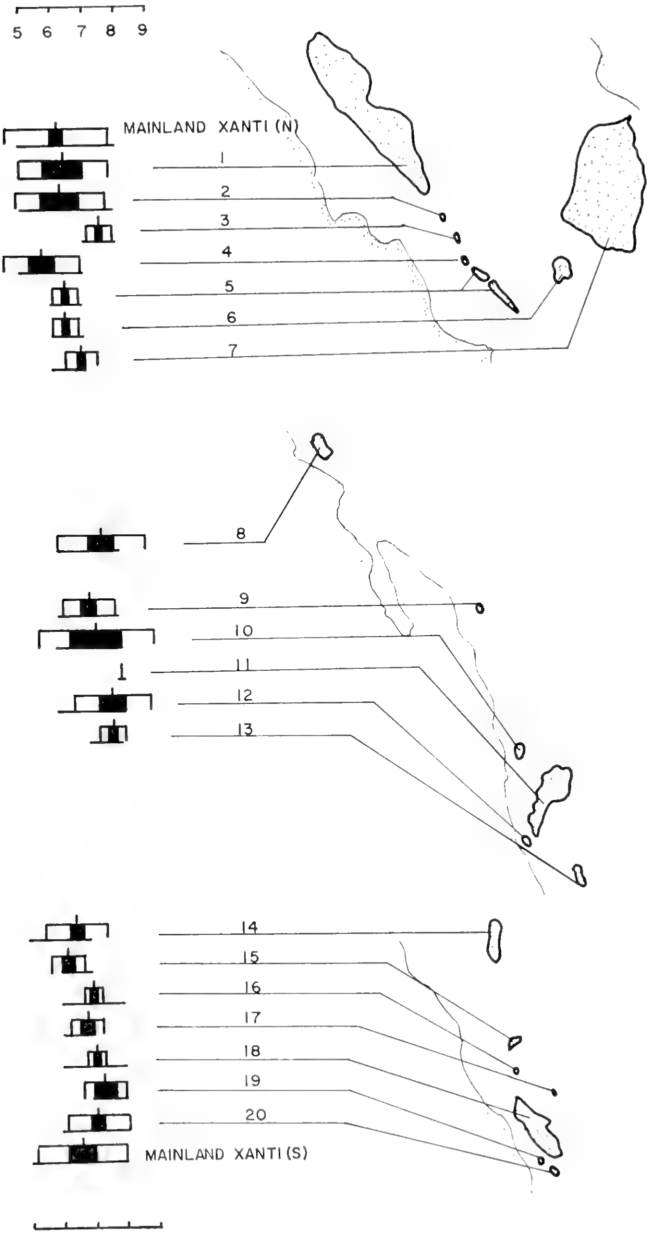
Dorsal surface of upper arm with flattened scales, forearm with larger tubercles interspersed among the smaller flattened scales; dorsal surface of thigh without tubercles dispersed among the smaller flattened scales, lower leg with a few tubercles interspersed among the granular scales; lamellae formula for hand 7-8-9-9-8, foot 7-9-11-12-10; claw short, visible when viewed from below; terminal pad large, slightly truncate at tips; tail tubercular rows reduced to zero at third proximal tail whorl.

Measurements (in mm.). Snout–vent length 46, axilla–groin length 21, length of leg 20, length of arm 15, length of tail 50, length of head 15, width of head 10.5, length of snout 5.0; diameter of eye 3.5, diameter of ear 1.4.

Color in life. Ground color gray, dorsum with 5 dark gray crossbands, broken medially; mid-dorsal line of dark gray from rear of head to pelvic region; snout reticulated with dark gray lines, top of head with minute grayish brown flecks; loreal stripe dark brown, short, from mid-snout to orbit; limbs ground color with a few scattered darker spots of brown; tail reticulated and spotted with grayish brown; venter cream white; white tipped tubercles not in evidence, but sometimes present in other specimens.

Range. Islas Salsipuedes, San Lorenzo (North and South), Gulf of California.

Specimens examined. (19), listed under type and paratypes.



SCALES BORDERING THE INTERNASALS

Figure 10. Variation in the number of scales bordering the internasals posteriorly (see figure 3 for explanation of analysis).

Phyllodactylus xanti estebanensis Dixon, new subspecies.

Holotype. Adult ♂, CAS no. 98481, collected by James R. Dixon and Donald W. Tinkle on Granite Boulders, August 14, 1964; on Isla San Esteban, Baja California.

Paratypes. San Esteban: CAS 50798, 84889–91, 98482–83; MCZ 82867; UCLA 15000–02; SDMNH 50870–71. Tiburon: CAS 98544–46; SDMNH 50852–53. Pelicano: BT 139 (Museum unknown).

Diagnosis: Average snout–vent length of 42.9 mm., differing from mainland races in having a much darker color pattern and a lower number of ventral scales and tubercles in a paravertebral row, and differing also from adjacent insular races in having a lower number of tubercles in a paravertebral row and scales across the belly.

Description of holotype. Rostral twice as wide as high, its dorsal edge with a slight depression and a short median vertical groove; 2 internasals, rounded, their median edges in broad contact, bordered posteriorly by 4 granules and postnasal of each side, nostril surrounded by rostral, labial, internasal, and 2 postnasals. First supralabial in narrow contact with ventral edge of nostril; shallow depression between eye and nostril, scales in posterior loreal region about 6 to 7 times larger than scales in midorbital region; 15 scales across snout at level of third labials, 15 scales at anterior edge of orbits, 19 interorbital scales; eye large, its diameter contained in length of snout one and one-half times; eyelid with 2 rows of granules and one larger outer row of scales; diameter of ear contained in eye diameter two times, ear opening not denticulate, scales on anterior and posterior edges rounded, subequal; rear of head granular with many larger intermixed tubercles; 7 supralabials and 6 infralabials to a point below center of eye; mental bell-shaped, wider than long; bordered posteriorly by 2 postmentals; postmental longer than wide, their median edges in broad contact, postmentals followed by transverse row of 8 scales, followed by second row of 12 smaller scales; postmentals contact first and second labials on each side.

Dorsum with 14 longitudinal rows of enlarged keeled tubercles that are somewhat flat; paravertebral row with 38 tubercles from rear of head to base of tail, 21 between axilla and groin; paravertebral rows separated from each other by 5 to 6 rows of granules; 8 rows of tubercles reach to rear of head, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 1 to 2 granules; postanal tubercles number 2 on each side, distinct; venter with 61 longitudinal and 31 transverse rows of scales.

Dorsal surface of upper arm with flattened scales, forearm with larger tubercles interspersed among the smaller flattened scales; dorsal surface of thigh with 4 to 5 tubercles dispersed among the smaller flattened scales, lower leg with several tubercles interspersed among the granular scales; lamellae formula for hand 9-10-10-9-7, foot 9-11-12-13-11; claw moderate, visible when viewed from below; terminal pad large, slightly longer than wide, truncate at

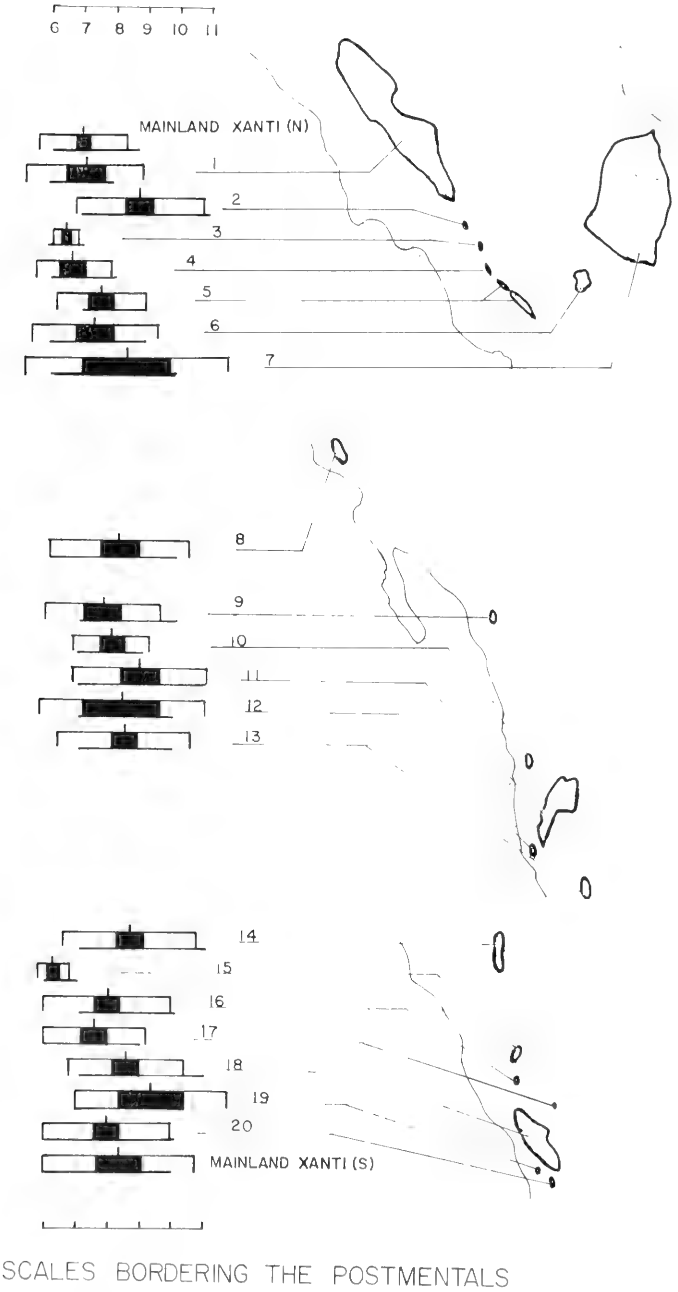


FIGURE 11. Variation in the number of scales bordering the postmentals posteriorly (see figure 3 for explanation of analysis).

tips; tail tubercular rows reduced to zero on the 3rd proximal whorl of the tail.

Measurements (in mm.). Snout–vent length 49, axilla–groin length 22, length of leg 19, length of arm 15, length of tail (one half missing), length of head 14.5, width of head 9.5, length of snout 6.0; diameter of eye 4.0 diameter of ear 2.0.

Color in life. Ground color tan with some darker flecks of chocolate brown intermixed; six chocolate brown dorsal bands, extending only across dorsal portion of back, broken into spots along sides; head reticulated with chocolate brown lines, darker color predominating over ground color; chocolate brown stripe from nostril, through eye to ear; dorsal surfaces of limbs similar, but not as distinctly marked; ventral surfaces of tail, belly, and limbs cream white, ventral surfaces of feet brownish.

Range. Islas San Esteban and Tiburon, Gulf of California.

Species examined. (15), listed under type and paratypes.

Phyllodactylus xanti circus Dixon, new subspecies.

Holotype. Adult ♀, SDMNH no. 50814, collected by Charles E. Shaw, April 2, 1962, from Isla Ildefonso, Baja California.

Paratypes. Ildefonso: CAS 51754–55, 84878; SDMNH 50809–12, 50815–17.

Diagnosis. Average snout–vent length of 46.4 mm., differing from mainland races in having fewer tubercles in a paravertebral row; fewer interorbital scales, and rows of enlarged dorsal tubercles; from adjacent insular races in having fewer tubercles in a paravertebral row from head to tail and axilla to groin.

Description of holotype. Rostral twice as wide as high, its dorsal edge forming a low "w" from a frontal view; 2 internasals, rounded posteriorly, their median edges in broad contact, bordered posteriorly by 4 granules and postnasal of each side, nostril surrounded by rostral, labial, internasal, and 2 postnasals. First supralabial barely in contact with ventral edge of nostril; shallow depression between internasals, slight depression in frontal region; 10 scales between eye and nostril, scales in posterior loreal region about 3 to 4 times larger than scales in midorbital region; 16 scales across snout at level of third labials, 14 scales at anterior edge of orbits, 19 interorbital scales; eye large, its diameter contained in length of snout almost 2 times; eyelid with 1 row of granules and 1 larger outer row of scales; diameter of ear contained in eye diameter slightly less than 2 times, ear opening not denticulate, scales on anterior and posterior edges rounded, subequal; rear of head granular with many larger intermixed tubercles; 7 supralabials and 6 intralabials to a point below center of eye; mental bell-shaped, longer than wide; bordered posteriorly by 2 postmentals; postmentals wider than long, their median edges in narrow contact, postmentals followed by transverse row of 10 scales, followed by second row of 13 smaller scales; postmentals contact only the first labial of each side.

Dorsum with 12 longitudinal rows of enlarged, keeled tubercles that are

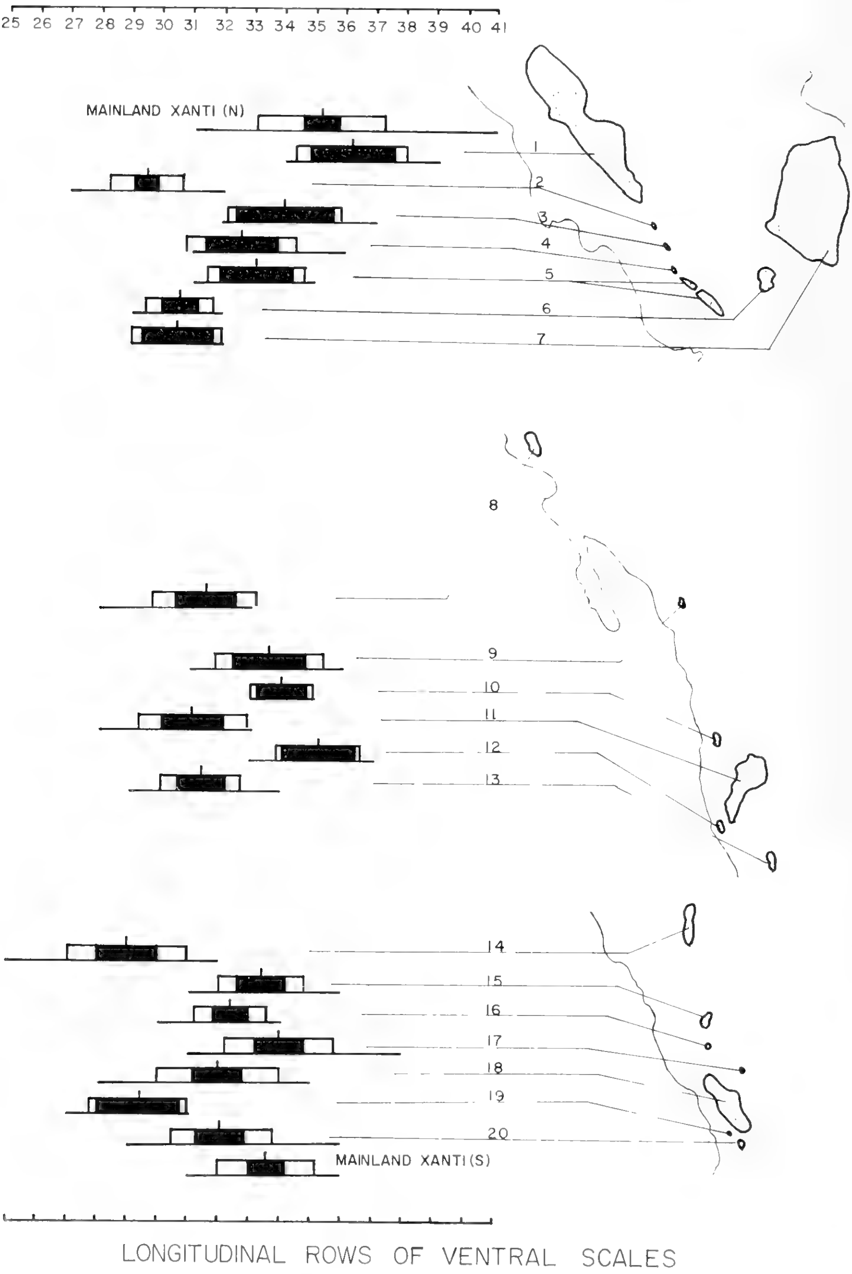


FIGURE 12. Variation in the number of longitudinal rows of ventral scales (see figure 3 for explanation of analysis).

somewhat flat; paravertebral row with 35 tubercles from rear of head to base of tail, 19 between axilla and groin; paravertebral rows separated from each other by 5 rows of granules; 10 rows of tubercles reach to rear of head, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 1 to 2 granules; postanal tubercles number 3 on each side, distinct; venter with 58 longitudinal and 35 transverse rows of scales.

Dorsal surface of upper arm with flattened scales, forearm with larger tubercles interspersed among the smaller flattened scales; dorsal surface of thigh with three to four tubercles dispersed among the smaller flattened scales, lower leg with a few tubercles interspersed among the granular scales; lamellae formula for hand 7-9-10-11-9, foot 6-8-10-13-10; claw short, visible when viewed from below; terminal pad large, slightly truncate at tip; tail tubercular rows reduced to zero on the 3rd proximal whorl of the tail.

Measurements (in mm.). Snout–vent length 47, axilla–groin length 22, length of leg 19, length of arm 17, length of tail (part missing), length of head 15, width of head 10, length of snout 6; diameter of eye 3.5, diameter of ear 2.0.

Color in alcohol. Ground color light brown; dorsum with five irregular crossbands of dark brown; dorsolateral areas of body reticulated with dark brown; limbs heavily spotted with dark brown; head reticulated with brownish lines; brownish loreal stripe from nostril to eye; tail with narrow brown crossbands, brown bands one-half the width of light interspaces. Venter cream yellow to dusky.

Range. Isla San Ildefonso, Gulf of California.

Specimens examined. (11), listed under type and paratypes.

Phyllodactylus xanti coronatus Dixon, new subspecies.

Holotype. Adult ♀, CAS no. 51803, collected by Joseph R. Slevin, May 18, 1921, from Isla Coronados, Baja California.

Paratypes. Coronados: CAS 51802, 51804–07.

Diagnosis. Average snout–vent length of 47.4 mm., differing from adjacent insular races in having a higher number of interorbitals, belly scales, paravertebral tubercles, and a lower number of snout scales; from mainland races in having a higher number of interorbitals, scales between eye and nostril and intermediate in number of snout scales.

Description of holotype. Rostral twice as wide as high, its dorsal edge with 2 internasals, rounded, their median edges in broad contact, bordered posteriorly by 4 granules and postnasal of each side, nostril surrounded by rostral, labial, internasal, and 2 postnasals. First supralabial in contact with ventral edge of nostril; shallow depression between internasals, moderate depression in frontal region; 11 scales between eye and nostril; scales in posterior loreal region about 5 to 6 times larger than scales in midorbital region; 17 scales across snout at level of third labials, 23 interorbital scales; eye large, its diameter contained in length of snout one and one-third times; eyelid with 2 rows of granules and 1 larger outer row of scales; diameter of ear contained in eye diameter one and one-third times, ear opening not denticulate, scales on anterior and posterior edges rounded, subequal; rear of head granular with many larger intermixed tubercles; 6 supralabials and 6 infralabials to a point below center of eye; mental bell-shaped, as wide as long; bordered posteriorly by 2 postmentals; postmental longer than wide, their median edges in broad contact, followed by transverse row of 8 scales, followed by second row of 14 smaller scales; postmentals contact only first labial of each side.

Dorsum with 14 longitudinal rows of enlarged, keeled tubercles that are somewhat flat, paravertebral row with 36 tubercles from rear of head to base of tail, 19 between axilla and groin; paravertebral rows separated from each other by 5 rows of granules; 10 rows of tubercles reach to rear of head, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 1 to 2 granules; postanal tubercles number 1 on each side, indistinct, venter with 63 longitudinal and 33 transverse rows of scales.

Dorsal surface of upper arm with flattened scales, forearm with larger tubercles interspersed among the smaller flattened scales; dorsal surface of thigh with two to four tubercles dispersed among the smaller flattened scales, lower leg with several tubercles interspersed among the granular scales; lamellae formula for hand 6-8-10-11-9, foot 6-9-11-13-10; claw short, visible when viewed from below; terminal pad large, slightly longer than wide. Tail tubercular row reduction to zero occurs on the first proximal whorl of tail.

Measurements (in mm.). Snout–vent length 52, axilla–groin length 23, length of leg 21, length of arm 16, length of tail (regenerated), length of head 15.5, width of head 10.0, length of snout 5.5; diameter of eye 3.6, diameter of ear 2.2.

Color in alcohol. Ground color grayish brown, dorsal pattern of six alternating pairs of brown spots, almost meeting across dorsum; head with brownish irregular lines, brown loreal stripe from nostril to eye, moderately distinct; limbs faintly marked with brown; venter brownish; tail light brown, regenerated.

Range. Isla Coronados, Gulf of California.

Specimens examined. (6), listed under type and paratypes.

Phyllodactylus xanti acorius Dixon, new subspecies.

Holotype. Adult ♂, CAS no. 98451, collected by James R. Dixon from a granite slab, August 9, 1964, from Isla San Diego, Baja California.

Paratypes. San Diego: CAS 52478–80, 98452–58, 98460–62; MCZ 82865; SDMNH 50827–29.

Diagnosis. Average snout–vent length of 41.2 mm., differing from mainland races in having a higher number of interorbitals, paravertebral tubercles, and rows of dorsal tubercles, a fewer number of ventral scales; from adjacent insular races in having a higher number of interorbitals, paravertebral tubercles, and vertebral tubercles.

Description of holotype. Rostral two and one-half times as wide as high, its dorsal edge with a short, vertical, median groove; 2 internasals, rounded posteriorly, their median edges in broad contact, bordered posteriorly by 5 granules and postnasal of each side, nostril surrounded by rostral, labial, internasal, and 2 postnasals. First supralabial in narrow contact with ventral edge of nostril; shallow depression between internasals, shallow depression in frontal region; 11 scales between eye and nostril, scales in posterior loreal region about 4 to 5 times larger than scales in midorbital region; 17 scales across snout at level of third labials, 15 scales at anterior edge of orbits, 19 interorbital scales; eye large, its diameter contained in length of snout one and one-third times; eyelid with 2 rows of granules and 1 larger outer row of scales; diameter of ear contained in eye diameter two and one-fourth times, ear opening not denticulate, scales on anterior and posterior edges rounded, subequal; rear of head granular with many larger intermixed tubercles; 7 supralabials and 6 infralabials to a point below center of eye; mental bell-shaped, and as wide as long; their median edges in narrow contact, postmentals followed by transverse row of 8 scales, followed by second row of 12 smaller scales; postmentals contact only the first labial on each side.

Dorsum with 16 longitudinal rows of enlarged, keeled tubercles that are somewhat flat, paravertebral row with 36 tubercles from rear of head to base of tail, 19 between axilla and groin; paravertebral rows separated from each other by 5 rows of granules; 8 rows of tubercles reach to rear of head, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 1 to 2 granules; postanal tubercles number 3 on each side, distinct; venter with 51 longitudinal and 32 transverse rows of scales.

Dorsal surface of upper arm with flattened scales, forearm with larger tubercles interspersed among the smaller flattened scales; dorsal surface of thigh with five to six tubercles dispersed among the smaller flattened scales, lower leg with several tubercles interspersed among the granular scales; lamellae formula for hand 6-8-10-11-10; foot 6-9-11-12-10; claw moderate, visible when viewed from below; terminal pad large, slightly truncate at tips; tail tubercular reduction to zero at the fifth proximal tail whorl.

Measurements (in mm.). Snout–vent length 46, axilla–groin length 21, length of leg 17, length of arm 14, length of tail (part missing), length of head 14, width of head 9, length of snout 5; diameter of eye 3.5, diameter of ear 1.5.

Color in alcohol. Ground color grayish tan; dorsum with an alternating series of small brown spots positioned along each paravertebral row of tubercles; limbs with faint or diffuse brown spots, head minutely spotted with brown; loreal stripe dark brown, short, from mid-snout to eye; tail faintly banded, with grayish brown; venter cream to white.

Range. Isla San Diego, Gulf of California.

Specimens examined. (18), listed under type and paratypes.

Phyllodactylus angelensis Dixon, new species.

Holotype. Adult ♂, SDMNH no. 19996, collected by Allan J. Sloan, March 22, 1963, from the north end of Isla Angel de la Guarda, Baja California.

Paratypes. Angel de la Guarda: CAS 50905–07, 98543; Isla Pond: SDMNH 50851.

Diagnosis. Average snout–vent length of 45.5 mm., differing from adjacent insular and mainland species in having a low number of rows of enlarged dorsal tubercles, a high number of longitudinal belly scales and tubercles in a paravertebral row from head to tail, and an intermediate number of snout scales, lamellae beneath the fourth toe, and scales between eye and nostril.

Description of holotype. Rostral almost twice as wide as high, its dorsal edge with slight depression and short, vertical, median groove; internasals rectangular, their median edges in broad contact, bordered posteriorly by 4 granules and postnasal of each side, nostril surrounded by rostral, labial, internasal, and 2 postnasals. First supralabial in narrow contact with ventral edge of nostril; shallow depression between internasals, moderate depression in frontal region; 12 scales between eye and nostril, scales in posterior loreal region about 4 to 5 times larger than scales in midorbital region; 18 scales across snout at level of third labials, 15 scales at anterior edge of orbits, 23 interorbital scales; eye large, its diameter contained in length of snout one and one-half times; eyelid with 2 rows of granules and one larger outer row of scales; diameter of ear contained in eye diameter 2 times, ear opening not denticulate, scales on anterior and posterior edges rounded, subequal; rear of head granular with many larger intermixed tubercles; 7 supralabials and 6 infralabials to a point below center of eye; mental bell-shaped, longer than wide; bordered posteriorly by 2 postmentals; postmentals wider than long, their median edges in narrow contact, postmentals followed by transverse row of 8 scales, followed by second row of 14 smaller scales; postmentals contact only the first labial on each side.

Dorsum with 12 longitudinal rows of enlarged, keeled tubercles that are somewhat flat; paravertebral row with 42 tubercles from rear of head to base of tail, 26 between axilla and groin; paravertebral rows separated from each other by 6 rows of granules; 10 rows of tubercles reach to rear of head, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 1 to 2 granules; postanal tubercles number 3 on each side, distinct; venter with 62 longitudinal and 36 transverse rows of scales.

Dorsal surface of upper arm with flattened scales, forearm with larger tubercles interspersed among the smaller flattened scales; dorsal surface of thigh without tubercles dispersed among the smaller flattened scales, lower leg with a few tubercles interspersed among the granular scales; lamellae formula for hand 6-9-10-11-10, foot 7-9-13-14-12; claw short, visible when viewed from below; terminal pad large, slightly longer than wide. Tail tubercular rows reduced to zero on the third proximal whorl of tail.

MEASUREMENTS (in mm.). Snout–vent length 52, axilla–groin length 24, length of leg 23, length of arm 18, length of tail (half of tail missing), length of head 16, width of head 11, length of snout 6; diameter of eye 4, diameter of ear 2.

COLOR IN ALCOHOL. Ground color tan, dorsum with six brown crossbands, broken along the midline, slightly irregular in shape; head reticulated with dark brown; loreal stripe indistinct; limbs with diffuse brownish spots; distal one-half of tail missing, proximal half banded with brown and interspaces of ground color.

RANGE. Isla Angel de la Guarda, Gulf of California.

SPECIMENS EXAMINED. (7), listed under type and paratypes.

Phyllodactylus partitus Dixon, new species.

HOLOTYPE. Adult ♂, CAS no. 98429, collected by James R. Dixon and Donald W. Tinkle on a rubble beach; August 18, 1964, on Isla Partida (N.), Baja California.

PARATYPES. Partida (N.): CAS 98430–50; LMK 6834–36, 39258, 39649, 40508; MCZ 13411; AHF–USC 50; SDMNH 50820–22.

DIAGNOSIS. A large gecko, average snout–vent length 53.3 mm., differing from all other insular forms in having a combination of a high number of snout scales and a low number of tubercles in a paravertebral row from rear of head to base of tail.

DESCRIPTION OF HOLOTYPE. Rostral twice as wide as high, its dorsal edge with a slight depression and a short median groove; internasals, rectangular, their median edges in broad contact, bordered posteriorly by 3 granules and postnasal of each side, nostril surrounded by rostral, labial, internasal, and 2 postnasals. First supralabial in broad contact with ventral edge of nostril; shallow depression between internasals, deep depression in frontal region; 13 scales between eye and nostril, scales in posterior loreal region about 2 to 3 times larger than scales in midorbital region; 25 scales across snout at level of third labials, 15 scales at anterior edge of orbits, 18 interorbital scales; eye large, its diameter contained in length of snout almost 2 times; eyelid with 3 rows of granules and one larger outer row of scales, last few without spines; diameter of ear contained in eye diameter slightly less than 2 times, ear opening not denticulate, scales on anterior and posterior edges rounded, subequal; rear of head granular with many larger intermixed tubercles; 6 supralabials and 5 infralabials to a point below center of eye; mental bell-shaped, longer than wide; bordered posteriorly by 2 postmentals; postmentals wider than long, their median edges in narrow contact, postmentals followed by transverse row of 9 scales, followed by second row of 12 smaller scales; postmentals contact first labial on right, and first and second on left side.

Dorsum with 14 longitudinal rows of enlarged, keeled tubercles that are somewhat flat; paravertebral row with 38 tubercles from rear of head to base of tail, 23 between axilla and groin; paravertebral rows separated from each other by 6 to 8 rows of granules; 6 rows of tubercles reach to rear of head, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 1 to 2 granules; postanal tubercles number 4 on each side, distinct; venter with 61 longitudinal and 30 transverse rows of scales.

Dorsal surface of upper arm with flattened scales, forearm with larger tubercles interspersed among the smaller flattened scales; dorsal surface of thigh with 5 to 6 tubercles dispersed among the smaller flattened scales, lower leg with many tubercles interspersed among the granular scales; lamellae formula for hand 8-10-11-12-8, foot 8-10-11-14-10; claw short, visible when viewed from below; terminal pad large, slightly longer than wide. Tail with a 6-4-2 reduction in tubercular rows; reduced to two for one-third length of the tail (in topotypes).

Measurements (in mm.). Snout–vent length 59, axilla–groin length 28, length of leg 23, length of arm 18, length of tail (missing), length of head 17.5, width of head 12, length of snout 7; diameter of eye 4, diameter of ear 2.5.

Color in life. Ground color brown, dorsum with eight chocolate brown crossbands that are interreupted along the median line; interspaces brown, and very narrow, mid-dorsal line obscure but lighter in color than interspaces; limbs heavily pigmented with chocolate brown, banding obscure; dorsal surfaces of hands and feet brownish; head dark brown, any other marks about head obscured by the dark ground color; tail more conspicuously marked with light and dark bands; venter cream yellow.

Range. Isla Partida (North), Gulf of California.

Specimens examined. (34), listed under type and paratypes.

Phyllodactylus tinklei Dixon, new species.

Holotype. Adult ♂, CAS no. 98463, collected by Donald W. Tinkle, from beneath a lava rock; August 19, 1964, on Isla Raza, Baja California.

Paratypes. Raza: CAS 51114, 98464–66; MCZ 82864.

Diagnosis. A medium-sized gecko, average snout–vent length of 47.5 mm., differing from all other insular forms in having each tubercle of each row white tipped, giving an appearance of many white lines on the body; and an incomplete white bar across the rear of the head; this species also has a high number of scales bordering the internasals and lamellae beneath the fourth toe.

Description of holotype. Rostral about two and one-half times as wide as high, its dorsal edge with slight depression and a short median groove; 2 internasals, rounded, their median edges in narrow contact, bordered posteriorly by 6 granules and postnasal of each side, nostril surrounded by rostral, labial, internasal, and 2 postnasals. First supralabial in very narrow contact with ventral edge of nostril; shallow depression between internasals, slight depression in frontal region; 12 scales between eye and nostril, scales in posterior loreal region about 5 to 6 times larger than scales in midorbital region; 16 scales across snout at level of third labials, 16 scales at anterior edge of orbits, 22 interorbital scales; eye large, its diameter contained in length of snout one and one-half times; eyelid with 2 rows of granules and one larger outer row of scales, last 5 to 6 without soft spines; diameter of ear contained in eye diameter about one and one-half times, ear opening not denticulate, scales on anterior and posterior edges rounded, subequal; rear of head granular with many larger intermixed tubercles; 8 supralabials and 7 infralabials to a point below center of eye; mental bell-shaped, as wide as long; bordered posteriorly by 2 postmentals; postmentals longer than wide, their median edges in broad contact, postmentals followed by transverse row of 7 scales, followed by second row of 13 smaller scales; postmentals contact first and second labials on each side.

Dorsum with 14 longitudinal rows of enlarged, keeled tubercles that are somewhat flat, paravertebral row with 38 tubercles from rear of head to base of tail, 22 between axilla and groin; paravertebral rows separated from each other by 5 to 7 rows of granules; 10 rows of tubercles reach to rear of head, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 1 to 2 granules; postanal tubercles number 4 on each side, distinct; venter with 63 longitudinal and 32 transverse rows of scales.

Dorsal surface of upper arm with flattened scales, forearm with larger tubercles interspersed among the smaller flattened scales; dorsal surface of thigh without tubercles dispersed among the smaller flattened scales, lower leg with several tubercles interpersed among the granular scales; lamellae formula for hand 7-9-10-11-9, foot 6-9-13-14-11; claw short, visible when viewed from below; terminal pad large, slightly longer than wide. Tail tubercular rows reduced from 4 to 0 in the proximal 3 whorls of tail.

Measurements (in mm.). Snout–vent length 52, axilla–groin length 24, length of leg 21, length of arm 17, length of tail 57, length of head 15.2, width of head 10, length of snout 5.5; diameter of eye 3.5, diameter of ear 2.2.

Color in life. Ground color brownish tan; dorsum with five obscure brownish bands; some interrupted medially; each tubercle of enlarged series of dorsum tipped with white; head brownish, white line from rear of eye curving upward and posteriorly towards parietals, almost forming a complete loop across the rear of head; loreal stripe obscure; limbs brownish with banding obscure; tail is distinctly banded with gray and darker brownish black bands; venter cream or white, lateral areas with a slight yellow cast.

Range. Isla Raza, Gulf of California.

Specimens examined. (6), listed under type and paratypes.

Phyllodactylus bugastrolepis Dixon, new species.

Holotype. Adult ♀, CAS no. 98485, collected by James R. Dixon under the bark of a Palo Verde, August 11, 1964, on Isla Catalina, Baja California.

Paratypes. Catalina: CAS 98486–90, 98492–95, 52340; MCZ 82862; SDMNH 44604–07, 44611–13, 50792–93.

Diagnosis. A small gecko, average snout–vent length of 45.1 mm., with exceptionally large belly scales that are few in number from gular region to anus; and in rows across the belly; a general pallid appearance in color pattern and color.

Description of holotype. Rostral slightly more than twice as wide as high, its dorsal edge with slight depression; and a short median groove; 2 internasals, rectangular, their median edges in broad contact, bordered posteriorly by 4 granules and postnasal of each side, nostril surrounded by rostral, labial, internasal, and 2 postnasals. First supralabial in narrow contact with ventral edge of nostril; shallow depression between internasals, moderate depression in frontal region; 10 scales between eye and nostril, scales in posterior loreal region about 4 to 5 times larger than scales in midorbital region; 20 scales across snout at level of third labials, 16 scales at anterior edge of orbits, 23 interorbital scales; eye large, its diameter contained in length of snout almost 2 times; eyelid with 2 rows of granules and 1 larger outer row of scales, without soft spines; diameter of ear contained in eye diameter two and one-fourth times, ear opening not denticulate, scales on anterior and posterior edges rounded, subequal; rear of head granular with many larger intermixed tubercles; 6 supralabials and 5 infralabials to a point below center of eye; mental bell-shaped, wider than long; bordered posteriorly by 2 postmentals; postmentals longer than wide, their median edges in narrow contact, followed by transverse row of 8 scales, followed by second row of 12 smaller scales; postmentals contact only the first labial on each side.

Dorsum with 15 longitudinal rows of enlarged, keeled tubercles that are somewhat flat; paravertebral row with 39 tubercles from rear of head to base of tail, 23 between axilla and groin; paravertebral rows separated from each other by 5 rows of granules; 10 rows of tubercles reach to rear of head, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 1 to 2 granules; postanal tubercles number 2 on each side, indistinct; venter with 48 longitudinal and 29 transverse rows of scales, ventral scales about 16 times larger than mid-dorsal granules.

Dorsal surface of upper arm with flattened scales, forearm with larger tubercles interspersed among the smaller flattened scales; dorsal surface of thigh with 2 to 3 tubercles dispersed among the smaller flattened scales, lower leg with many tubercles interspersed among the granular scales; lamellae formula for hand 7-8-10-10-9, foot 7-9-12-14-10; claw short, visible when viewed from below; terminal pad large, slightly longer than wide. Tail with a 4-2-0 reduction in tubercles on the proximal 3 whorls.

Measurements (in mm.). Snout–vent length 49, axilla–groin length 22, length of leg 19, length of arm 14, length of tail 39, length of head 15, width of head 10.5, length of snout 6; diameter of eye 3.5, diameter of ear 1.5.

Color in alcohol. Ground color brownish gray; dorsum with scattered small, dark brown spots; limbs faintly spotted with brown; head faintly spotted with minute brown flecks; brown loreal stripe from nostril to ear; tail with faint banding above, slate below; venter flesh to cream.

Range. Isla Santa Catalina, Gulf of California.

Specimens examined. (26), listed under type and paratypes.

Phyllodactylus santacruzensis Dixon, new species.

Holotype. Adult ♀, CAS no. 98468, collected by James R. Dixon, from beneath an exfoliating granite slab, August 9, 1964, from Isla Santa Cruz, Baja California.

Paratypes. Santa Cruz: CAS 52390, 98469–73, 98475–76; MCZ 82863; SDMNH 50872–73.

Diagnosis. Average snout–vent length of 47.5 mm., differing from all other species of the *xanti* complex in having a significantly higher number of paravertebral tubercles, and lower number of scales bordering the postmentals.

Description of holotype. Rostral almost twice as wide as high, its dorsal edge with a slight depression, and a short median groove; internasals, somewhat rectangular, their median edges in broad contact, bordered posteriorly by 4 granules and postnasal of each side, nostril surrounded by rostral, labial, internasal, and 2 postnasals. First supralabial in broad contact with ventral edge of nostril; shallow depression between internasals, slight depression in frontal region; 12 scales between eye and nostril, scales in posterior loreal region about 5 to 6 times larger than scales in midorbital region; 19 scales across snout at level of third labials, 16 scales at anterior edge of orbits, 21 interorbital scales; eye large, its diameter contained in length of snout one and three-fourths times; eyelid with 2 rows of granules and one larger outer row of scales; diameter of ear contained in eye diameter 2 times, ear opening not denticulate, scales on anterior and posterior edges rounded, subequal; rear of head granular with many larger intermixed tubercles; 8 supralabials and 5 infralabials to a point below center of eye; mental bell-shaped, longer than wide; bordered posteriorly by 2 postmentals; postmentals longer than wide, their median edges in broad contact, postmentals followed by transverse row of 6 scales, followed by second row of 11 smaller scales; postmentals contact first labial on right, first and second labials on left side.

Dorsum with 15 longitudinal rows of enlarged, keeled tubercles that are somewhat flat; paravertebral row with 44 tubercles from rear of head to base of tail, 25 between axilla and groin; paravertebral rows separated from each other by 5 to 6 rows of granules; 8 rows of tubercles reach to rear of head, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 1 to 2 granules; postanal tubercles number 3 on each side, distinct; venter with 57 longitudinal and 34 transverse rows of scales.

Dorsal surface of upper arm with flattened scales, forearm with larger tubercles interspersed among the smaller flattened scales; dorsal surface of thigh with 3 to 4 tubercles dispersed among the smaller flattened scales, lower leg with several tubercles interspersed among the granular scales; lamella formula for hand 8-9-9-11-9, foot 7-9-13-14-11; claw moderate, visible when viewed from below; terminal pad large, slightly longer than wide. Tail tubercular rows reduced to zero by the third proximal whorl of tail.

Measurements (in mm.). Snout–vent length 51, axilla–groin length 24, length of leg 21, length of arm 17, length of tail 46, length of head 16, width of head 11, length of snout 7; diameter of eye 4, diameter of ear 2.

Color in alcohol. Ground color light gray; dorsum with four brownish black linear stripes broken into a series of three to six linear spots; arm with longitudinal blackish reticulations; leg faintly spotted with brown; tail very spotty with dark brown, head with brownish reticulations from nostril to midorbital region; rear of head spotted with brown; dark loreal stripe from nostril to ear; venter white or cream.

Range. Isla Santa Cruz, Gulf of California.

Specimens examined. (12), listed under type and paratypes.

Phyllodactylus apricus Dixon, new species.

Holotype. Adult ♂, SDMNH no. 44623, collected by Chris Parrish and G. E. Lindsay, June 27, 1964, from Isla Las Animas, Baja California.

Paratypes. Las Animas: SDMNH 44620–22, 44624, 50830–42, 50844–49.

Diagnosis. Average snout–vent length of 48.7 mm., differing from *P. xanti* of Isla San Jose, having a significantly higher number of ventral scales, dorsal tubercle rows, paravertebral tubercles, and lower number of interorbitals, snout scales, and scales bordering the postmentals; from *P. bugastrolepis* in having a higher number of ventral scales and lower number of snout scales, interorbitals, dorsal tubercle rows, paravertebral tubercles, and scales bordering the postmentals.

Description of holotype. Rostral almost twice as wide as high, its dorsal edge with slight median groove; internasals, rounded posteriorly, their median edges in broad contact, bordered posteriorly by 7 granules and postnasal of each side, nostril surrounded by rostral, labial, internasal, and 2 postnasals. First supralabial in broad contact with ventral edge of nostril; shallow depression between internasals, moderate depression in frontal region; 11 scales between eye and nostril, scales in posterior loreal region about 5 to 6 times larger than scales in midorbital region; 19 scales across snout at level of third labials, 18 scales at anterior edge of orbits, 21 interorbital scales; eye large, its diameter contained in length of snout one and one-half times; eyelid with one row of granules and one larger outer row of scales, last 4 to 5 of which are not pointed; diameter of ear contained in eye diameter two and one-fourth times, ear opening not denticulate, scales on anterior and posterior edges rounded, subequal; rear of head granular with many larger intermixed tubercles; 6 supralabials and 5 infralabials to a point below center of eye; mental bell-shaped, slightly wider than long, bordered posteriorly by 2 postmentals; postmentals longer than wide, their median edges in broad contact, followed by transverse row of 8 scales, followed by second row of 11 smaller scales; postmentals contact first labial on right side, first and second labial on left side.

Dorsum with 14 longitudinal rows of enlarged, keeled tubercles that are somewhat flat, paravertebral row with 40 tubercles from rear of head to base of tail, 22 between axilla and groin; paravertebral rows separated from each other by 4 rows of granules; 10 rows of tubercles reach to rear of hear, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 1 to 2 granules; postanal tubercles number 2 on each side, indistinct; venter with 62 longitudinal and 38 transverse rows of scales.

Dorsal surface of upper arm with flattened scales, forearm with larger tubercles interspersed among the smaller flattened scales; dorsal surface of thigh without tubercles dispersed among the small flattened scales, lower leg with 2 to 3 tubercles interspersed among the granular scales; lamellae formula for hand 7-9-10-11-10, foot 7-11-13-14-11; claw short, visible when viewed from below; terminal pad large, slightly wider than long. Tail with 4-2-0 reduction of tubercle rows on proximal two whorls of tail.

Measurements (in mm.). Snout–vent length 50, axilla–groin length 24, length of leg 19, length of arm 16, length of tail 47, length of head 15, width of head 10, length of snout 5; diameter of eye 3.5, diameter of ear 1.5.

Color in alcohol. Ground color brownish tan; dorsum with four bands, interrupted medially, dark brown; and generally diffuse in appearance; each enlarged dorsal tubercle white tipped; upper arm with faint diffuse brownish bands, thigh similar to dorsum; spots more diffuse, tail brownish gray, with scattered darker flecks; head slightly darker than dorsum; with scattered diffuse dark brown spots; diffuse brown line from nostril to eye; ventral surfaces with each scale whitish posteriorly, dusky otherwise, with a few scattered black dots in each scale.

Range. Isla Las Animas, Gulf of California.

Specimens examined. (24), listed under type and paratypes.

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 14, pp. 453–480; 1 table May 12, 1966

NEW NON-MARINE MOLLUSCA FROM THE ESMERALDA FORMATION, NEVADA

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Abstract: Two new species of Pelecypoda, *Sphaerium stewartensis* and *Pisidium leslieae*, and 5 new species of Gastropoda, *Vorticifex stewartensis*, *Planorbis webbi*, *Bulimnea webbi*, *Goniobasis reticulata*, and *Goniobasis leslieae*, are described from the non-marine late Tertiary Esmeralda Formation, Nye and Mineral counties, Nevada. The 7 new species are part of a non-marine molluscan fauna of 34 taxa, here referred to as the Cedar Mountain molluscan fauna. On the basis of associated fossil mammals this fauna ranges in age from Barstovian through Clarendonian (late Miocene though early Pliocene). The Cedar Mountain molluscan fauna is closely related to that of the Truckee Formation of western Nevada. The character and field relationships of the lacustrine sediments where the molluscs occur indicates lake margin or shallow water environment.

Introduction

A large non-marine fauna, including 7 new species, was collected from lacustrine sediments of the Esmeralda Formation in the vicinity of the Cedar Mountains during 1961. The area is located in west central Nevada, approximately 22 miles east of the town of Mina and 35 miles southeast of Hawthorne (see index map).

Collections were made at 42 localities in Stewart and Ione valleys. Surface prospecting techniques were employed at all localities and were augmented by dry screening at localities B-2051 and B-2052. Laboratory preparation depended on the use of small hand tools, as weak solutions of acetic acid and immersion in water were unsatisfactory for the separation of fossils from the matrix.

Specimens and locality numbers refer to collections of the Museum of Paleontology, University of California at Berkeley (*UCMP*) and the California Academy of Sciences at San Francisco (*CAS*).

I am indebted to J. Wyatt Durham, Department of Paleontology, University of California, Berkeley, for his critical reading of this manuscript. Thanks are also due J. E. Mawby and S. D. Webb, of the University of California, Berkeley, for their determinations of the fossil mammals. Financial support was graciously given by the Museum and Department of Paleontology, University of California, Berkeley.

Occurrence

The Esmeralda Formation in the area of the Cedar Mountains is represented by a series of tuffaceous sandstones, siltstone, limestones, thin beds of volcanic ash, and shale. These lacustrine beds have a thickness of over 1,400 feet in Stewart Valley and more than 1,600 feet in Ione Valley. In both valleys the sediments overlie an irregular surface of igneous rocks, and crop out on both the east and west flanks of the Cedar Mountains, from Gabbs Valley south to Big Smokey Valley, the terminus of the Cedar Mountains. The molluscs are generally abundant in the sandstones and limestones throughout the lacustrine sediments, becoming rare in the siltstones and shale and absent in the volcanic ash.

The Esmeralda Formation in this region ranges in age from late Miocene through early Pliocene. Major evidence for dating the Esmeralda Formation of this area is provided by the occurrence of fossil mammals in the same beds with the molluscs. Two North American mammalian ages, the Barstovian and the Clarendonian (as defined by Wood, *et al.*, 1941), are represented by the characteristic fossil mammals, which are listed systematically below. A geologic map of that portion of the Esmeralda Formation in Mineral County has been compiled by Ross (1961, pl. 2).

Precise locality data for all localities where molluscs were collected are given in the appendix.

List of Barstovian (late Miocene) Mammals from the Stewart Springs and Bell Springs Faunas.

- Insectivora
  - Erinaceidae
    - *Meterix latidens*
  - Soricidae
    - *Limnoecus* species
  - Talpidae
- ? Insectivora, genus undetermined
    - *Arctoryctes* species
- ? Chiroptera
- Rodentia
- Rodentia
  - Sciuridae
    - Sciuridae, genus and species undetermined
    - *Tamias ateles*
- Carnivora
  - Canidae
    - *Tomarctus* species
    - *Aelurodon* species
    - *Vulpes* species
  - Procyonidae
    - *Bassariscus parvus*
  - Mustelidae
    - Mustelidae, genus and species undetermined
- Proboscidea
  - Gomphotheriidae
    - *Gomphotherium* species
- Perissodactyla
  - Equidae
    - *Hypohippus* species, compare *H. osborni*

Aplodontidae
Liodontia species
Mylagaulidae
Mylagaulus species
Castoridae
Monosaulax pansus
Anchitheriomys species
Heteromyidae
Perognathoides species
Geomyidae
Cricetineae
Lagomorpha
Leporidae
Hypolagus species
Merychippus brevidontus
M. californicus
Rhinocerotidae
Teleoceras species
Artiodactyla
Camelidae
Procamelus species
Aepycamelus species
Palaeomerycidae
Palaeomerycidae, genus and species undetermined
Antilocapridae
Merycodus furcatus
M. loxoceras

List prepared by S. D. Webb.

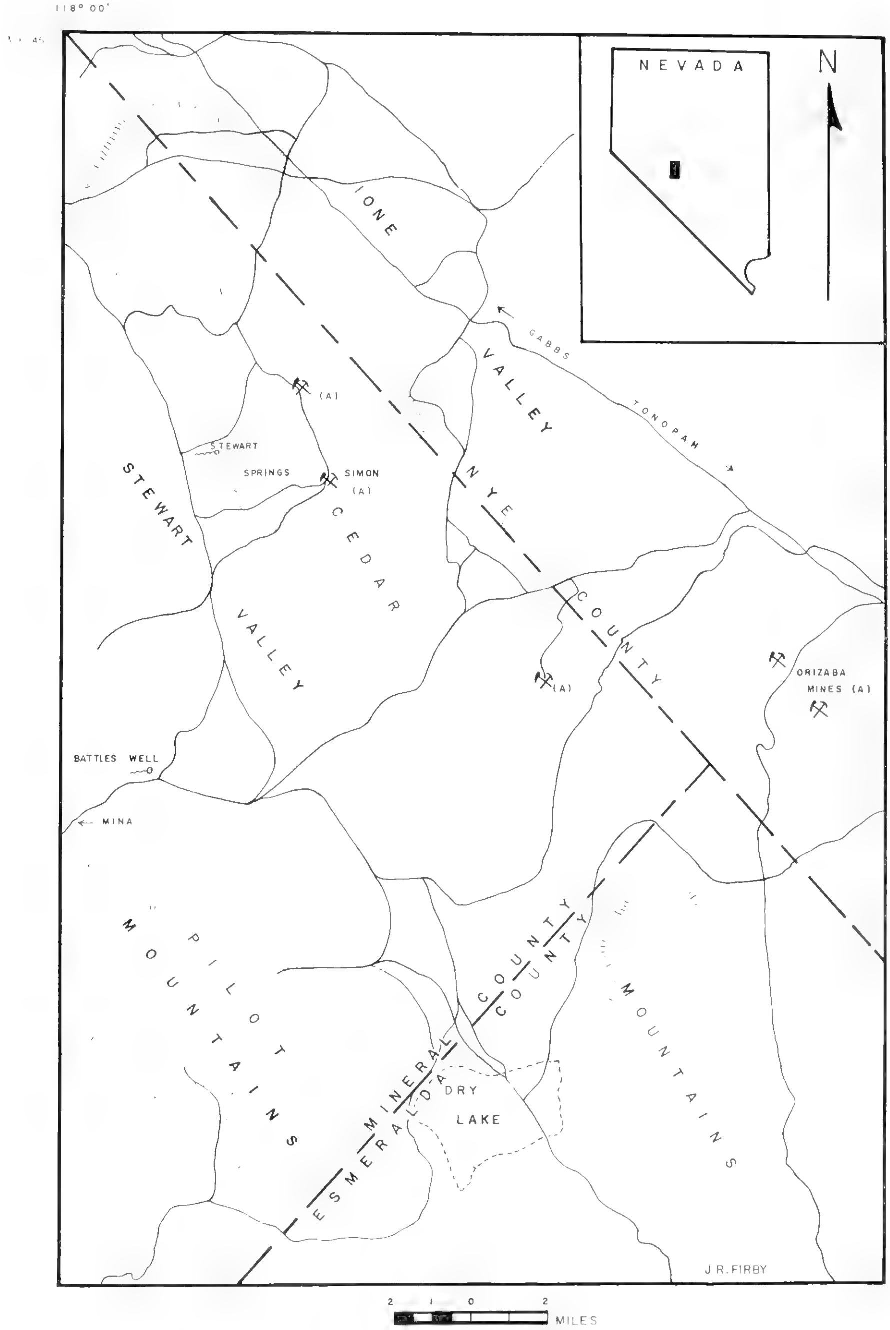
List of Clarendonian (early Pliocene) Mammals from the Cedar Mountain Esmeralda Beds.

Insectivora
Soricidae
Limnoecus tricuspis
Rodentia
Sciuridae
Sciuridae, genus and species undetermined
Tamias ateles
Heteromyidae
Perognathus species, compare *P. minutus*
Cupidinimus species
Perognathoides quartus
P. cuyamensis
Dipidomyine
Dipidomyine, genus and species undetermined
Castoridae
Eucastor dividerus
Cricetidae
Peromyscus dentalis
Lagomorpha
Leporidae
Hypolagus species
Carnivora
Canidae
?*Tomarctus* species
Vulpes species
Aelurodon taxoides
Aelurodon species
Mustelidae
Mustelidae, genus and species undetermined
Felidae
Pseudaelurus species
Sansanosmilus species
Proboscidea
Gomphotheriidae
Gomphotheriidae, genus and species undetermined
Perissocactyla
Equidae
Megahippus species
Pliohippus species, compare *P. tantalus*
Pliohippus species
Neohipparion species
Hypohippus nevadensis
Rhinocerotidae
?*Aphelops* species
Artiodactyla
Camelidae
Procamelus coartatus
Procamelus species
Protolabis species
Antilocapridae
Merycodus species

List prepared by J. E. Mawby.

Related Faunas

The molluscan fauna of the Esmeralda Formation in the Cedar Mountain area is most closely related to that of the Truckee Formation to the north. The



Index map. Collecting area from the Esmeralda Formation, Nevada.

limited assemblage from the Silver Peak area to the south is also similar. Both faunas are probably contemporaneous, at least in part, with the Cedar Mountain molluscan fauna. Stratal continuity between the Esmeralda Formation at its type area in the Silver Peak region and lacustrine sediments at Cedar Mountain is affirmed by Buwalda (1914). The Silver Peak region is approximately 40 miles south of the Cedar Mountain area.

Portions of the Truckee Formation have been referred to a probable late Clarendonian age by Macdonald (1956), who records *Eucastor* near *E. leconti* and *Osteoborous diabloensis* from the Nightingale and Brady Pocket localities. In the upper sequence at Cedar Mountain the beaver *Eucastor dividerus*, the horses *Megahippus, Pliohippus* species *cf. P. tantalus*, *Pliohippus* species, and *Neohipparion* species indicate a Clarendonian Age. This is in sharp contrast to the fauna of the lower sequence at Cedar Mountain (Stewart Spring Fauna, Stirton, 1940) in which the beaver *Monosaulax pansus*, and the horses *Merychippus brevidontus* and *M. californicus* leave little doubt of a Barstovian Age. There are no known faunas of comparable antiquity in beds referred to the Truckee Formation. It would seem, therefore, that the upper portion of the Esmeralda Formation at Cedar Mountain is a possible correlative of the Truckee Formation. That both are Clarendonian seems certain. However, the lack of stratal continuity between the Esmeralda and the Truckee makes any further refinement impractical and possibly misleading.

Yen (1950, p. 181) records the following 18 species from the Fossil Hill locality, which he considers to be the type area of the Truckee Formation: *Sphaerium rugosum* Meek, *Valvata* species *cf. V. incerta* Yen, *V. truckeensis* Yen, *Amnicola truckeensis* Yen, *Fluminicola yatesiana inflata* Yen, *Hydrobia truckeensis* Yen, *Lacunorbis nevadensis* Yen, *Goniobasis sculptilis* (Meek), *Goniobasis* species *cf. G. arnoldiana* Pilsbry, *Lanx undulatus* (Meek), *Gyraulus* species undetermined, *Menetus* species undetermined, *Vorticifex binneyi* (Meek), *Vorticifex tryoni* (Meek), *Vorticifex tryoni concava* (Meek), *Vorticifex tryoni planus* Yen, *Vorticifex globosus* Yen, and *Vorticifex menetoides* Yen.

In addition to those species recorded by Yen, Hannibal (1912) records *Helisoma* (*Perrinilla*) *cordillerana* and *Viviparus turneri* from the "Truckee Lake beds, Nevada."

Comparison of the Cedar Mountain molluscan fauna with that of the type Truckee shows 8 of 29 species, or 36 per cent of the specifically identifiable taxa are identical. Eight of 17 genera are the same.

Fossil molluscs from the type area of the Esmeralda Formation at Silver Peak include *Viviparus turneri*, *Lanx undulatus*, *Valvata truckeensis*, *Vorticifex tryoni*, and an indeterminate species of *Sphaerium* which may be the same as *S. stewartensis*, new species.

PALEOECOLOGY

Pelecypoda

Sphaeriidae.

Sphaerium and *Pisidium.*

The family Sphaeriidae is represented in the Cedar Mountain molluscan fauna by *Sphaerium stewartensis* and *Pisidium leslieae.* The ecologic requirements for the two genera are so similar they do not warrant separate treatment.

The living members of the Sphaeriidae are found in a variety of habitats ranging from deep to shallow water, but the majority prefer water less than 6 feet deep (Pennak, 1953). The Sphaeriidae are tolerant of a wide range of bottom environments. Rock or clay are the only extremes in substrate which they cannot tolerate. Although the sphaeriids prefer water that is somewhat alkaline, they have been recorded from water with a pH of 6.0 (*ibid.*, p. 705).

La Rocque (1960, pp. 20, 21) states that the sphaeriids are not abundant in sediments of lacustrine origin, preferring the running water of streams. Baker (1902) and Pennak (1953) make no such distinction, and the widespread occurrence of these pelecypods in the Cedar Mountain Esmeralda does not support such an inference. The sphaeriids of the Cedar Mountain molluscan fauna have relatively thin, inflated shells, more typical of lake dwellers than of inhabitants of running water.

Gastropoda

Planorbidae.

North American members of this family are littoral, seldom being found at depths greater than 15 feet, with about 6 feet being the optimum. Distribution of individuals within this depth range is determined largely by the food supply. Members of the Planorbidae may be found living in permanent or subpermanent ponds, lakes, and streams. A silty or fine grained sandy substrate where there is an abundance of rooted vegetation is generally the most favorable habitat; however, the Planorbidae are highly tolerant of a wide range of environmental conditions.

The Planorbidae are represented in the Cedar Mountain mollucan fauna by the genera *Planorbis*, *Vorticifex*, *Carinifex*, *Perrinilla*, *Rostroapertura*, and *Promenetus*. Of these 6 genera only 3, *Carinifex*, *Promenetus*, and *Planorbis* are represented by living species and thus offer basis for uniformitarian interpretation of the paleoecology. Beyond the general remarks given above, little may be said of the 3 extinct genera. Since the extinct genera are found in association not only with one another but also with representatives of the extant genera, I believe it reasonable to assume similar habits and habitats for the extinct genera.

Carinifex.

Found principally in a quiet water, littoral habitat with an abundance of rooted vegetation. Exclusively fresh-water. Tolerant of wide temperature variations. The present range of *Carinifex* is western North America, from California east to Wyoming.

Promenetus.

The basis for the ecologic interpretation of *Promenetus kansasensis* is the living species, *P. exacuous* (Say), from the High Plains. Its environment is described by Taylor (1960, p. 59) as follows: "*Promenetus exacuous* is found in shallow, perennial or subpermanent, quiet water bodies, such as ponds, oxbow lakes, marshes, and sloughs or backwaters along streams. It is usually on the submerged vegetation in such habitats." *Promenetus kansasensis* is found only at locality B-2051, in the Barstovian of Stewart Valley. This locality was probably at or near the mouth of a stream, as indicated by the cross-bedding of the enclosing beds. The water could not have been as quiet as that cited by Taylor for *P. exacuous*, which may account for the paucity of specimens.

Planorbis.

Planorbis may be found in streams, ponds, and lakes, preferably where there is an abundance of rooted vegetation and silty or fine grained sandy substrate. It may live in permanent or subpermanent bodies of fresh-water. Species of this genus are highly tolerant of a wide range of environmental conditions.

Planorbis is apparently cosmopolitan in its distribution. As with many other fresh-water gastropods, birds play a major role in the dispersal of *Planorbis*. Passive dispersal of *Planorbis* (as well as *Carinifex* and most other members of the family) is further aided by rafting and by the transport of eggs on the elytra of water beetles. Active dispersal occurs through water channels.

LYMNAEIDAE.

Lymnaea, *Galba*, and *Bulimnea*.

Members of this family are ubiquitous in fresh to brackish water, in either permanent or temporary bodies, from North to South America, eastern Siberia, Greenland, Iceland, and Europe. Species of *Lymnaea*, *Galba*, and *Bulimnea* vary greatly in their habitat preferences. Many species are euryopic. In view of their ability to exist under a wide range of environmental conditions, it is surprising that the Lymnaeidae are not better represented in the Cedar Mountain molluscan fauna.

LANCIDAE.

Lanx.

Lanx may be found in both quiet and running water, clinging to sticks, stems of water weed, fresh-water crustaceans, stones, or anything that provides a suitable substrate. Although *Lanx* is a pulmonate gastropod, it is also able to extract oxygen directly from the water, thus eliminating the need to come to the surface to respire. Baker (1928, p. 397) records rafting, birds, and the elytra of water beetles as agents of dispersal.

VIVIPARIDAE.

Viviparus.

Exclusively fresh-water; found in rivers, streams, lakes, ponds, pools, marshes, backwaters, and bodies of permanent water. *Viviparus* is abundant in areas with heavy growth of aquatic rooted vegetation or concentrations of algae; occasionally it is carnivorous. It is found at various depths, apparently controlled by the availability of food. Respiration is by means of ctenidia, with the mantle serving as a secondary respiratory organ (Prashad, 1928, p. 155). Although reasonably tolerant of substrate, *Viviparus* prefers silty or sandy bottoms.

Methods of passive dispersal available to members of this family are limited. As the young are shed alive after undergoing torsion and development of an embryonic shell, dispersal of an egg mass is impossible. It is the opinion of Prashad (1928, p. 157) that the embryonic shells are too delicate to endure long transport. The older (and larger) individuals are, therefore, the only ones capable of surviving long transport. Successful passive dispersal of *Viviparus*, although possible, is rendered improbable by several factors; their size, their sexual differentiation, and the required size of the transporting agent. As these gastropods are unisexual, successful transport must involve a gravid female or a mature male and female. Shells of the genus generally exhibit sexual dimorphism, with that of the female being larger. As the adults of most species of this genus are large (*V. turneri* reaching a shell height of 2½ inches), the transporting agent would have to be of large size. I believe that transport by birds is, in this instance, highly improbable.

The most plausible, and therefore most widely accepted, means of dispersal for the genus is active dispersal through water channels. Although passive dispersal by rafting in fresh-water is possible, it is unrecorded.

Distribution of the family is essentially world-wide, excepting the polar regions. The distribution of *Viviparus* in the strict sense encompasses Europe, Africa, Asia, Australia, and North America. No North American species of *Viviparus* have been found north of 52° north latitude, and Recent species are further restricted to east of the Rocky Mountains.

PLEUROCERIDAE.

Goniobasis.

Living representatives of this genus are found in waters of varying salinity, ranging from estuarine (species such as *Goniobasis virginica*) to strictly fresh-water (*G. laurae*). They are generally tolerant of extremely adverse conditions, such as excessive turbidity (La Roque, 1960, p. 27). Respiration is by means of ctenidia.

Dispersal of these pleurocerids is not as easily accomplished as in the Planorbidae or Lancidae. Egg masses are attached to stones, shells, sticks, and on occasion to other individuals of *Goniobasis*. Unlike *Planorbis* or *Lanx* there are no records of *Goniobasis* attaching an egg mass to the elytra of a water beetle. Rafting is a possible means of passive dispersal, but its importance has never been evaluated. *Goniobasis* is not known to be transported by birds. The main method of dispersal, therefore, would appear to be active dispersal through water channels.

VALVATIDAE.

Valvata.

The family Valvatidae is represented in the Cedar Mountain molluscan fauna by at least 2, and possibly 3, distinct species of *Valvata*. Recent forms of *Valvata* are found almost exclusively in large permanent water bodies such as rivers and lakes. A substrate of mixed rock, fine grained sand or silt is preferred, although almost any substrate is tolerated.

It is significant that *Valvata* is almost universally intolerant of waters having a pH of less than 7.0. This supports the hypothesis that the lacustrine sediments of the Cedar Mountain Esmeralda Formation were deposited in alkaline waters.

Dispersal of this genus is usually through water channels. Passive dispersal, primarily through the agency of birds, is probably of secondary importance. I know of no recorded instance of egg masses being transported on the elytra of water beetles.

AMNICOLIDAE.

Amnicola.

Species of this genus are found clinging to stems or leaves of aquatic plants, bathed by a gentle current. In contrast to *Valvata*, *Amnicola* is tolerant of a wide range of hydrogen ion concentrations, from a pH of 5.7 to a pH of 8.3 (Pennak, 1953, p. 681). It is surprising that only one recognizable specimen of *Amnicola* was found in the Cedar Mountain Esmeralda as it is abundant in the Truckee beds where much the same environment prevailed. Dispersal of this genus is similar to that of *Valvata*.

In summary, the Cedar Mountain molluscan fauna inhabited a large permanent lake. Their general preference was for shallow, relatively quiet water, with an abundance of rooted aquatic vegetation. The climate was more equable then than now, a fact well documented by associated fossil flora.

Drainage

It is my opinion that the Stewart and Ione basins drained externally during the Barstovian and Clarendonian. If the drainage had been predominantly internal, the resultant concentration of dissolved salts would have precluded the presence of such exclusively fresh-water genera as *Carinifex* and *Viviparus*. Both of these genera, however, are represented by numerous individuals at many localities in both basins.

Additional support for a hypothesis of external drainage is provided by the hydrogen ion concentration tolerance of the molluscan fauna. An excessive concentration of dissolved carbonates (greater than a pH of 8.0) would be intolerable to most fresh-water gastropods. A noted exception to this is *Amnicola*, which has been recorded from water with a pH of 8.3. Certainly carbonates in solution were available for concentration, and without external drainage a high concentration would be expected. The surrounding mountain ranges, which served as a major source of sediment for the Stewart and Ione basins, have extensive areas of Mesozoic limestones which probably would have provided dissolved carbonates throughout the Tertiary depositional history of these basins. At the same time we may assume that the water of these basins was slightly alkaline, as such aggregations of molluscs, both in number of species and individuals, are atypical of waters with a pH of less than 7.0. Additional evidence is provided by the presence of *Valvata*, which cannot tolerate water with a pH of less than 7.0.

SYSTEMATIC PALEONTOLOGY

Class PELECYPODA

Family Sphaeriidae

Genus **Sphaerium** Scopoli

Type *Tellina cornea* Linnaeus, 1758

Sphaerium stewartensis Firby, new species.

(Figures 12, 15, 17, 18.)

Description. Shell ovoid; beaks almost central, slightly anterior; sculpture of closely spaced growth lines, more prominent dorsally than ventrally; right valve with single triangular arched cardinal tooth anterior to beak; two elongate anterior lateral teeth, two low elongate posterior lateral teeth; posterior lateral teeth one-third longer than anterior lateral teeth; left valve with small single pointed cardinal tooth, single prominent anterior lateral, single prominent posterior lateral; posterior margin flatter than anterior margin.

Holotype *UCMP* 37869. Paratypes *UCMP* 37870, 37871; *CAS* 12757, 12758.

Measurements

Length	Height	Length	Height
10.8 mm. right valve	10.3 mm.	12.0 mm. right valve	11.0 mm.
11.7 mm. " "	11.3 mm.	12.9 mm. " "	12.2 mm.

9.9 mm. " "	9.9 mm.	9.3 mm. " "	8.8 mm.
10.5 mm. left valve	10.1 mm.	10.8 mm. left valve	10.1 mm.

Discussion. This species resembles *Sphaerium rugosum* Meek, 1877, but differs in having the beaks more central, a less trigonal outline, and heavier lateral teeth. The less pronounced costae of *S. stewartensis* may be due, in part, to a greater amount of available carbonates. *Sphaerium stewartensis* is larger than *S. rugosum*, being closest in size to *S. malheurensis* Henderson and Rodeck, 1934, from the Pliocene of Oregon. *Sphaerium stewartensis* is common throughout the Cedar Mountain Esmeralda beds, occurring in beds of Barstovian and Clarendonian age.

Occurrence. The type specimen is from *UCMP* B-2051, Barstovian of Stewart Valley. Preservation of the shells is excellent at this locality, and numerous complete left and right valves were collected. Other localities: *UCMP* B-2052, B-8305, B-8306, B-8307, B-8310, B-8314, B-8315, B-8317, B-8318, B-8321, B-8328, B-8329, B-8331, B-8335.

Genus **Pisidium** Pfeiffer, 1821
Type *Tellina amnica* Müller, 1774

Pisidium leslieae Firby, new species.
(Figures 2, 3, 6, 7, 10.)

Description. Shell trigonal, inflated; beaks high, two-thirds distant from anterior margin; surface of shell with prominent concentric sculpture, regularly spaced, uniform in size near beak, stronger towards margin; hinge arched, with cardinal area almost straight; posterior margin slightly curved; right valve with two posterior and two anterior laterals, posterior laterals slightly more massive than anterior; cavity between both posterior and anterior laterals deep; dorsal laterals low, ventral laterals roundly pointed; crescent-shaped shallow ligamental groove from cardinal tooth extends anteriorly to, but does not meet, anterior lateral; 2 triangular, pointed cardinal teeth; anterior cardinal extended to form low ridge which joins anterior lateral, forming ventral boundary of the anterior ligamental groove.

Holotype *UCMP* 37872. Paratypes *UCMP* 37873, 37874; *CAS* 12759, 12760.

Measurements

Length	Height	Length	Height
6.4 mm. right valve	6.2 mm.	5.9 mm. right valve	6.4 mm.
7.1 mm. " "	6.9 mm.	6.7 mm. left valve	6.4 mm.
6.2 mm. left valve	5.9 mm.	6.0 mm. " "	5.6 mm.
4.1 mm. " "	3.5 mm.		

Discussion. Numerous well preserved specimens were found in Barstovian beds in Stewart Valley. This form is like *Pisidium curvatum* Hanna, 1923, from the late Miocene of Sonoma County, California, but differs from it by having the cardinal tooth directly under the beak, and more strongly curved anterior and posterior margins. It is proportionally shorter than *P. curvatum* in height to width ratio. That it is slightly more inflated than *P. curvatum* is of little taxonomic value, as this feature is largely controlled by environment and may vary considerably within a species.

Occurrence. Type locality *UCMP* B-2051, Barstovian of Stewart Valley. Other localities: *UCMP* B-8317, B-8318, B-8325, B-8326.

Class GASTROPODA

Family Planorbidae

Genus **Vorticifex** Meek, 1870

Type *Carinifex* (*Vorticifex*) *tryoni* Meek, 1870
(= *Choanomphalus* (*Carinifex*) *tryoni* Fischer, 1887)

Vorticifex stewartensis Firby, new species.
(Figures 1, 5, 9.)

Description. Shell ultradextral; whorls 4 to 4½, rapidly increasing in size, flatly convex; sculpture of strong axial ribs; body whorl with rounded shoulder, flattened sides obscurely angulate at base; body whorl does not descend; spire depressed approximately one-sixth total shell height; sutures deep, impressed; aperture roundly sub-quadrate; umbilicus wide, one-half diameter of shell, deep, funicular, showing preceding whorls.

Holotype *UCMP* 37875. Paratypes *UCMP* 37876, 37877; *CAS* 12761.

Measurements

Diameter	Height
12.3 mm.	5.8 mm.
12.8 mm.	5.7 mm.
12.0 mm.	5.1 mm.

Discussion. This form resembles *Vorticifex menetoides* Yen, 1950, but differs in being distinctly concave in apical view, owing to the depressed spire, and has a much wider umbilicus. *Vorticifex stewartensis* is found with *V. tryoni* and *V. binneyi*, and is distinctly larger and more robust.

Occurrence. Type locality *UCMP* B-2051. Other localities *UCMP* B-8326, B-8332.

Genus **Planorbis** Geoffrey, 1767

Type *Helix Planorbis* Linnaeus, 1758

Planorbis webbi Firby, new species.
(Figures 11, 14.)

Description. Shell large for genus, discoidal; spire flat or slightly raised; 4½ to 5½ whorls; whorls flatly convex above, rounded below; periphery of whorls obscurely angulate; last one-quarter of last whorl slightly descending, expanded, becoming flatly concave above aperture; sculpture of regularly spaced, prominent, prosocline axial ribs; aperture cardiform, deflected; umbilicus one-third diameter of shell, funicular, deep, exposing early whorls.

Holotype *UCMP* 37878. Paratypes *UCMP* 37879; *CAS* 12762.

Measurements

Maximum diameter	Height	Maximum diameter	Height
17.4 mm.	7.5 mm.	15.2 mm.	6.8 mm.
15.2 mm.	6.8 mm.	15.0 mm.	8.0 mm.
15.0 mm.	6.2 mm.	14.3 mm.	7.0 mm.
13.7 mm.	7.4 mm.	13.3 mm.	5.4 mm.

Discussion. *Planorbis webbi* appears to be close to *P. utahensis* Meek, 1877, from the Bridger group of southern Wyoming. *Planorbis webbi* is distinguished by the slight concavity on the ventral surface of the body whorl just over the aperture, and the expansion of the last one-quarter of the body whorl. Only 9 specimens were found, preserved as casts.

Occurrence. Type locality *UCMP* B-8333, Clarendonian. Only locality.

Family Lymnaeidae
Genus **Bulimnea** Haldeman, 1841
Type *Bulimnea megasoma* (Say)

Bulimnea webbi Firby, new species.
(Figures 4, 8.)

Description. Shell thin, turbinate; spire high, slightly over one-third shell height; whorls rapidly enlarging, becoming increasingly more convex abapically, sutures well defined, deeply impressed to form a shoulder; body whorl inflated; aperture ovoid, slightly oblique; inner lip with thickened parietal callus; umbilicus reduced to a small chink; sculpture not known.

Holotype *UCMP* 37880. Paratypes *UCMP* 37881; *CAS* 12763.

Measurements

Height	Maximum diameter	Height of aperture
24.8 mm.	15.6 mm.	13.5 mm.
27.5 mm.	11.8 mm.	14.0 mm.
16.8 mm.	11.5 mm.	10.8 mm.

Discussion. *Bulimnea webbi* is strongly reminiscent of *B. megasoma* (Say) in size and proportion. It differs in having a more inflated body whorl and less acute spire angle. The fossils are preserved as opalized internal casts, with fragments of shell material adhering in small patches, especially portions of the parietal callus. *Bulimnea webbi* has a much higher spire and a much less inflated body whorl than *Radix junturae* Taylor, which occurs stratigraphically higher.

Occurrence. Type locality *UCMP* B-8325, Barstovian. Only locality.

Family PLEUROCERIDAE
Genus **Goniobasis** Lea, 1862
Type *Melania olivula* Conrad, 1834

Goniobasis reticulata Firby, new species.
(Figures 13, 16.)

DESCRIPTION. Shell imperforate, 6 to 8 whorls; spire high, four-fifths total shell height; whorls convex, with marked reticulate sculpture formed by strong, regularly spaced axial ribs intersecting slightly less pronounced spiral cords; 25 to 35 axial ribs on body whorl, ceasing abruptly at basal portion of body whorl; basal portion of body whorl concave, delineated by strong spiral cord, 4 to 5 inferior spiral cords on basal portion of body whorl; sculpture of threadlike, very closely spaced growth lines parallel to axial ribs for entire length of shell; aperture ovoid, slightly produced abapically; inner lip reflexed, callused; outer lip not expanded, continuous; sutures distinct, grooved; columella smooth; angle of spire 20° to 22°.

HOLOTYPE *UCMP* 37882. PARATYPES *UCMP* 37883, 37884; *CAS* 12764.

MEASUREMENTS

Height	Maximum diameter
9.9 mm. (3 whorls)	5.5 mm. (type)
13.9 mm. (4 ″)	5.5 mm.
17.0 mm. (4½ ″)	7.2 mm.
16.2 mm. (4 ″)	6.8 mm.
6.7 mm. (5½ ″)	3.3 mm.
6.6 mm. (5 ″)	3.4 mm.

DISCUSSION. This species has features in common with both *G. simpsoni* and *G. sculptilis* of Meek, from the Kaw-soh Mountains. The concavity of the abapical portion of the body whorl and the anterior production of the aperture distinguish *G. reticulata* from *G. simpsoni.* Greater convexity of whorls, lesser spire angle, stronger spiral sculpture and abrupt cessation of axial ribs on basal portion of the body whorl distinguish it from *G. sculptilis.*

OCCURRENCE. Type locality *UCMP* B-2051, Barstovian. Other localities: *UCMP* B-2050, B-8301, B-8305, B-8309, B-8310, B-8311, B-8312, B-8315, B-8317, B-8318, B-8321, B-8322, B-8329, B-8332, B-8335, B-8337.

Goniobasis leslieae Firby, new species.
(Figures 19, 20.)

DESCRIPTION. Shell imperforate, elongate, conical; spire high, gradually tapered to apex, with spire angle of 12° to 16°; 8 to 10 markedly convex whorls; early whorls with sculpture of slightly raised axial ribs, intersected by faint spiral threads; apical whorl distinguished by a peripheral angulation two-thirds of distance from preceding suture; whorls marked by opisthocyrt, crowded, threadlike growth lines, becoming sigmoidal on body whorl; aperture ovoid, slightly oblique; inner lip reflexed, callused; outer lip not expanded, continuous; sutures linear, slightly grooved; basal portion of body whorl convex.

Holotype *UCMP* 37885. Paratypes *UCMP* 37886, 37887; *CAS* 12765.

Measurements

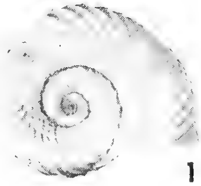
Height	Maximum diameter
15.6 mm. (8 whorls, apex broken)	5.6 mm.
16.5 mm. (9 " " ")	5.8 mm.
8.5 mm. (8 " complete)	3.2 mm.

Discussion. *Goniobasis leslieae* is similar to *G. simpsoni* Meek, 1877, but is slenderer, with a spire angle 10° less than that reported by Meek. Sculpture of specimens from the type locality is fairly uniform, with only minor variations in the height and persistence of the axial ribs. Specimens from the type locality retain the shell, and show surface ornamentation clearly.

Occurrence. Type locality *UCMP* B-2051, Barstovian. Only locality.

Localities	Barstovian																						Clarendonian																			
Molluscan Fauna	B-2050	B-2051	B-2053	B-8300	B-8301	B-8302	B-8303	B-8304	B-8305	B-8306	B-8317	B-8318	B-8324	B-8325	B-8326	B-8327	B-8328	B-8329	B-8334	B-8335	B-8336	B-8337	B-2052	B-8307	B-8308	B-8309	B-8310	B-8311	B-8312	B-8313	B-8314	B-8315	B-8316	B-8319	B-8320	B-8321	B-8322	B-8323	B-8330	B-8331	B-8332	B-8333
Pelecypoda																																										
Sphaerium stewartensis, new species		X							X	X	X	X					X	X		X			X	X			X		?		X	X		?	?	X				X		
Sphaerium species						X	X																					X														
Pisidium leslieae, new species		X									X	X		X	X																											
Pisidium leslieae?										X						X	X				X																					
Gastropoda																																										
Carinifex malheurensis																							X								?								X	X	X	
Carinifex species						X																																				
Perrinilla cordillerana	X			X	X			X			?												X	X				?	X	X	X	X	?	X		X			X	X		X
Perrinilla (?) species																												X										X				
Promenetus kansasensis		X																																								
Rostroapertura mawbyi				X		X																																				
Rostroapertura species							X																																			
Vorticifex tryoni		X					?		X	X	X	X	X	X	X	?	X	?				X	X	X		X					X	X	?		?	X	X				X	
Vorticifex binneyi		X								X	X		X	X	X							?		X																	X	
Vorticifex globosus																															X											
Vorticifex stewartensis, new species		X								X																X															X	
Vorticifex species compare *V. tryoni*													X						X														X					X				
Vorticifex species																X																										
Planorbis webbi, new species																																										X
Planorbis (?) species																									X																	
Radix junturae									X																																	
Bulimnea webbi, new species														X																												
Valvata truckeensis									X											X																						
Valvata incerta			X									X																													X	

Valvata species																							·								
Viviparus turneri	·	·				×		·	·			?	·		·	×						·				·					
Viviparus species												·			·																
Goniobasis reticulata, new species	·	·		·	?		·		·	·	?		·		·	×		·	×	·	·			·	?		·	·		·	·
Goniobasis leslieae, new species		·																													
Goniobasis species			×	×			·							·															·		
Lymnaea vetusta (?)		×																													
Galba species																	·														
Lanx undulatus										·		×																			
Lanx species												×																			
Amnicola species, compare *A. truckeensis*																							·								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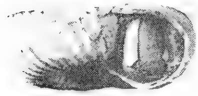
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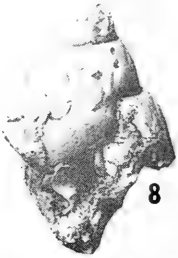
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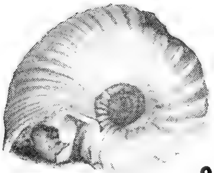
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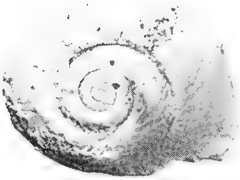
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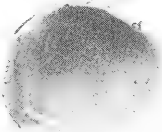
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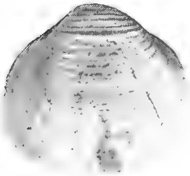
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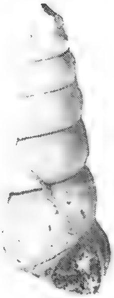
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APPENDIX

REGISTER OF LOCALITIES

All coordinates refer to United States Geological Survey Tonopah Quadrangle, scale 1:250,000, 1959 edition, Nye and Mineral counties, Nevada.

LOCALITY:

B-2050: N.W. ¼ section 21, Range 38 E., Township 9 N., Nye County. Along county road to Mina 5.6 miles, west from junction with Nevada State Highway 89, approximately 500 feet north of road.

Lithology: Well-indurated, poorly bedded fine to medium grained tuffaceous sandstone, light grey to blue grey, weathering to brown.

Age: Barstovian.

B-2051: S.E. ¼ of S.E. ¼ section 20, Range 36 E., Township 9 N., Mineral County. East side of Stewart Valley road, adjacent to road, 11.5 miles north from junction with county road to Mina.

Lithology: Sequence of fore-set beds of calcareous cemented sandstone, vitric ash, tuff, thin beds of pebble conglomerate.

Age: Barstovian. Associated fossil mammals.

B-2052: Center section 15, Range 38 E., Township 8 N., Nye County. West from junction with Nevada State Highway 89, 2.5 miles along county road to Mina, just south of road in low bluff.

Lithology: Moderately well-indurated grey tuffaceous sandstone, well bedded.

Age: Clarendonian.

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FIGURES 1, 5, 9. *Vorticifex stewartensis* Firby, new species, ×2. Holotype *UCMP* no. 37875, locality B-2051.

FIGURES 2, 3, 10. *Pisidium leslieae* Firby, new species, left valve.

FIGURES 3, 10, ×2; FIGURE 2, ×5. Paratype *UCMP* no. 37873, locality B-2051.

FIGURES 6, 7. *Pisidium leslieae* Firby, new species, right valve.

FIGURE 7, ×2; FIGURE 6, ×5. Holotype *UCMP* no. 37872, locality B-2051.

FIGURES 4, 8. *Bulimnea webbi* Firby, new species, ×2. Holotype *UCMP* no. 37880, locality B-8325.

FIGURES 11, 14. *Planorbis webbi* Firby, new species, ×2. Holotype *UCMP* no. 37878, locality B-8333.

FIGURES 12, 15. *Sphaerium stewartensis* Firby, new species, left valve.

FIGURE 15, ×5; FIGURE 12, ×2. Paratype *UCMP* no. 37870, locality B-2051.

FIGURES 17, 18. *Sphaerium stewartensis* Firby, new species, right valve, ×2. Holotype *UCMP* no. 37869, locality B-2051.

FIGURES 13, 16. *Goniobasis reticulata* Firby, new species, ×2. Holotype *UCMP* no. 37882, locality B-2051.

FIGURES 19, 20. *Goniobasis leslieae* Firby, new species, ×2. Holotype *UCMP* no. 37885, locality B-2051.

B-2053: S.W. corner of S.E. ¼ section 33, Range 36 E., Township 9 N., Mineral County. Approximately 300 feet north of Stewart Springs road, 0.3 miles up road from junction with Stewart Valley road. This junction is 9.8 miles north along Stewart Valley road from intersection with county road to Mina.

Lithology: Coarse grained well-indurated tuffaceous sandstone, indistinctly bedded.

Age: Barstovian. Associated fossil mammals.

B-8300: N.E. ¼ section 22, Range 36 E., Township 9 N., Mineral County. In canyon on east side of abandoned mining road between Warrior Mine and Stewart Valley, 5.3 miles west along road from Warrior Mine. Up west fork of canyon approximately ¼ mile, on top of ridge, west side of canyon.

Lithology: Well-indurated fine to medium grained grey to brown sandstone, cemented by $CaCO_3$.

Age: Barstovian.

B-8301: N.W. ¼ of S.E. ¼ section 22, Range 36 E., Township 9 N., Mineral County. Approximately ½ mile up west fork of canyon described above, near top of west wall.

Lithology: Moderately well-indurated, well-bedded tuffaceous sandstone.

Age: Barstovian.

B-8302: N.W. ¼ section 23, Range 36 E., Township 9 N., Mineral County. Approximately 400 yards up canyon described above, in east wall of canyon.

Lithology: Well-bedded diatomite.

Age: Barstovian.

B-8303: N.E. ¼ section 23, Range 36 E., Township 9 N., Mineral County. In east side of canyon described above, just past low diatomite ridge, east wall of canyon.

Lithology: Grey tuffaceous sandstone interbedded with thin beds of vitric ash.

Age: Barstovian.

B-8304: S.E. ¼ section 22, Range 36 E., Township 9 N., Mineral County. West fork of canyon described for *UCMP* locality B-8300. One mile up canyon from road, 50 feet above canyon floor in west wall.

Lithology: Coarse, well-indurated sandstone and conglomerate, cemented by $CaCO_3$.

Age: Barstovian.

B-8305: Center section 22, Range 36 E., Township 9 N., Mineral County. West fork of canyon described for *UCMP* locality B-8300, ¾ mile up canyon, top of ridge west side of canyon.

Lithology: Thin beds of well-indurated limestone capping tuffaceous sandstone.

Age: Barstovian.

B-8306: N.E. ¼ section 29, Range 36 E., Township 9 N., Mineral County. In basal portion of high cliff on north side of canyon, 11.2 miles from junction of Stewart Valley road with county road to Mina and 0.3 miles south of *UCMP* locality B-2051.

Lithology: Sequence of fine grained, poorly bedded tuffaceous sandstone, tuff, conglomerate, massive grey limestone, diatomite, and well-bedded "paper shale."

Age: Barstovian.

B-8307: N.E. ¼ section 11, Range 38 E., Township 8 N., Nye County. East of Nevada State Highway 89, 1.6 miles north along road from junction with county road to Mina and 5.2 miles along road from *UCMP* locality B-2052.

Lithology: Well-bedded, moderately well-indurated tuffaceous sandstone cemented by $CaCO_3$.

Age: Clarendonian. Associated fossil mammals.

B-8308: N.E. ¼ section 9, Range 38 E., Township 8 N., Nye County. Top of small butte approximately 1.5 miles W.S.W. of *UCMP* locality B-8307.

Lithology: Resistant dark grey massive limestone.

Age: Clarendonian?

B-8309: N.W. ¼ section 15, Range 38 E., Township 8 N., Nye County. In south side of cut-bank, approximately ½ mile N. 50° W. from *UCMP* locality B-2052.

Lithology: Fine grained grey tuffaceous sandstone, 30 feet thick, cemented by $CaCO_3$.

Age: Clarendonian.

B-8310: S.E. ¼ of N.E. ¼ section 15, Range 38 E., Township 8 N., Nye County. In south side of cut-bank, approximately ¼ mile downstream from *UCMP* locality B-8309.

Lithology: Grey, poorly bedded tuffaceous sandstone, weakly cemented by $CaCO_3$.

Age: Clarendonian.

B-8311: S.W. ¼ of S.W. ¼ section 15, Range 38 E., Township 8 N., Nye County. West 2.8 miles along county road to Mina from junction with Nevada State Highway 89. At base of low hill 1,800 feet south of road.

Lithology: Small lenticular body of diatomite.

Age: Clarendonian.

B-8312: S.E. ¼ of S.W. ¼ section 15, Range 38 E., Township 8 N., Nye County. Locality essentially the same as for *UCMP* locality B-8311, but on east flank of same low hill.

Lithology: Well-bedded impure diatomite.

Age: Clarendonian.

B-8313: N.W. ¼ section 21, Range 38 E., Township 8 N., Nye County. Top of butte on north side of county road to Mina, approximately 4 miles west along road from junction with Nevada State Highway 89.

Lithology: Massive grey limestone.

Age: Clarendonian.

B-8314: Center N.W. ¼ section 21, Range 38 E., Township 8 N., Nye County. Approximately 4 miles west along county road to Mina from junction with Nevada State Highway 89. At head of gully approximately 1,000 feet south of road.

Lithology: Medium to coarse grained moderately well-bedded tuffaceous sandstone.

Age: Clarendonian?

B-8315: Center section 21, Range 38 E., Township 8 N., Nye County. In south bank of small wash ½ mile S.E. of *UCMP* locality B-8314.

Lithology: Coarse grained, poorly sorted tuffaceous sandstone.

Age: Clarendonian.

B-8316: N.E. ¼ section 21, Range 38 E., Township 8 N., Nye County. In cut-bank on north side of east-west trending wash, ¾ mile S. 32° E. from *UCMP* locality B-8314.

Lithology: Sandy limestone, containing numerous sub-angular pebbles less than ½ inch in diameter.

Age: Clarendonian.

B-8317: S.E. ¼ of N.W. ¼ section 29, Range 36 E., Township 9 N., Mineral County. In canyon west of Stewart Valley road, ¼ mile S.W. of *UCMP* locality B-2051.

Lithology: Fine grained tuffaceous sandstone with small lenticular bodies of limestone.

Age: Barstovian. Associated fossil mammals.

B-8318: N.E. ¼ section 4, Range 36 E., Township 8 N., Mineral County. Approximately 200 yards south of Stewart Springs road described for *UCMP* locality B-2053.

Lithology: Grey to brown fine grained sandstone, well-bedded, cemented by $CaCO_3$.

Age: Barstovian.

B-8319: S.E. corner of N.W. ¼ section 15, Range 38 E., Township 8 N., Nye

County. West 2.5 miles along county road to Mina from junction with Nevada State Highway 89. Approximately 300 feet north of road.

Lithology: Grey, well-bedded tuffaceous sandstone, cemented by $CaCO_3$. Sandstone contains numerous concretions.

Age: Clarendonian.

B-8320: N.E. corner of N.W. ¼ section 14, Range 38 E., Township 8 N., Nye County. Approximately 100 yards west of junction of county road to Mina and Nevada State Highway 89, in west flank of low hill near road.

Lithology: Medium to coarse grained well-indurated tuffaceous sandstone, moderately well bedded.

Age: Clarendonian.

B-8321: S.W. ¼ section 11, Range 38 E., Township 8 N., Nye County. Approximately 2 miles along county road to Mina from junction with Nevada State Highway 89, north of road.

Lithology: Well-bedded, moderately well-indurated tuffaceous sandstone cemented by $CaCO_3$.

Age: Clarendonian.

B-8322: N.E. ¼ of N.W. ¼ section 28, Range 38 E., Township 8 N., Nye County. Approximately 2 miles south of county road to Mina and 1 mile north of abandoned road known locally as "South Road," on south side of east-west trending canyon.

Lithology: Well-bedded diatomite, 20 feet thick, overlying grey sandy limestone.

Age: Clarendonian.

B-8323: S.W. ¼ section 21, Range 38 E., Township 8 N., Nye County. In same canyon as *UCMP* locality B-8322, but ½ mile south.

Lithology: Poorly sorted, indistinctly bedded tuffaceous sandstone, cemented by $CaCO_3$, moderately well-indurated.

Age: Clarendonian? Associated fossil mammals.

B-8324: N.W. ¼ section 29, Range 36 E., Township 9 N., Mineral County. West side of Stewart Valley road, 11.2 miles from junction with county road to Mina. Approximately ½ mile west up canyon, near top of low ridge, north side of canyon.

Lithology: Coarse grained, poorly sorted grey sandstone cemented by $CaCO_3$, above a brown unconsolidated silt.

Age: Barstovian. Associated fossil mammals.

B-8325: N.W. ¼ section 29, Range 36 E., Township 9 N., Mineral County. Same geographic location as *UCMP* locality B-8324, but 20 feet higher in the section.

Lithology: Brown, moderately well-sorted medium grained tuffaceous sandstone.

Age: Barstovian.

B-8326: S.W. ¼ section 29, Range 36 E., Township 8 N., Mineral County. South side of canyon to west of Stewart Valley road, 11.2 miles north along road from junction with county road to Mina. In base of small butte ½ mile up canyon.

Lithology: Brown, medium grained tuffaceous sandstone, cemented by $CaCO_3$.

Age: Barstovian. Associated fossil mammals.

B-8327: S.E. ¼ of N.W. ¼ section 32, Range 38 E., Township 8 N., Nye County. Immediately south of "South Road," 3.5 miles west along road from junction with a ½ mile long road connecting "South Road" with county road to Mina.

Lithology: Coarse grained grey tuffaceous sandstone, cemented by $CaCO_3$, interbedded with diatomite.

Age: Barstovian.

B-8328: S.W. ¼ section 29, Range 38 E., Township 8 N., Nye County. On a bearing of N. 25° W., 4,920 feet from *UCMP* locality B-8326 towards point of a high, isolated, lava capped butte.

Lithology: Well-indurated, moderately well-bedded grey, sandy limestone.

Age: Barstovian.

B-8329: S.W. ¼ section 29, Range 38 E., Township 8 N., Nye County. On a bearing of N. 25° W., 5,250 feet from *UCMP* locality B-8326 towards point of same lava capped butte as above.

Lithology: Well-indurated, well-bedded, grey sandy limestone.

Age: Barstovian. Associated fossil mammals.

B-8330: S.W. ¼ of N.W. ¼ section 29, Range 38 E., Township 8 N., Nye County. On a bearing of N. 20° W., 8,200 feet from *UCMP* locality B-8326. Stratigraphically and unconformably above a fine grained brown siltstone.

Lithology: Grey, medium to fine grained tuffaceous sandstone, cemented by $CaCO_3$.

Age: Clarendonian.

B-8331: Center of boundary between sections 28 and 29, Range 38 E., Township 8 N., Nye County. South of "South Road" 200 feet, 2½ miles west along "South Road" from junction with road connecting with county road to Mina.

Lithology: Grey, medium to fine grained tuffaceous sandstone, cemented by $CaCO_3$.

Age: Clarendonian.

B-8332: Center section 29, Range 38 E., Township 8 N., Nye County. One-half mile north of "South Road," 3 miles west along road from junction with short road connecting with county road to Mina.

Lithology: Moderately well-bedded grey sandy limestone.

Age: Clarendonian. Associated fossil mammals.

B-8333: S.W. ¼ of N.W. ¼ section 22, Range 38 E., Township 8 N., Nye County. Approximately ½ mile north of "South Road," slightly west of north from *UCMP* locality B-8331. Stratigraphically the same as *UCMP* locality B-8332.

Lithology: Medium to fine grained, grey tuffaceous sandstone interbedded with lighter grey sandy limestone.

Age: Clarendonian. Associated fossil mammals.

B-8334: S.E. ¼ of N.E. ¼ section 21, Range 36 E., Township 8 N., Mineral County. In low bluff on east side of Stewart Valley road, 3.1 miles south of intersection of Stewart Valley road with road to Stewart Springs.

Lithology: Grey, well-bedded limestone and fine grained tuffaceous sandstones.

Age: Barstovian.

B-8335: S.E. ¼ of N.E. ¼ section 4, Range 36 E., Township 8 N., Mineral County. In north-south trending wash, ¼ mile south from road to Stewart Springs and approximately ¼ mile east of Stewart Valley road.

Lithology: Extremely well-bedded, well-indurated, grey tuffaceous sandstone, cemented by $CaCO_3$.

Age: Barstovian.

B-8336: N.E. ¼ of S.E. ¼ section 9, Range 36 E., Township 8 N., Mineral County. In east bank of canyon, approximately 200 yards east of Stewart Valley road. Canyon is 1.4 miles south of intersection of Stewart Valley road with Stewart Springs road.

Lithology: Extremely well-bedded green to grey "paper shale."

Age: Barstovian.

B-8337: N.W. ¼ section 4, Range 36 E., Township 8 N., Mineral County. South bank of canyon west of Stewart Valley road approximately ¼ mile, due west of *UCMP* locality B-8318.

Lithology: Grey, poorly bedded fine grained tuffaceous sandstone, weakly cemented by $CaCO_3$.

Age: Barstovian. Associated fossil mammals.

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 15, pp. 481–498; 14 figs. July 8, 1966

THE *PEDALIS*-GROUP OF *HYGROTUS*, WITH DESCRIPTIONS OF TWO NEW SPECIES AND A KEY TO THE SPECIES (COLEOPTERA: DYTISCIDAE)

By

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In 1901 Fall described a medium-sized species of *Hygrotus* from the coast of California, *H. pedalis,* in which the middle tibiae of the male are produced inwardly at the tip (fig. 10). In 1928 Darlington added *H. thermarum* from material taken by C. T. Brues at hot springs in central and western northern Nevada; the front femora, and middle tibiae and femora of the male, are strikingly modified (figs. 1, 14). In 1938 Leech described *H. curvipes* from near the mouth of the San Joaquin River in the San Francisco Bay region of California; the middle tibiae (fig. 9) and the femora of both front and middle legs of the males are modified.

A new species closely resembling *H. thermarum* (Darlington), but from hot springs in northeastern Mono County, California, is described in the following pages. Since even the Nevada records for *H. thermarum* are some 500 miles west of the Rocky Mountains, it is of particular interest to report on a new species from a stream in northeastern Wyoming, about 175 miles east of the Continental Divide at that point. It is the largest of the group, has the front (figs. 5, 6) and middle femora of the male modified and has dual elytral punctation, a character not found in the others.

The above species I propose to call the *H. pedalis* group. Currently it may be defined as containing those species of *Hygrotus* in which the male genitalia has the apical part of the aedeagus very thin in profile, ligulate, with the tip blunt instead of pointed (compare figs. 2A and 3A). Males differ from all other described Nearctic species but one in the curiously formed front and middle femora and tibiae. The male of *H. femoratus* (Fall) has peculiarly shaped legs (figs. 7, 11), but does not belong to this group; it is discussed later.

Hygrotus diversipes Leech, new species.

A species allied to *H. pedalis* (Fall), *H. thermarum* (Darlington), *H. fontinalis,* new species, and *H. curvipes* (Leech) by the secondary sex characters of the legs of the male, and by the male genitalia; of the size and general aspect of *H. nubilus* (Le Conte).

HOLOTYPE, male, WYOMING, NATRONA COUNTY. DUGOUT CREEK, 8.5 MILES NORTHWEST OF MIDWEST, 27.VII.1964 (H. B. Leech). Deposited in the California Academy of Sciences, Entomology.

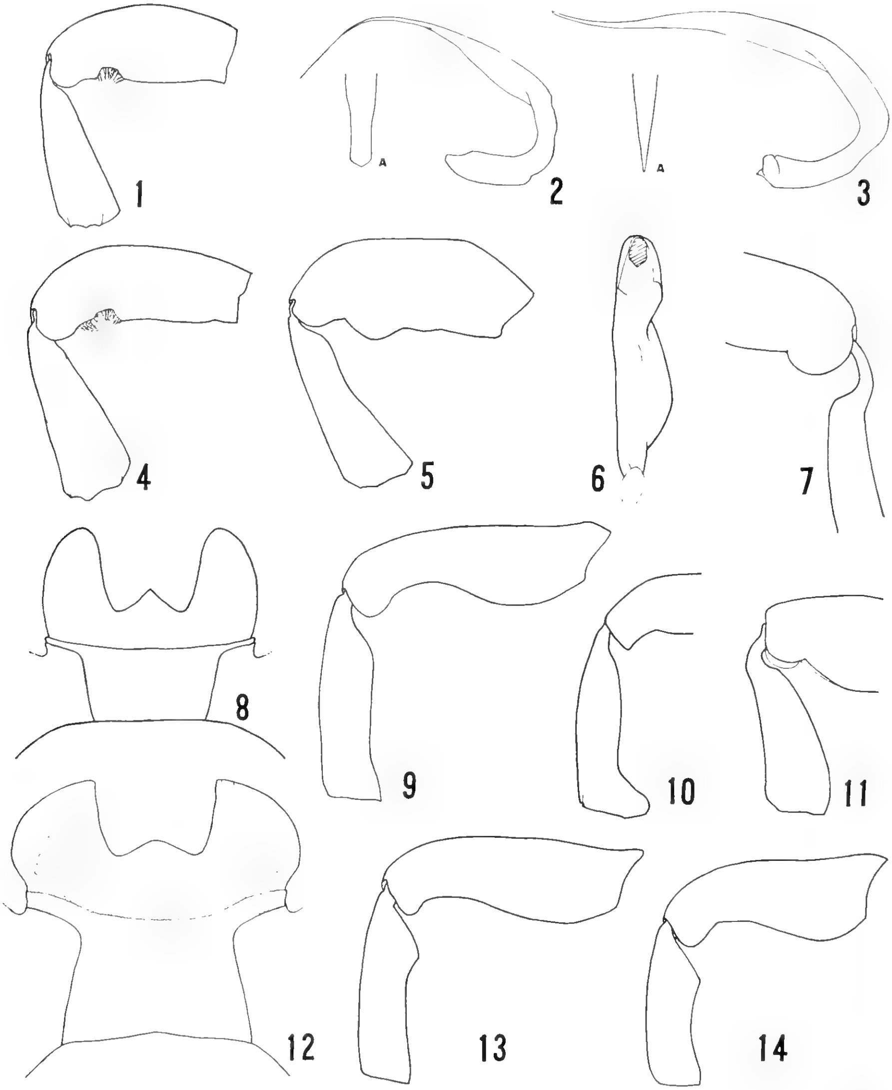
Length 4.46 mm., width 2.1 mm. Form ovate, strongly elongate. *Color*: head rufo-testaceous, with an elongate piceous area paralleling and slightly separated from inner margin of eye, as long as and half as wide as an eye; apical palpal segment piceous except at bases; first four antennal segments pale testaceous, next four progressively darker, last three piceous. Pronotum pale rufo-testaceous, palest laterally, with a narrow longitudinal piceous mark extending from just before middle of disk to basal three-fourths. Elytra pale yellowish testaceous except as follows: each elytron with an oblique elongate semitransparent area just before base, from near suture to near humerus; suture narrowly piceous; a small elongate fuscous sublateral spot at basal quarter; and a large fuscous mark extending from basal third to apical sixth, one-third longer than broad, well separated from suture, tridentate anteriorly, broad and a little emarginate posteriorly, bulging on its outer side at middle, and with a tiny pale inclusion behind middle. Epipleura and legs yellowish testaceous, pro- and mesofemora infuscate apically. Metasternum, hind coxal plates, and abdomen rufo-piceous to black.

Head shining, finely punctate, punctures separated by a little more than their own diameters, except in a transverse area just before an imaginary line joining hind margins of eyes, where they are coarser, closer set, and in short series. Clypeus not margined. *Pronotum* shining, punctation about as on much of head, sparsest on a slightly inflated area near each side of front part of discal piceous mark; with a shallow, narrow longitudinal impression in front half of discal piceous mark. Pronotum wider at base than at apex (8 : 5.5), sides straight to near front angles, gradually converging; hind angles slightly obtuse; lateral marginal bead narrow, about as wide as a facet of eye. *Elytra* shining, basal half finely, densely punctate, punctures separated by about their own diameters; subsutural, discal, humeral, and sublateral longitudinal series of coarse punctures apparent, the punctures two to three times as large as fine ones between series; in addition, there are irregularly scattered coarse punctures among fine ones on interspaces in basal half of elytra, but in apical half almost all punctures are large. Epipleura finely, densely punctate.

Metasternum coarsely punctate laterally, many of punctures behind mesocoxae confluent and longitudinally serial; posterior half of midmetasternum shining, impunctate, bordered by a linear area of fine punctures, and lateral to this with another impunctate area. Metacoxal plates coarsely, closely punctate except near posterior margin where surface is merely finely reticulose. Metacoxal lines together lyriform, intralineal area with line of coarse punctures at each side, rest with greatly elongated small punctures; median line impressed. First abdominal sternum as coarsely punctate as are metacoxal plates; second sternum nearly as coarsely punctate laterally, sparsely and more finely toward median line; following sterna progressively more finely punctate, four and five each with a few long golden hairs arising from a puncture on median line near middle. Prosternal process broadest at middle, margined, tectiform along median line, apex pointed.

Protrochanter with line of golden hairs along ventral edge. Profemur broad, inflated at middle on anterior face, ventral side coming to an edge, sinuate in outer third, edge outcurved at apical third, then broadly, shallowly notched before apex (figs. 5, 6), a few short golden hairs in emargination; posterior face with lower third opaque, crescentically emarginate for reception of tibia; lateral wing of apical groove in which tibia articulates, very large. Protibia as an oblique-topped elongate triangle, apical angles rounded, inner margin slightly sinuate (fig. 5), posterior face smooth, inflated, lower margin except near base with a compact linear brush of golden hairs. Protarsi narrow, as wide as first segment of metatarsus; claws simple, anterior one a little shorter, broader, and more strongly curved at base than its fellow. Mesotrochanter as in protrochanter. *Mesofemur* broad, flat, widest at basal two-sevenths, where it is a little more than twice as wide as an epipleuron near base, lower edge slightly sinuate; lower side flat, as wide as an epipleuron, posterior edge with thin fringe of golden hairs; posterior lateral wing of apical groove large. Mesotibia simple. *Metatrochanter* almost one and one-half times as long as broad, not bearded, apex bluntly pointed. Metafemur strongly narrowed at base, anterior margin broadly concave in basal third, anterior (lower) face inflated medially, lightly impressed on anterior half at apical three-fourths, sides nearly parallel in median two-thirds; surface shining, with series of short oblique impressions in basal two-thirds; thence finely reticulose; an inconspicuous longitudinal median line of setose punctures present. Metatibia gradually widening from base to apex, arcuate, with concavity outward; outer face near apex of anterior margin with a few punctures, each with a small spine. *Male genitalia*: aedeagus curved, strongly dorsoventrally flattened and exceedingly thin in apical three-elevenths, ligulate; apex blunt, subangulate (figs. 2, 2A).

Allotype, female, same data as for holotype; in California Academy of Sciences, Entomology. Length 4.2 mm., width 2.1 mm. Almost exactly like



FIGURES 1–14. Structures of males of *Hygrotus* species. Fig. 1. Front femur and tibia of *H. thermarum.* Fig. 2. Profile of aedeagus of *H. diversipes*; 2A, ventral view of apical portion. Fig. 3. Same as 2, for *H. nubilus.* Fig. 4. Front femur and tibia of *H. fontinalis.* Fig. 5. Same, *H. diversipes.* Fig. 6. Ventral view of front femur of *H. diversipes*, apex and fossa for tibial insertion at top. Fig. 7. Apex of femur and base of tibia of hind leg of *H. femoratus.* Fig. 8. Mentum and submentum of *H. curvipes.* Fig. 9. Middle femur and tibia of *H. curvipes.* Fig. 10. Same, *H. pedalis.* Fig. 11. Front tibia and femur of *H. femoratus.* Fig. 12. Mentum and submentum of *H. pedalis*; the stippled area is semicircularly impressed just anterior to the transverse curved sutures. Fig. 13. Middle femur and tibia of *H. fontinalis.* Fig. 14. Same, *H. thermarum.*

the male, except for sex characters; head and prothorax slightly darker than in type; elytra with rufous tinge adjacent to suture; large elytral infuscation bidentate anteriorly, the outer of the two projections larger, extending forward to level of small sublateral spot. Profemur with slight projection on lower anterior face at apical third, and small notch between that and apex; mesotibia broad, flat, lower margin distinctly sinuate. Metatibia less strongly arcuate than in male.

Paratypes, eight males, ten females, all with the same data as the type. Paratypes will be placed in the following collections: United States National Museum, Canadian National Collection, F. N. Young, R. D. Anderson.

Variation. One paratype male is 4.6 mm. long, four are of the same length as the type, two are 4.2 mm. and 4.3 mm., respectively, and one is only 3.75 mm. The paratype females vary in length from 4.0 to 4.25 mm., most of them being near the upper limit. There is an appreciable variation in elytral coloration, but because all specimens in the type series are teneral it is hard to assess. In both the holotype and allotype there is a semitransparent area on each elytron near the base, but this is not a taxonomically significant character, even though some paratypes show it. Other paratypes have extensive and irregular semitransparent areas, or none at all; one has the right elytron semitransparent except narrowly near the suture, and the left elytron more yellowish testaceous (the usual fuscous markings are present on both). One specimen with semitransparent elytra was soaked in ether for a few moments, and then dried; parts of the elytra became yellowish testaceous again for a time, but later faded out. The facts that all specimens are teneral, and that they were placed in 70 per cent alcohol immediately upon being collected, may have something to do with this coloration.

There is considerable variation in the curvature (as in the holotype) or straightness (as in the allotype) of the metacoxal lines in the anterior two-thirds of their course, but the variation is not sex-linked.

One paratype female has a teratological right antenna. It has eight instead of 11 segments; segments 1 to 7 and 11 appear to be normal, but 8 to 10 have fused to form an elongate, somewhat irregular segment about as long as 8 and 9 together would normally be.

Remarks. *Hygrotus diversipes* is clearly to be associated with *H. pedalis, H. thermarum, H. fontinalis,* new species, and *H. curvipes* by the peculiarly formed femora and tibiae of the males. In addition, each of these species has the aedeagus of the male ligulate, recurved, and blunt apically, while all other Nearctic species known to me have the aedeagus ligulate or acicular, but always sharply pointed in dorsal or ventral view (compare figs. 2A, 3A). However, *H. diversipes* will not trace readily to couplet 8 of Fall's key, where *H. pedalis* is placed. It goes easily to division 5 but not through it to 7 and 8, because the elytral punctation is obviously dual; neither does it fit the first choice in division 5, because the elytra have well-defined markings. With males at hand the crural characters will place it (figs. 5, 6); females may be associated by the dual punctation of the midelytral disk, the elytral markings, the finely and densely punctate epipleura, and the slight bump and associated small emargination near the outer end of the lower front margin of the profemora.

Two species resembling *H. diversipes* in facies occur in the same stream with it, *H. nubilus* (Le Conte) and *H. patruelis* (Le Conte). *Hygrotus nubilus* is well epitomized by Fall (1919, p. 15): "The elongate form, rather large size [4.0 to 4.4 mm.], evenly rather finely punctate elytra, and pale head, form a combination of characters which separate this species from all other except *femoratus*, . . ."; in using division 3 of Fall's key (*loc. cit.*, p. 2) one must guard against tracing specimens to the third choice, rather than to the second as necessary, since many examples have the elytral markings decidedly vittiform. *Hygrotus patruelis* is a little smaller, 3.5 to 4.0 mm. long; the head is infuscated on each side near the eyes, and as in *H. nubilus* the protarsi of the male are much wider than those of the female and have the anterior claw thickened and abruptly bent.

Males of *H. diversipes* may be separated from those of both of Le Conte's species by their modified front femora (figs. 5, 6), narrow protarsi, and simple anterior claw. Females of *H. diversipes* may be recognized by their dual elytral punctation, the basic fine punctation of which is much smaller than that of *H. nubilus* or *H. patruelis*. The shallow preapical profemoral notch and the broad flat mesotibiae with lower (inner) margin slightly but distinctly sinuate, are also diagnostic.

The type locality of *H. diversipes* is Dugout Creek, Natrona County, Wyoming. This stream is a tributary of Salt Creek, *i.e.*, of the Missouri River drainage system. In late July, 1964, the stream at Highway 87 was a series of disconnected pools in a clay and gravel bed. The water was mineralized enough to have left a white deposit on the shores and stones as it evaporated, but contained young fish, apparently those of the flathead chub, *Platygobio gracilis* (Richardson) (determination by W. I. Follett).

Hygrotus pedalis (Fall).

Cœlambus pedalis FALL, 1901. Calif. Acad. Sci., Occ. Papers, no. 8, p. 212.
Coelambus pedalis Fall, FALL, 1919. N. Amer. spp. *Coelambus*, pp. 3 (key), 13–14.
Cœlambus pedalis Fall, LEECH, 1938. Pan-Pacific Ent., vol. 14, no. 2, p. 86.
Cœlambus curvipes LEECH, 1938 (*partim*). Pan-Pacific Ent., vol. 14, no. 2, pp. 85, 86.
Hygrotus pedalis (Fall), LEECH, 1956. *In*: Aquatic Ins. Calif., p. 316.

Hygrotus pedalis is more broadly ovate than other species in the group, notably obtusely rounded anteriorly because of the large head; it is also the darkest in color. Females may be separated from those of other species of the genus in coastal California by a combination of features. The elytra are finely, very densely punctate except for the usual longitudinal series of coarser punctures; the head is dark basally, without a pale spot at the middle (teneral specimens are not typical); the epipleura are finely, densely punctate over the whole area except in front of the basal carina; the mesofemora are darkest in the basal two-thirds.

Females of *H. pedalis* and *H. curvipes* are structually very similar, and upon collecting a pure culture of the former in 1954, I realized that the "form C" of the female in my description of *H. curvipes* was in fact that of *H. pedalis.* Females of *H. pedalis* may be distinguished by the darker head, and by the mesofemora being darkest in the basal two-thirds; in *H. curvipes* the femora are darkest in the apical quarter. See also the following comments.

There are two other characters in *H. pedalis,* one especially striking in the male, which have not been noted before. The surface of the mentum, instead of being shiny like the surrounding areas is in all other species of *Hygrotus* which I have examined, is here differentiated, very finely granular and yellowish white in color, giving a peculiar "cheesy" appearance. In the male almost the entire mentum is semicircularly impressed, the curved posterior margin of this impression encroaching upon the usual straight transverse suture separating it from the submentum (compare figs. 8, 12). The lateral lobes of the mentum are very broadly rounded anteriorly; the outer anterior part and a small median area just behind the labial palpi have the surface shining, not granular. In the female the mentum is smaller, not semicircularly impressed, the lateral lobes are not so expanded, and the differentiated area is small and harder to see. Nevertheless, once the feature is recognized, it is of great help in identification.

The hind coxal plate of *H. pedalis* is more coarsely punctate than in other species of the group; the area between the punctures are mostly convex, giving a subrugose appearance. Starting at each outer margin beside the epipleura and extending halfway across the plate toward the middle coxa there is an impression; the punctures in it are smaller and confluent. This oblique narrow impression will separate both sexes of *H. pedalis* from any other species of the genus within its distribution.

Fall recorded *H. pedalis* from Pomona (type), Riverside, Naples, and San Diego in southern California, and Vine Hill, Contra Costa County, in the San Francisco Bay region. A male from Riverside, dated 5.6.90 and from the type series, was given to me by Mr. Fall in 1937 and is before me. I have seen examples from the following additional localities: Poway, San Diego County (F. E. Blaisdell); Pasadena, Los Angeles County, April and May (A. Fenyes); Sunol, Alameda County, September 14, 1919 (J. O. Martin); Oakley, Contra Costa County, September 5, 1936 (H. B. Leech; female form "C" of *H. curvipes* paratypes), and August 21, 1938 (E. C. Van Dyke); Danville, Contra Costa County, June–July, 1951 (F. X. Williams); Martinez, Contra

Costa County, September 17, 1962 (R. Brown); also from the following eight localities all in Marin County: Smith Lake, Manor, November 21, 1955 (H. B. Leech); Novato Creek, 2 miles south of Novato, February 21, 1954 (H. B. Leech); Olema, August 14, 1946 (H. P. Chandler); Marshall, October 20, 1963 (H. B. Leech); Tamales [sic!], Bay near Marshalls, September 11, 1938 (E. C. Van Dyke); Stemple Creek, 1.5 miles north of Tomales, September 28, 1964 (H. B. Leech); Dillon Beach, June 24 and October 19, 1963 (H. B. Leech); Inverness, July 21, 1963 (P. H. Arnaud, Jr.), in small freshwater pond with extensive algal mats.

The Oakley specimens were from a cattle-fouled pool in which *Typha* sp. grew; those from Stemple Creek in a cattle-fouled pool in the dry stream bed. Novato Creek is affected by the tides and was brackish in the part sampled; the Dillon Beach specimens were taken from pools near the foot of the large Sand Point dunes and only a few above sea level. The single example from Marshall was in a pool in a flowing stream, just above the tidal effect.

Hygrotus curvipes (Leech).

Cœlambus curvipes LEECH, 1938. Pan-Pacific Ent., vol. 14, no. 2, pp. 84–86.
Cœlambus pedalis Fall, LEECH, 1938 (*partim*). *Loc. cit.*, p. 86.
Hygrotus curvipes (Leech), LEECH, 1956. *In*: Aquatic Ins. Calif., p. 316.

As explained under *H. pedalis,* the type series of *H. curvipes* actually contained several females of the very similar *H. pedalis.* The middle femur and tibia of a male of *H. curvipes* are shown in figure 9.

To the best of my knowledge *H. curvipes* has been taken only at the type locality, a shallow, muddy pool at Oakley, Contra Costa County, California. I collected the original series on September 5, 1936; Dr. E. C. Van Dyke went to the pond on August 21, 1938, and obtained males and females of both *H. curvipes* and *H. pedalis.* The diagnostic characters are given under the latter species.

Hygrotus thermarum (Darlington).

Coelambus thermarum DARLINGTON, 1928. Psyche, vol. 35, no. 1, pp. 1–3.
Coelambus thermarum Darlington, BRUES, 1928. Proc. Amer. Acad. Arts & Sci., vol. 63, no. 4, p. 170. BRUES, 1932. *Loc. cit.*, vol. 67, no. 7, p. 259.
Cœlambus thermarum Darlington, LEECH, 1938. Pan-Pacific Ent., vol. 14, no. 2, p. 86.

Hygrotus thermarum should have been included in my 1956 key to the California species, but I overlooked Brues's 1932 record for a specimen from the outflow of a hot spring 5 miles east of Cedarville, Modoc County, in the northeastern corner of California. Thanks to the kindness of Dr. P. J. Darlington, Jr., of the Museum of Comparative Zoology, I have seen the beetle; it belongs indeed to *H. thermarum* (as would be expected on distributional grounds), and is a female. The mesotibia of a male is shown in figure 14.

In his 1932 paper (p. 259) Brues lists the temperature, specific gravity, and pH of the water in which he took this species.

Spring number and location	Temperature	Specific gravity	pH
20. Twenty-nine miles south of Winnemucca, Nevada	38.0° C.	1.0014	8.6
23a. About 36.5 miles south of Battle Mountain, Nevada	30.0°	1.0021	8.6
103. Forty-five miles northeast of Austin, at Cortez, Nevada	44.5°	1.0041	8.5
113. Soldier Meadows, Nevada, about 35 miles north of Gerlach	19.2°	1.0007	8.8
120b. Five miles east of Cedarville, California	28.4°	1.0034	8.2

It is clear that water temperature is not a deciding factor in the beetles' occurrence, although the 44.5° figure is remarkably high for a carnivorous species, a point made by Tuxen (1944). Indeed, Brues found only two species of water beetles surviving in water above 45°, and none above 46°. Of more significance so far as *H. thermarum* is concerned would be a knowledge of the water temperature at which the immature stages develop successfully. The pH figures are near the optimum for species occurring in hot springs. Of Harney Lake Hot Springs, Oregon, Malkin (1959, p. 34) reports three species of water beetles ". . . swimming cheerfully along the shore of the hot springs in the temperature as high as 52.2° Centigrade."

Specimens have been seen from the following Oregon localities: Twelve miles south of Blue Mt. Pass, Malheur County, July 20, 1956 (Hugh B. Leech; flying specimens attracted to the light of a "Coleman" lantern); hot spring 4 miles north of Fields, Harney County, July 16, 1957 (Ken Goeden); Hot Lake, 5 miles north of Fields, Harney County, July 17, 1959 (J. D. Lattin).

Also before me are two females from a freshwater pool on the southeast shore of Lake Abert, Lake County, Oregon, July 17, 1950 (H. B. Leech). In Hatch's key to the species of the Pacific Northwest (1953, pp. 198–202) they run to *H. bonnelli* Hatch, 1951, and agree well with the original description. It would be desirable to verify that they belong to *H. thermarum* by the collection of males. Hatch based *H. bonnelli* on a pair from alkaline Lake Abert, but did not mention any percularities in the legs of the male; however, it may be noted that both sexes of *H. thermarum* run to *H. bonnelli* in his key.

A male from a spring at Deep Springs, Inyo County, California, August 19, 1963 (H. B. Leech) extends the known distribution southward by some 180 airline miles from the nearest Nevada locality, and is about 90 miles south of the type locality for *H. fontinalis.* The 180 miles does not seem impressive until one considers the possibilities for these beetles of finding suitable habitats in a desert area where sources of water of any sort are small, and widely and irregularly scattered. There must be colonies in the intervening area.

Hygrotus fontinalis Leech, new species.

A species closely resembling *H. thermarum,* differing chiefly in the structure of the legs. Known from north central Mono County, California.

Holotype, male, CALIFORNIA, MONO COUNTY. TRAVERTINE HOT SPRINGS, 2 MILES SE. OF BRIDGEPORT, ALTITUDE 6,700 feet, 11.VIII.1962 (H. B. Leech). Deposited in the California Academy of Sciences, Entomology.

Length 3.85 mm., width 1.95 mm. *Form* ovate, elongate. *Color:* Head black, dark rufo-piceous near front margin, paler above antennal insertions, with a small reddish yellow spot on vertex; labrum and palpi reddish yellow, the former infuscate at middle, the latter apically; first four antennal segments pale testaceous, remainder progressively darker to piceous. Pronotum piceous, vaguely paler laterally. Elytra pale yellowish brown, slightly more than basal fifth of discal area semitransparent, suture narrowly piceous; each elytron with an irregular, elongate infuscate cloud from basal fifth to apical sixth, the cloud bidentate anteriorly, its median lateral projection nearly disconnected; a faint sublateral infuscate mark shows at basal fifth; lateral margin along an area opposite first to about middle of sixth abdominal sterna, narrowly piceous. Epipleura dull yellowish brown from base to opposite first abdominal sternite, then piceous to apex (*i.e.,* adjacent to about middle of sixth sternum and opposite the internal elytral ligula). Prolegs rufo-piceous, femora dark, tibiae paler, especially at base; mesofemora black, mesotibiae rufo-piceous, tarsi infuscate.

Head shining, finely and somewhat unevenly punctate, puncture finer and denser in a depressed area inward from emargination near front of each eye, and in a narrow longitudinal area near inner margin of each eye. Clypeus not margined. Pronotum shining, finely and rather evenly closely punctate except on slightly tumid sparsely punctate part on each side of middle of disk; anteriorly and posteriorly from a point just outward from the tumid areas, punctures are coarser, as are usual transverse series paralleling anterior margins; middle of disk with a short longitudinal impressed mark. Pronotum wider at base than at apex (7 : 4.75), sides weakly arcuate; hind angles obtuse; lateral marginal bead narrow, not as wide as two facets of an eye.

Elytra shining, finely densely punctate, punctures of nearly uniform size and spacing from base to near apex, except for the usual longitudinal series of coarser ones (subsutural, discal, humeral, sublateral), separated by less than their own diameters. Epipleura punctate, a little more sparsely and finely so than elytra. *Prosternal process* narrow, widest near base, weakly margined, median line tectiform, apex pointed, almost acuminate. Protrochanter with an inconspicuous line of hair along ventral edge. *Profemur* with upper side weakly arcuate from base toward apex (fig. 4), lower margin nearly straight, anterior face strongly inflated in middle part, broadly impressed on lower two-thirds before apex, its surface finely reticulose, the impression funneling to a deep notch in anterior lower margin, notch set with short stiff golden setae (fig. 4); there is a small tooth just posterior to it; lower edge of median part of femur flattened, with slight posterior slope, surface finely granular, its posterior edge fringed with long golden hairs. Protibia widest apically, lower anterior corner flattened and turned under; posterior face with longitudinal brush of dense, long golden hairs arising from a sinuate line along middle; trochanter with a thin line of short hairs along ventral edge; tarsus narrow, segments hardly broader than those of female, basal segment broadest, next two progressively narrower; claws simple, of equal length, anterior one very slightly more curved than its fellow. Mesotrochanter with an inconspicuous line of hairs along ventral edge. *Mesofemur* flattened, dorsal margin arcuate, ventral margin strongly arcuately lobed in basal third, narrowest in apical third, outer angles produced downward (fig. 13); ventral side broadened, impressed to receive subbasal projection of mesotibia, surface of broadened area finely granulate; ventral margin between broadened area and trochanter with fringe of long silky hairs. Mesotibia very slightly arcuate, nearly parallel-sided in apical half, ventral side lobately produced on anterior margin at basal two-thirds, thence rapidly narrowed to base (fig. 13); ventral margin broadening from base to apex, somewhat flattened, and with a line of long golden hairs starting behind lobe on anterior edge; anterior face, in lower apical half punctate and with a patch of golden hair; upper edge of posterior face with a line of fine golden hairs. *Metafemur* with anterior margin shallowly concave in basal half, sides nearly parallel in median two-thirds; surface shining, with series of short oblique impressions on median area, finely reticulose in apical quarter; an inconspicuous longitudinal median line of setose punctures present. Metatibia gradually widening from base to middle, thence nearly parallel-sided to apex; arcuate, with concavity outward; outer face near anterior margin with a few punctures, each with a spine. *Metasternum* very finely punctate along each side of median line, impunctate on an area lateral of this, side wings coarsely punctate; median line impressed more deeply posteriorly. Metacoxal plates coarsely punctate except for an area paralleling hind margin, comprising half the width of the coxa internally and narrowing externally, which is impunctate; metacoxal interlineal area three-quarters as wide at narrowest point (before metacoxal lobes) as anteriorly at hind margin of metasternum, punctate, median line impressed; metacoxal lines slightly curved. First two abdominal sterna as coarsely punctate as are metacoxal plates, remaining sterna more densely but much more finely punctate; sterna 4 and 5 each with a few golden hairs arising from a puncture on median line near middle. *Male genitalia*: Aedeagus curved, strongly dorsoventrally flattened and exceedingly thin in apical three-elevenths, ligulate; apex blunt subangulate.

ALLOTYPE, female, data the same as for the holotype; in California Academy of Sciences, Entomology. Length 3.80 mm., width 1.92 mm. Almost exactly like the male except for sex characters; head and pronotum slightly paler, elytral markings a little more extensive.

PARATYPES, 9 males, 16 females, all with the same data as for the holotype. Also 25 males and 54 females, all topotypical but collected on August 15, 1963. Paratypes will be distributed to the United States National Museum, The Canadian National Collection, the British Museum (Nat. Hist.), the Museum of Comparative Zoology, F. N. Young, R. D. Anderson, and M. H. Hatch.

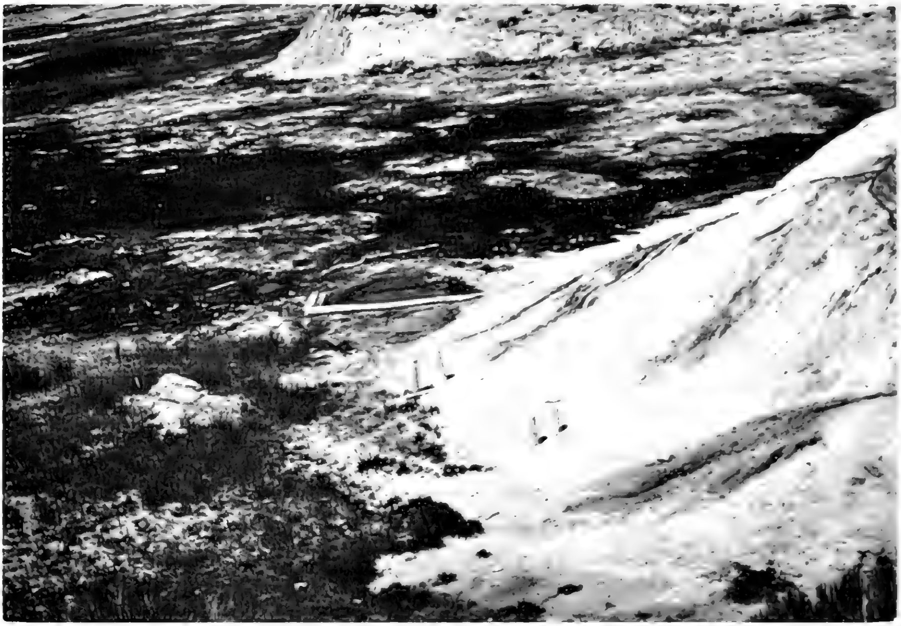
VARIATION. There is very little variation among the specimens. In some, anterior prolongations of the infuscate markings may extend to the basal tenth of the elytra, but are never more reduced than in the holotype; they are usually more extensive in the females than in the males. The smallest female is 3.60 mm. long, the largest 3.90 mm.

REMARKS. *Hygrotus fontinalis* closely resembles *H. thermarum* but may be recognized in both sexes by the longer front and middle legs (figs. 4 and 13 *vs.* 1 and 14), and by the curvature of the upper side of the front femur (fig. 4 *vs.* 1). Males of *H. fontinalis* have the same type of femoral and tibial modifications found in *H. thermarum* and *H. curvipes,* but the profemoral notch is larger, deeper, and more strongly ciliate than in Darlington's species, while the body shape, the bicolored front and middle legs, and differences in habitat and distribution mark *H. curvipes.*

→

PLATE 1. UPPER FIGURE. Detail of the left center foreground of the lower picture, from a different angle. The pool with a small log across it is the type locality for *H. fontinalis* as it was in August, 1963. The species also occurs in the shallow sedge pools just beyond.

LOWER FIGURE. General view of three tufa ridges at Travertine Hot Springs, about 2 miles southeast of Bridgeport, Mono County, California. The tiny hot spring mentioned in the text is in the crack at the top of the white section in the center foreground. Water is channeled to the right to the "bathtub," or to the left to the pool which is the type locality for *Hygrotus fontinalis.* The trees in the background are singleleaf pine (*Pinus monophylla* Torrey) and western juniper (*Juniperus occidentalis* Hooker); altitude 6,700 feet.



Hygrotus fontinalis occurs in the runoff pools from hot springs in a limestone outcrop. The type locality is a most interesting spot on slopes of andesitic lava, with a background of hills covered with the singleleaf pine (*Pinus monophylla* Torrey) and western juniper (*Juniperus occidentalis* Hooker), at an altitude of 6,700 feet. I am indebted to Mrs. Grace Crocker, one of the owners of the land, for permission to collect there.

The prominent ridges of calcareous tufa, or in more colorful language banded onyx marble, have apparently formed as mineral-laden waters flowed out of long fissures, which have narrowed with height as the sides built up. To one familiar with the signs of pocket gophers (*Thomomys* spp.) in the western mountains, it is easy to imagine a giant race at work during the winter, filling their snow tunnels with excavated dirt, the "gopher cores" of summer (see Storer and Usinger's "Sierra Nevada Natural History," fig. 23 on page 329). The low gray ridges are shown in the lower figure of plate 1. A longitudinal vertical fissure can be seen at the top of the middle ridge, while the white section in the foreground is still actively growing by deposit from a tiny hot spring in the crevice.

The above-mentioned photograph was taken in 1963. It is interesting to compare it with one made in the period 1908–1910, and comprising figure A, plate IX, of G. A. Waring's 1915 report on the springs of California. He stated the flow from the little hot spring to be about one gallon a minute. "It deposits lime carbonate on troughs and barrels which have been arranged so that the water can be used in preparing sheep dip. This deposit is said to form at the rate of nearly an inch a month."

Analysis of water from spring from crevice in travertine ridge, Hot Springs near Bridgeport, Mono County, California. Analyst and authority, F. M. Eaton (1910). Constituents are in parts per million.

Temperature	64° C.	(148° F.)
Properties of reaction:		
Primary salinity		48
Secondary salinity		0
Tertiary salinity		0
Primary alkalinity		44
Secondary alkalinity		8
Tertiary alkalinity		6

Constituents	By weight	Reacting values
Sodium (Na)	1,109	48.22
Potassium (K)	35	0.90
Calcium (Ca)	60	3.01
Magnesium (Mg)	19	1.56

Iron (Fe) Aluminium (Al)	1.8	0.06
Sulphate (SO_4)	939	19.55
Chloride (Cl)	214	6.04
Carbonate (CO_3)	844	28.14
Silica (SiO_2)	89	2.96
	3,310.8	------
Carbon dioxide (CO_2)	Present	Present

The site is currently known as "the bathtub," because someone has excavated a neat hole of the size and shape of a bathtub at the southeast corner of the tufa ridge. It shows in the lower photograph, at the right-hand end of the narrow iron-stained water course leading from the little hot spring at the top. At the left foot of the ridge there is a larger natural pool formed by an independent cool spring, but it also receives most of the water from the hot spring when it is not flowing to the bathtub. This pool shows in Waring's photograph (as do the wooden posts in the upper of my two photographs, but in 1910 they supported a long squared timber), and is the actual type locality of *Hygrotus fontinalis*. Normally the water is cool, the bottom muddy and soft with a flocculent deposit, easily roiled, and beetles are common throughout.

When not wanted for the bathtub the water from the hot spring can be returned to its normal course by plugging the narrow cut channel with mud and stone, as shown in the photographs. In 1962 it flowed broadly over the side of the mound to the pool below. On the sodden slope were many dead specimens of *H. fontinalis,* killed by the hot water when they landed in it, attracted no doubt by its glistening wetness as they flew nearby.

Unfortunately, the bathtub holds only one person, so in 1963 some late visitor, also wanting to relieve his arthritic pains by soaking in the hot mineralized water, cut a direct channel from the hot spring to the type-locality pool. It worked—the water was hot and I saw a man in it. In fact it was so hot that all but a few beetles around the edges were killed. Luckily a population continues in adjacent sedge-covered overflows, which show in the upper photograph as dark places among the white carbonate deposits.

At least five species of aquatic beetles have been taken with *H. fontinalis* at the type locality: Dytiscidae, *Bidessus* sp., a form belonging to the *B. affinis* complex; *Hygrotus tumidiventris* (Fall); *Deronectes striatellus* (Le Conte); Limnebiidae, *Ochthebius bruesi* Darlington; Hydrophilidae, *Enochrus* sp.

Travertine Hot Springs is some 10½ miles west of Nevada, and about 175 miles southwest of the nearest reported locality for *H. thermarum*. The latter species I have taken in southeastern Oregon, flying to the light of a

"Coleman" gasoline lantern at some distance from a known hot spring, so *H. fontinalis* can be expected in any suitable springs in the Bridgeport area. On August 15, 1963, I took a female attracted to light at The Hot Springs, a group of springs about a mile and a half south of the type locality, and to my knowledge the species occurs in at least the largest (called Big Hot) warm pool there.

Hygrotus femoratus (Fall).

Cœlambus femoratus Fall, 1901. Calif. Acad. Sci., Occ. Papers, vol. 8, p. 212.
Coelambus femoratus Fall, Fall and Wickham, 1907. Trans. Amer. Ent. Soc., vol. 33, nos. 2 and 3, p. 162. Fall, 1919. N. Amer. spp. Coelambus, p. 4 (in key), 15–16 (description).

By chance described on the same page of Fall's 1901 paper, though widely separated in his 1919 revisional study, *H. femoratus* and *H. pedalis* were the only species known to have the femora and tibiae of the males modified. With the descriptions of *H. thermarum* and *H. curvipes,* and in this paper of two more species, all having peculiarly shaped front and middle legs, it seemed probable that *H. femoratus* also belonged to the *H. pedalis* group. *Hygrotus femoratus* closely resembles *H. nubilus,* and apparently both occurred at Albuquerque, New Mexico (Fall and Cockerell, *loc. cit.*, under *Coelambus nubilus*: ". . . . The Albuquerque insect was, at least in part, *femoratus*.") *Hygrotus diversipes,* new species, also resembles *H. nubilus* and was taken with it in central Wyoming.

Fall described *H. femoratus* from a single male, and in 1919 mentioned that "A second example, taken at the same place is a female and is probably correctly associated; it is slightly larger and noticeably duller than the male." These are the only specimens recorded in over 60 years.

Through the kindness of Drs. P. J. Darlington, Jr. and J. F. Lawrence of the Museum of Comparative Zoology, I have been able to study the type. The femoral apices of all three pairs of legs are distinctive, and unlike those of any other described Nearctic species (figs. 7, 11); Fall calls them laminate, but this is hardly true. The lateral wings of the apical articulation are big (though not larger than in *H. diversipes*), unusually thick, and inflated internally so there is only a narrow, shallow groove for the pedunculate tibial bases to fit into. The middle and hind tibiae are almost parallel-sided after the pedunculation, but the front tibia gradually enlarges toward the apex.

All species grouped in this paper with *H. pedalis* have one feature in common, in addition to the tibial and femoral modifications: the aedeagus of the male is always very thin and blunt apically, ligulate (fig. 2A). In all other Nearctic species of *Hygrotus* known to me the aedeagus is thin or acicular apically but always pointed (fig. 3A). It is thus a great surprise to find that *H. femoratus* belongs to the second group; in fact, the aedeagus is very like that of *H. nubilus* (fig. 3), but more gradually narrowing apically.

It seems probable that this aedeagal character is more significant of relationships than the leg modifications, so I do not include *H. femoratus* in the *H. pedalis* group. In my key it will not fit either choice in the first couplet; the elytral punctures are of almost uniform size and distribution, but the anterior protarsal claw of the male is short, broad, and strongly curved as in *H. nubilus*. In the male all femora have the apical articular flanges large, and the tibiae pedunculate basally (figs. 7, 11).

The following key is an attempt to enable students to place both males and females of species of the *H. pedalis* group. Males are most easily identified by comparison with the drawings of femora and tibiae (figs. 1, 4, 5, 6, 9, 10, 13, 14).

Key to the Species of the *Hygrotus pedalis* Group

1. Elytral punctures (other than the usual longitudinal series of coarser ones) fine, dense, of almost uniform size and distribution from base to apex; anterior protarsal claw of male simple and like posterior claw; profemur of male not as in figures 5, 6; mesotibia obviously modified (figs. 9, 10, 13, 14). Nevada, Oregon, California 2

1′. Elytral disk with intermixed fine, dense, and scattered coarse punctures on the areas between the usual longitudinal series of subsutural, discal, humeral, and sublateral coarse punctures; anterior protarsal claw of male a trifle shorter, broader, and more sharply bent than posterior claw; profemur of male as in figures 5, 6, mesotibia slightly sinuate on lower margin. Wyoming .... *H. diversipes*, n. sp.

2(1). Profemur of male shining, with a funneled impression on anterior face ending in a ciliated notch at apical third of lower edge (figs. 1, 4); ventral half of posterior face of protibia covered with long golden hairs, mesotibia not strongly produced inwardly at apex (figs. 9, 13, 14); mentum shining, its median area not differentiated (fig. 8); head with median pale spot near base; hind coxal plate not impressed at outer edge 3

2′. Profemur of male not notched, but with outer half of anterior face broadly, shallowly impressed, and surface finely granulate; protibia without patch of golden hairs on posterior face; mesotibia of male produced inwardly at apex of lower side (fig. 10); median area of mentum differentiated (extensively in the male, fig. 12), its surface dull, anterior lateral lobes large, very broadly rounded; head normally without pale spot at base; hind coxal plate with an oblique impression starting adjacent to the epipleura. Coast of California, San Diego north to at least Marin County .... *H. pedalis* (Fall)

3(2). Mesotibia of male almost parallel-sided in apical half, then lobately produced on lower (inner) margin and obliquely narrowed to base (figs. 13, 14). Pronotum usually uniformly rufo-piceous to piceous, pale only near lateral margins; pro- and mesofemora uniformly colored. From hot springs in northwestern Nevada, southeastern Oregon, and the northeastern edge of California 4

3′. Mesotibia of male almost parallel-sided in apical two-thirds, thence obliquely narrowed to base on ventral side (fig. 9). Pronotum usually pale with piceous mark in middle of disk; pro- and mesofemora usually strongly bicolored, basal three-fourths testaceous, apical fourth piceous to black. As yet known only from a muddy pool at Oakley, Contra Costa County, in the San Francisco Bay region of California .... *H. curvipes* (Leech)

4(3). Pro- and mesolegs relatively long (figs. 4, 13). Preapical notch on ventral margin of profemur of male large, deep, strongly ciliate (fig. 4); lower half of anterior face of mesotibia of male, from near ventral lobe to apex, with covering of long golden hairs (do not confuse with dense brush on posterior face). Anterior margin of profemur of female weakly arcuate, nearly parallel-sided in median part, as in figure 4. Northeastern Mono County, California .... *H. fontinalis*, n. sp.

4′. Pro- and mesolegs shorter (figs. 1, 14) than in *H. fontinalis*. Preapical notch in profemur of male shallow, more weakly ciliate (fig. 1); mesotibia of male without long golden hairs obscuring surface of anterior face in lower apical half. Anterior margin of profemur of female more strongly arcuate, as in figure 1. Northwestern Nevada, southeastern Oregon, eastern Modoc County and northeastern Inyo County, California .... *H. thermarum* (Darlington)

ACKNOWLEDGMENTS

I am indebted to Dr. P. J. Darlington, Jr., of the Museum of Comparative Zoology, Harvard University, for comparing specimens with the type of his *Coelambus thermarum,* and to him and Dr. J. F. Lawrence for an opportunity to see the type of *H. femoratus* (Fall). Mrs. Grace Crocker of Bridgeport, California, generously allowed me to collect at her Travertine Hot Springs property. Mr. C. W. Chesterman gave information on the thermal springs of the Bridgeport region, and Mr. W. I. Follett of the California Academy of Sciences was so kind as to identify the immature fishes from Dugout Creek.

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 16, pp. 499–534; 8 figs.; 1 table July 8, 1966

A REVIEW OF THE GENUS *OPHIOMORUS* (SAURIA: SCINCIDAE), WITH DESCRIPTIONS OF THREE NEW FORMS

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Abstract: The genus *Ophiomorus* is distributed from mainland Greece through southwest Asia. Three new forms are described herein, and a total of nine species are recognized. The genus contains two major adaptive radiations: the three western species living under rocks and having the greatest limb reduction; the six eastern species inhabiting sand dunes and having the greatest structural modification of the head.

From the morphology of the animals, and from their present geographical distribution, it is speculated that the group originated in the region now occupied by the Plateau of Iran and the mountainous regions of southwest Asia. Morphology and the present pattern of prevailing winds suggest that the sand-dwelling species have been distributed south and east from their center of origin on the Plateau of Iran as a result of dune migration through the agency of wind action.

Introduction

The genus *Ophiomorus,* a group of very elongate skinks with greatly reduced appendages, is restricted to mainland Greece and southwest Asia. Consequently, the relationships of its species and their distribution are of interest to students of zoogeography of this region. The only previous review of the genus is that of Boulenger (1887b).

Recently, additional specimens of these infrequently encountered lizards have been collected by the Street Expedition of the Chicago Natural History Museum to Iran, by John Gasperetti, and more recently by the Clark Expedition to Afghanistan, by Sherman A. Minton and Jeromie A. Anderson in

Pakistan, and others. This new material has served to elucidate some of the relationships within the genus, and makes possible the recognition of three previously undescribed populations. It seems advantageous to review the entire genus at this time, in the hope of providing a framework for the interpretation of future collections.

An attempt has been made to list all previously recorded localities which can be definitely associated with each species. Those localities which could be located with reasonable certainty are shown on the map (fig. 1).

Measurements and counts for all specimens examined are given in table 1; they are also summarized in the discussions of each of the recognized forms.

Thanks are due Charles M. Bogert and Richard Zweifel of the American Museum of Natural History (AMNH), Doris Cochran and James Peters of the United States National Museum (USNM), Alice G. C. Grandison and E. M. Noble of the British Museum (BM), Robert Inger and Hymen Marx of the Chicago Natural History Museum (CNHM), P. Kuenzer of the Zoologisches Institut und Museum der Universität Göttingen (MUG), Ernest E. Williams of the Museum of Comparative Zoology, Harvard University (MCZ), and Ilja Darevsky, Zoological Institute, Academy of Sciences, Leningrad (ZIL) for permission to examine specimens in their care. We particularly want to thank Jeromie A. Anderson for collecting the new species from west Pakistan at our request. Specimens in the collection of the California Academy of Sciences are designated with the letters CAS.

Maurice Giles of the California Academy of Sciences kindly prepared the photographs.

Genus *Ophiomorus* Duméril and Bibron

Ophiomorus DUMÉRIL and BIBRON, 1839, Erp. Gen., vol. 5, p. 799 (type species, *O. miliaris* Duméril and Bibron, by monotypy [= junior objective synonym of *Anguis punctatissimus* Bibron and Bory St. Vincent, 1833]).

Sphenocephalus (*nec* Agassiz, 1838) BLYTH, 1853, J. Asiatic Soc. Bengal, vol. 22, p. 654 (type species *S. tridactylus* Blyth, by monotypy).

Hemipodion STEINDACHNER, 1867, Sitzb. Akad. Wiss. Wien, vol. 55, p. 265 (type species *H. persicum* Steindachner, by monotypy).

Zygnopsis BLANFORD, 1874, Ann. Mag. Nat. Hist., ser. 4, vol. 14, p. 33 (type species *Z. brevipes* Blanford, by monotypy).

Sphenoscincus PETERS, 1875, Monatsb. Akad. Wiss. Berlin, 1875, p. 553 (type species *Sphenocephalus tridactylus* Blyth, by monotypy).

Zygnidopsis BLANFORD, 1879, J. Asiatic Soc. Bengal, vol. 48, p. 128 (proposed as a corrected spelling of *Zygnopsis* Blanford, 1874; type species *Zygnopsis brevipes* Blanford, 1874, by reason of its proposal as a substitute name [spelling]).

Palatine bones not meeting on the midline of the palate; pterygoid teeth

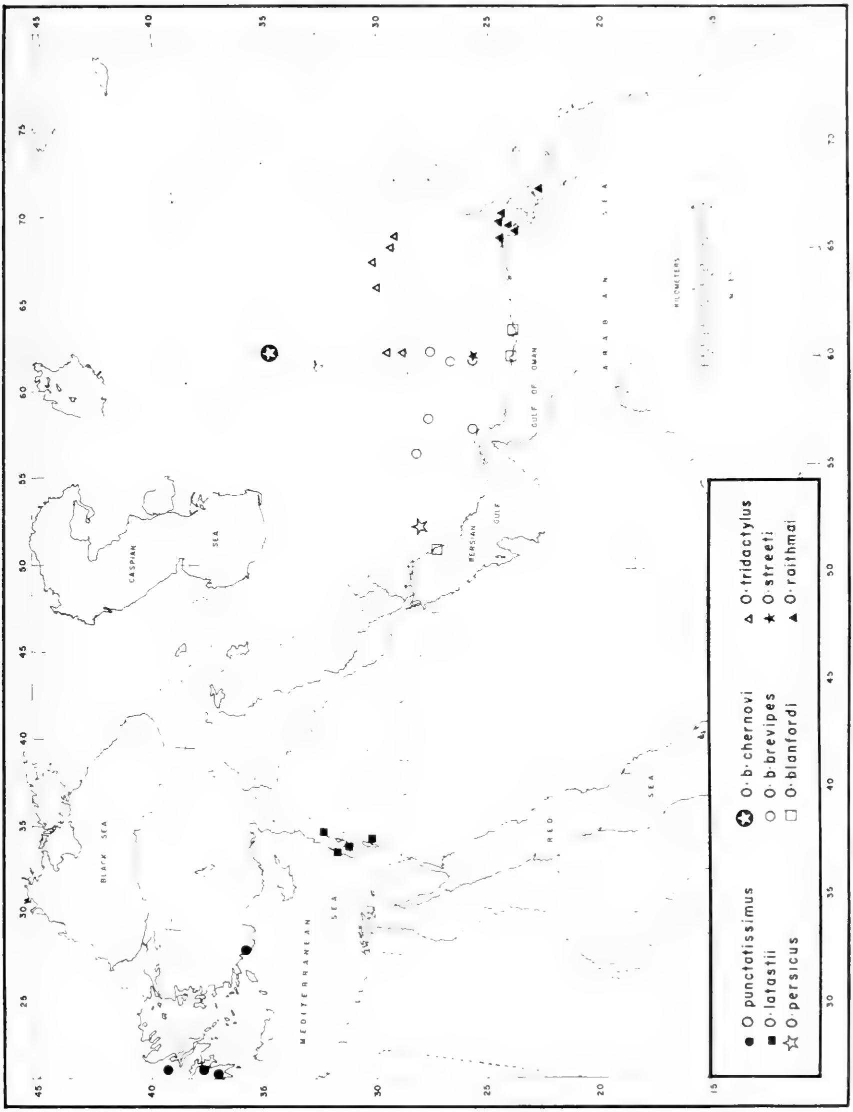

Figure 1. Map of southwest Asia showing distribution, based on available locality records, of the currently recognized species of *Ophiomorus*.

usually present. Teeth conical, or with obtuse crowns. Eye small; lower eyelid with an undivided, transparent disc. Ear opening absent or hidden. Nostril in the suture between the nasal and supranasal, close to the rostral; prefrontals usually distinct; frontoparietal and parietal distinct. Body elongate. Limbs greatly reduced or absent.

RANGE. From Greece through southwest Asia to northwestern India.

REMARKS. There are two major adaptive trends within the genus. One group, consisting of the three westernmost species, *Ophiomorus persicus, O. punctatissimus,* and *O. latastii,* have extremely elongate cylindrical bodies and blunt, conical snouts. The peritoneum and mesenteries are darkly pigmented. In *O. punctatissimus* and *O. latastii* the limbs have been lost entirely, while in *O. persicus* they are greatly reduced. Judging from their morphology and the little that is known of their habits, they are adapted to living under rocks, and perhaps burrowing in loose soil. The remaining species are adapted to living in loose windblown dune sand, moving through this medium with strong lateral undulations. This mode of locomotion has earned them the appellation "sand-fish" in some areas, a name also applied to members of the genus *Scincus*. Their wedge-shaped snouts, elongate body form, extremely smooth imbricate scales, prominent ventrolateral edge to the body from snout to groin, and the small grooves into which fit the forelimbs during subsurface locomotion, are adaptations which facilitate their progress through loose sand. The peritoneum and mesenteries of these species are devoid of dark pigment.

Ophiomorus punctatissimus and *O. latastii* retain external ear openings (hidden by scales), while *O. persicus,* in most respects the least specialized member of the genus, lacks them, as do all of the sand-dwelling forms.

All of the species exhibit sexual dimorphism in the number of dorsal scales, the females having a higher count than the males of the same species.

In using the number of longitudinal scale rows as a character for distinguishing populations of *Ophiomorus,* it is essential that the position on the body at which the counts are made be constant. This is because of the fact that reduction of the number of scale rows takes place as body circumference decreases posteriorly. The positions of reduction are relatively constant within a population, but vary from one population to another. An expanded discussion of scale row reduction in the Scincidae is planned for a later date. For purposes of the diagnoses and key used in this paper, mid-body counts are made at a point exactly halfway between the vent and the end of the snout. Table 1 also includes counts made at one-third and two-thirds the distance from snout to vent.

The genus *Ophiomorus* appears to be related most closely to the genera *Eumeces, Scincus,* and *Chalcides*. The relationships among these genera await further study. Neither *Scincus,* with its highly modified snout and fringed digits, nor *Chalcides,* with its greater modification of the head shields, appears representative of a type directly ancestral to *Ophiomorus*.

Key to the Species of the Genus *Ophiomorus*

1a. Limbs absent; scale rows less than 20 at mid-body.[1]
  2a. Small prefrontals present; frontonasal half, or less than half as long as the frontal; scale rows 18 at posterior third of body .... *O. punctatissimus*
  2b. No prefrontals; frontonasal much more than half as long as the frontal; scale rows 16 at posterior third of body .... *O. latastii*
1b. Limbs present; scale rows 20 or more at mid-body.
  3a. Fingers 4, toes 3.
    4a. Scale rows 20 at mid-body .... *O. blanfordi*
    4b. Scale rows more than 20 at mid-body.
      5a. Scale rows 22 at mid-body .... *O. brevipes*
      5b. Scale rows 24 at mid-body .... *O. chernovi*
  3b. Fingers 3; toes 2 or 3.
        6a. Toes 2 .... *O. persicus*
        6b. Toes 3.
          7a. Parietals in contact posteriorly. Prefrontals not in contact with upper labials (20 scale rows at mid-body) .... *O. streeti*
          7b. Parietals not in contact behind interparietal; prefrontals in contact with upper labials; usually 22 scale rows at mid-body (occasionally 20).
            8a. Parietal in contact with anterior temporal; postocular scale about as large as posterior suboculars; usually 7 or 8 scales on third (longest) toe .... *O. tridactylus*
            8b. Parietal not in contact with anterior temporal (posterior temporal intervenes); postocular scale much larger than posterior suboculars; usually 4 to 6 scales on third (longest) toe .... *O. raithmai*

Brevipes Group

Ophiomorus chernovi[2] Anderson and Leviton, new species.

(Figures 2a, 2b, 3a.)

Ophiomorus brevipes Boulenger, 1891, Proc. Zool. Soc. London, p. 631. Nikolsky, 1899, Fedtschenko's Reise in Turkestan, vol. 2, p. 44; 1915 (in part), Faune de la Russie, vol. 1, pp. 515–516, fig. 69. Terentjev and Chernov, 1949, Diag. Rept. Amph., pp. 174–175, map 25. Bogdanov, 1962, Presm. Turkmen, p. 106.

Distribution. Known only from the type locality, in Turkmen, near the Iranian and Afghan borders.

Holotype. British Museum number 91.10.6.25, Turkmen: Pul-i-Khatun, at confluence of Geshef-Rud and Hari-Rud, collected by M. C. Eylandt, 1891.

Paratypes (6). BM 91.10.6.24, 91.10.6.26–91.10.6.27, 91.10.6.29, CAS 100806, same data as holotype; BM 1940.2.24.23, same locality data as holotype, collected by P. Nesteroff, 1940.

Diagnosis. Snout cuneiform, a slight labial edge; interparietal broader than long. Twenty-four scales round the middle of the body. Fingers four; toes three.

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[1] Counts must be made exactly midway between snout and vent.

[2] This form is named for the late Dr. S. A. Chernov, former Curator of Herpetology in the Zoological Museum at Leningrad, in recognition of his numerous contributions to the herpetology of the USSR.

TABLE 1. *Counts and measurements of material examined of* Ophiomorus.

Species	*Museum Number*	*Sex*	*Length*		*Scale Rows*[3]			
			S–V	*Tail*	*1*	*2*	*3*	*4*
O. blanfordi	BM 91.9.14.5	♀	83	—[4]	102	22	20	20
"	CNHM 43437	♀	96	—	103	21	20	20
"	USNM 148660	juv	49	42	96	22	20	20
"	MUG 83	—[5]	50[6]	—	100	22	20	20
"	MUG 85	—	48[6]	—	102	22	20	20
O. brevipes	CAS 86593	♂	76	—	107	24	22	22
"	CNHM 141548	♀	85	78	110	24	22	22
"	CNHM 141549	♀	80	89	112	24	22	22
"	CNHM 141550	♀	91	—	114	22	22	22
"	CNHM 141552	♂	82	—	106	24	22	22
"	CAS 101792	♀	83	—	112	24	22	22
O. chernovi	BM 91.10.6.24	juv	54	—	116	24	24	22
"	BM 91.10.6.25[7]	♀	91	—	118	25	24	23
"	BM 91.10.6.26	juv	62	—	115	25	24	22
"	BM 91.10.6.27	♀	95	—	115	25	23	23
"	CAS 100806	♀	90	—	113	25	24	22
"	BM 91.10.6.29	♂	87	—	109	25	23	22
"	BM 1940.2.24.23	♀ (?)	84	—	112	24	24	22
O. latastii	CAS 87417	♂	102	—	117	18	16	16
"	CNHM 74419	♀	81	—	121	18	16	16
"	AMNH 88382	♀	96	—	122	18	16	16
O. persicus	CNHM 141555	♀	75	—	120	22	20	20
"	CAS 101793	♂	68	—	122	22	20	20
"	CNHM 141557	♀	75	—	122	22	20	20
"	CAS 101794	♀	75	—	119	22	20	20
"	CNHM 141559	♂	61	—	112	22	20	20
"	CNHM 141560	♀	73	80	121	22	20	20
"	CNHM 141561	♀	79	—	122	22	20	20
"	CAS 101795	♂	72	—	114	22	20	20
"	CNHM 141563	♂	66	83	113	22	20	20
"	CAS 101796	♀	82	—	120	22	20	20
"	CNHM 141565	♀	80	—	124	20	20	20
"	CAS 101797	♂	69	—	117	22	20	20
"	CNHM 141577	♂	56	—	115	22	20	20
"	CNHM 141578	juv	41	—	116	22	20	20
"	CNHM 141579	♀	77	—	118	22	20	20
"	CNHM 141580	♂	60	—	114	22	20	20
"	CAS 101798	juv	46	—	113	22	20	20
"	CNHM 141582	♀	78	—	121	22	20	20
O. punctatissimus	CAS 12752	♀	50	—	113	20	18	18

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[3] Categories of scale rows are as follows:
1) Number of transverse rows of dorsal scales from parietals to level of vent.
2) Number of longitudinal scale rows around anterior third of body.
3) Number of longitudinal scale rows around mid-body.
4) Number of longitudinal scale rows around posterior third of body.

[4] Tail regenerated, damaged, or largely missing; presence of dash (—) indicates no measurements taken.

[5] Specimen poorly preserved, presence of dash (—) indicates it could not be sexed.

[6] Specimen poorly preserved and could not be measured properly; these measurements are approximations.

[7] Holotype.

TABLE 1. *Continued.*

Species	*Museum Number*	*Sex*	*Length*		*Scale Rows*[6]			
			S V	*Tail*	*1*	*2*	*3*	*4*
"	USNM 31956	♂	72	79	105	20	18	18
"	USNM 37299	♂	77		102	20	18	18
"	AMNH 17819	♂	53	55	102	20	18	18
"	MCZ 25933	♂	76	80	107	20	20	18
"	MCZ 38517	♂	67	—	105	20	18	18
O. raithmai	CAS 99835	♀	99	—	112	22	22	22
"	CAS 99834[7]	♂	83	—	107	22	22	22
"	CAS 99836	♀	81	66	114	22	22	22
"	CAS 99838	♂	85	—	107	22	22	22
"	CAS 99840	♂	65	—	110	22	22	22
"	CAS 99841	♀	70	—	111	22	22	22
"	CAS 99842	♀	63	—	111	22	22	22
"	CAS 99843	♀	65	55	111	22	21[8]	20
"	CAS 99844							
"	CAS 99845	specimens living at time of this report.						
"	CAS 99846							
"	MCZ 84027	♀	90	—	113	22	22	22
"	ZIL	♀	89	—	111	22	22	22
"	BM 70.11.29.39	—	76	—	106	22	22	20
"	BM 70.11.29.39A	—	76	—	106	21	22	22
"	BM 70.11.29.39B	—	64	—	109	22	22	22
"	BM 70.11.29.39C	—	66	—	109	22	22	22
"	BM 1934.3.4.3	♀	74	54	113	22	22	22
"	BM 1934.3.4.4	♀	84	—	113	22	22	22
"	AMNH 82205	♂	81	—	107	22	22	22
"	AMNH 85843	♂	84	—	108	22	22	22
"	AMNH 85844	—	—	—	—	—	22	—
"	AMNH 85845	♂	78	—	105	22	22	22
"	AMNH 85846	♀	81	64	111	22	22	22
"	AMNH 85847	♀	90	—	111	21	20	20
"	AMNH 85848	♂	64	—	107	22	22	22
"	AMNH 86876	♀	94	—	112	22	22	22
"	AMNH 86877	juv	44	—	113	22	22	22
"	AMNH 86878	juv	40	—	102	22	22	22
"	AMNH 86879	♀	90	—	111	22	22	22
"	AMNH 86880	♀	76	—	110	23	22	22
O. streeti	CAS 100024	♀	90	—	112	22	20	20
"	CNHM 141551[7]	♀	85	—	109	20	20	20
O. tridactylus	CAS 84669	♂	91	—	114	22	22	22
"	CAS 84670	♀	84	—	115	22	22	22
"	CAS 84671	♂	79	54	107	22	22	22
"	CAS 84672	♀	76	—	114	22	22	22
"	CAS 84673	♂	80	61	114	22	22	22
"	CAS 84674	♂	83	66	101	22	22	22
"	CAS 84675	♂	71	—	114	22	22	22

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[8] Owing to fusion of two scales.

TABLE 1. *Continued.*

Species	Museum Number	Sex	Length		Scale Rows[3]			
			S-V	Tail	1	2	3	4
"	CAS 97973	♂	81	—	110	22	22	22
"	AMNH 74578	♂	78	—	112	24	22	22
"	AMNH 75607	—	92	—	122	22	22	22
"	AMNH 75608	—	—	—	118	—	22	—
"	AMNH 75609	—	—	—	120	—	22	—
"	AMNH 75610	—	—	—	118	—	22	—
"	AMNH 75611	—	—	—	115	—	22	—
"	AMNH 77109	♂	84	—	113	22	22	22
"	BM 68.4.3.71	♀	88	—	113	22	22	22
"	BM 1936.9.11.1	♀	87	—	118	22	22	22
"	CNHM 141376	♀	85	—	121	22	22	22
"	CNHM 731	♀	88	—	116	22	22	22
"	MCZ 13963	♂	91	—	113	20	20	21

Color as in *Ophiomorus brevipes.*

DESCRIPTION OF HOLOTYPE. Head depressed; snout cuneiform, with a distinct, but rounded, labial edge; mouth inferior. Rostral with a triangular, convex, superior portion equal in length to two-thirds the width, the inferior portion not concave, lying entirely in front of the mouth, and equal in length to about two-fifths the width; the posterior angle of the rostral does not partially separate the supranasals, which are broadly in contact; frontonasal septagonal, about two-thirds as long as broad, twice as long as the suture formed by the supranasals; frontal ten-sided, longer than broad, as long as the distance between its anterior border and the tip of the snout; interparietal broader than long, three-fourths as long as frontal, its straight anterior border forming a broad suture with the straight posterior border of the frontal; a pair of elongate parietals, less than one-third as broad as long, obliquely situated, as long as the distance between eye and nostril, and not in contact behind the interparietal; a single enlarged nuchal on each side of the midline. Nostril in the suture between the nasal and the supranasal, separated from the rostral; nasal more than three-fourths the length of the supranasal, much longer than high, truncate behind; supranasal longer than broad; prefrontals pentagonal, much longer than broad, pointed behind, broadly separated from the supralabials by the loreal and the preocular, broadly separated from one another by the suture formed by the frontal and frontonasal; loreal longer than high, higher than the preocular, which is also longer than high, and is as long as the loreal; three supraoculars, the second largest; two small frontoparietals, widely separated from one another, and much larger than the postocular; five elongate supraciliaries on the right, six on the left; upper eyelid rudimentary; lower lid with a large transparent scale, surrounded by several much smaller scales; a small postocular, about equal to the posterior suboculars; temporals 1 + 3, the anterior highest, the upper posterior longest, the anterior and two upper posterior temporals in contact with the parietal. Eight supralabials, the 5th and 6th below the eye, the 5th much the longest, the 1st and 8th much the smallest. No ear opening.

Mental quadrangular, with a straight posterior border; two azygous postmentals, the posterior the larger, and irregular in this specimen, being excluded from contact with the infralabials on the left side by the intervention of the first left submaxillary shield; four enlarged submaxillaries on the right, five on the left, bordering the infralabials. Seven infralabials on the right, six on the left.

Body very elongate, the ventrolateral edge not sharply defined. Length of hind limb goes slightly more than four times into distance between axilla and groin. All scales of body perfectly smooth, imbricate, more than twice as broad as long. Twenty-four longitudinal straight series of scales round the middle of the body (measured halfway between tip of snout and vent); 25 round the body counted exactly one-third the distance from snout to vent, 23 at two-thirds the distance from snout to vent; 118 scales between interparietal and the level of the vent. A pair of enlarged preanal scales.

Tail slightly depressed, scales subequal to those of body; a median subcaudal series of slightly enlarged scales.

Forelimb about two-thirds length of hind limb; four fingers, the one on ulmar side shortest, the two middle fingers nearly equal, the outer slightly the longer; seven lamellae beneath the longest finger, four beneath the shortest on the right hand, three beneath the shortest on the left.

Three toes, the toe of the tibial side the shortest, less than half the length of the toe of the fibular side, which is longer than the middle toe. Ten lamellae beneath the longest toe, eight scales on the outer aspect; four lamellae under the shortest toe, six under the middle toe. All fingers and toes clawed.

Color (in alcohol) cream above, each scale of the two median dorsal rows with a brown spot, these forming two distinct lines the length of the body and tail. The scale rows immediately lateral to these median rows lack dark markings, except for a few occasional scattered faint dots. The next three lateral rows each with a dark marking on each scale, forming three lines in such close approximation as to appear as a single broad stripe the length of the body. Immaculate cream below. A dark line from nostril through eye and temporal region, contacting lateral stripe on body. A single dark line on frontonasal and anterior portion of frontal, bifurcating on posterior part of frontal and on interparietal; a dark dot on posterior part of interparietal. Limbs speckled with brown on dorsal surfaces.

Measurements of holotype. Snout–vent: 91; tail: 63 (terminal two-fifths regenerated); head (tip of snout to angle of jaw): 8; hind limb: 16; eye (opening between lids): 2; snout (tip of snout to orbit): 4.

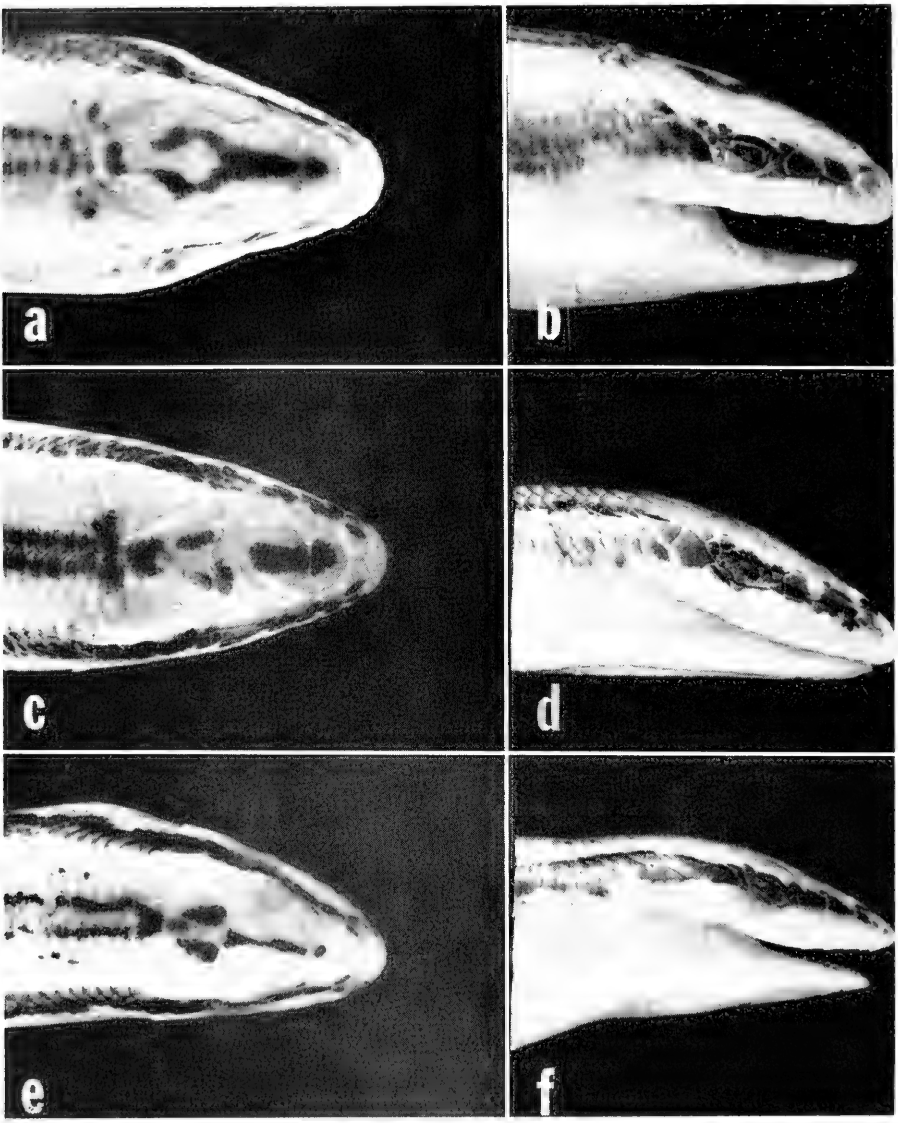

Figure 2. "*Brevipes*" group of the genus *Ophiomorus*; dorsal and lateral views of head: a and b) *O. chernovi*; c and d) *O. brevipes*; e and f) *O. blanfordi*.

Remarks. This form differs from *Ophiomorus brevipes* in possessing a greater number of longitudinal scale rows. Of all material of *Ophiomorus* examined, this population is the most variable in the positions on the body at which scale row reduction takes place, both as regards different individuals and the two sides of the same animal. For example, in BM 91.10.6.27 the

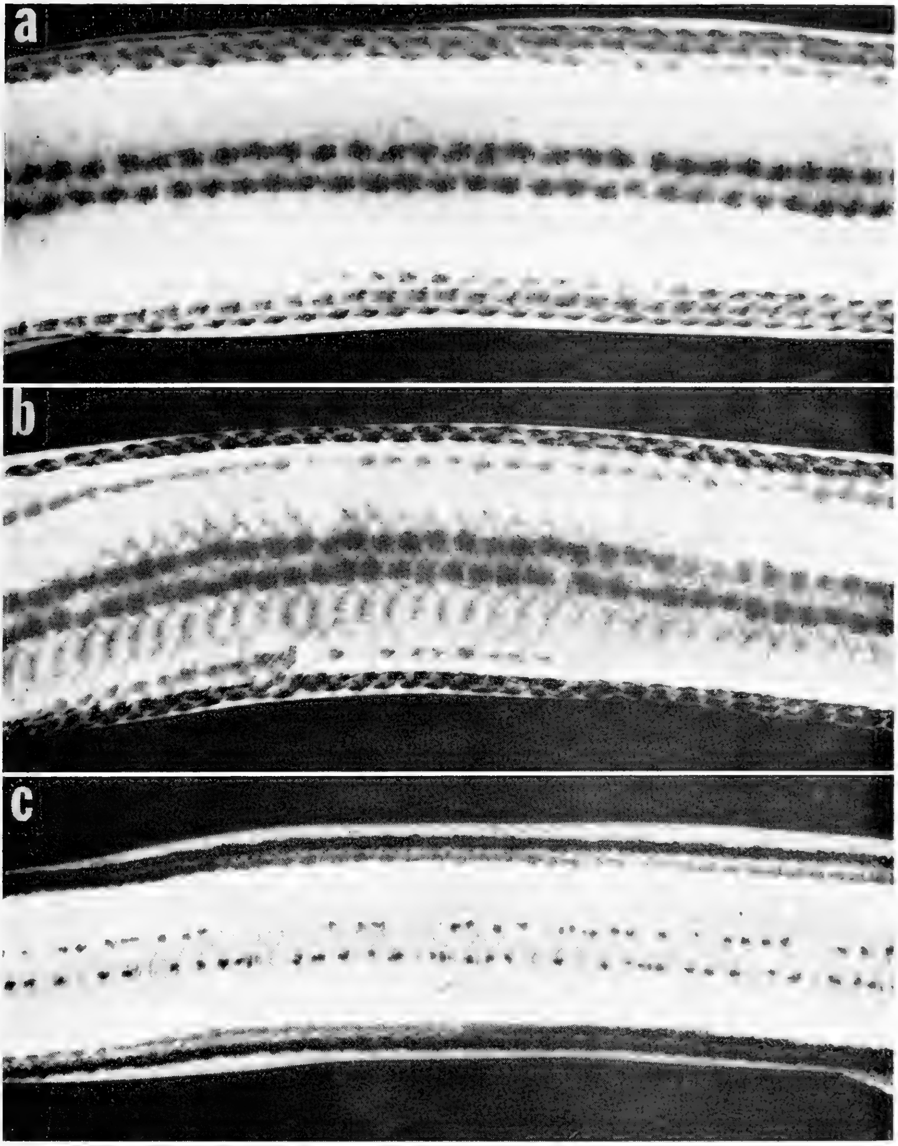

Figure 3. "*Brevipes*" group of the genus *Ophiomorus*; mid-body sections showing typical color patterns: a) *O. chernovi*; b) *O. brevipes*; c) *O. blanfordi*.

count drops from 24 scale rows to 23 anterior to mid-body, but the full reduction to 22 occurs only in the posterior third of the body. There is also a greater tendency to fusion of the head shields; BM 91.10.6.29 has complete fusion of the right prefrontal with the frontal; BM 1940.2.24.23 has the frontal partially fused with the frontonasal. In BM 91.10.6.24 the postocular is enlarged and elongated, interposed between the anterior temporal and the parietal in such a way that these latter scales are not in contact. Whether this greater variability is a reflection of genetic or developmental diversity cannot be determined from this material, of course. The fact that this is the most northern population of this species known, presumably living in a colder environment than the other populations examined, suggests that perhaps developmental differences account for the observed variation.

Snout–vent length (mm.): ♂: 87; ♀: 84–95; dorsal scales from occipital region to a point at the level of the vent: ♂: 109; ♀: 112–118 (mean 114.5).

BM 91.10.6.27 contains ovarian eggs, the largest approximately 2 mm. in diameter.

Ophiomorus brevipes (Blanford).

(Figures 2c, 2d, 3b.)

Zygnopsis brevipes BLANFORD, 1874, Ann. Mag. Nat. Hist., ser. 4, vol. 14, p. 33 (type locality: Iran: Sáadatabad, southwest of Kerman); 1876, Eastern Persia, vol. 2, Zool. and Geol., pp. 397–399, pl. 27, fig. 4.

Ophiomorus brevipes BOULENGER, 1887, Cat. Lizards British Mus., vol. 3, pp. 395–396; 1887, Bull. Soc. Zool. France, vol. 12, pp. 525–526. NIKOLSKY, 1899, Ann. Mus. Zool. Acad. Imp. Sci. St. Pétersbourg, vol. 4, pp. 401–402; 1915 (in part), Faune de la Russie, vol. 1, pp. 515–516, fig. 69. SMITH, 1935, Fauna British India, vol. 2, p. 348. WERNER, 1936, Festschrift Strand, vol. 2, p. 201. FORCART, 1950, Verh. Naturf. Ges. Basel, vol. 61, p. 148. WETTSTEIN, 1951, Sitzber. Österr. Akad. Wiss. Mathem.-Natur. Wien, vol. 160, p. 441. ANDERSON, 1963, Proc. California Acad. Sci., ser. 4, vol. 31, pp. 464–465, fig. 13.

DISTRIBUTION. Sandy regions of eastern Iran.

KNOWN LOCALITIES. IRAN: Sáadatabad, between Kerman and Shiraz, about 100 miles southwest of Kerman, 29°40′ N., 55°51′ E., 5,500 ft. elevation (Blanford, 1874, type locality); Kirman (Nikolsky, 1915); Schur (Sargad) (Nikolsky, 1915); Bazman, 27°49′ N., 60°12′ E. (Nikolsky, 1915); Kuh-i-Tuftan, 28°36′ N., 61°06′ E. (Nikolsky, 1915); Kerman Province; between Zahedan and Chahbar (Forcart, 1950); Sabzavaran, 28°37′ N., 57°45′ E. (Wettstein, 1951); Minab, 27°09′ N., 57°07′ E. (Anderson, 1963); 11 miles west of Iranshahr, 27°12′ N., 60°30′ E.

MATERIAL EXAMINED (6). CAS 86593, Iran: Minab, collected by Steven C. Anderson, October 21, 1958. CNHM 141548–141550, 141552–141553, Iran: 11 miles west of Iranshahr, collected by the Street Expedition to Iran, November 27–December 4, 1962.

DIAGNOSIS. Snout cuneiform, a slight labial edge; interparietal broader than long. Twenty-two scales round the middle of the body. Fingers four; toes three.

Cream or pale brown above in preservative, each scale of the two median dorsal rows with a central brown spot, these forming two distinct lines the length of body and tail. The scale rows immediately lateral to these median rows lack dark markings. The next three lateral rows each with a dark marking on each scale, forming either three distinct lateral stripes, or a single broad stripe the length of body and tail. Immaculate white below. A dark line from nostril through eye and temporal region, contacting lateral stripes on the body. A single line on frontonasal and frontal, divided on posterior portion of frontal, reuniting on posterior portion of interparietal.

Remarks. In *Ophiomorus brevipes* the interparietal is considerably broader than long, and the frontonasal is approximately twice as broad as long.

Smith (1935) says that the dark longitudinal lines occupy 10 dorsal scale rows. In all of the specimens examined here, the second dorsal scale row on either side of the vertebral line is without a dark line. Occasionally there are scattered dark spots on a few of the scales of this row.

Snout–vent length (mm.): ♂: 76–82; ♀: 80–91; dorsal scales from the occipital to a point level with the vent: ♂: 106–107 (mean 106.5); ♀: 110–114 (mean 112).

The following specimens contain ovarian eggs: CNHM 141548, 141549, 141553, the largest egg slightly less than 2 mm. in diameter.

Ophiomorus brevipes is intermediate in the number of longitudinal scale rows and in its geographical distribution between *O. chernovi* and *O. blanfordi.*

Ophiomorus blanfordi Boulenger.

(Figures 2e, 2f, 3c.)

Zygnidopsis brevipes Blanford, 1879, J. Asiatic Soc. Bengal, vol. 48, p. 128 (type locality: southern Persia or Baluchistan, here restricted to Iran: Baluchistan: Chah Bahar, 25°18′ N., 60°37′ E.).

Ophiomorus blanfordi Boulenger, 1887, Cat. Lizards British Mus., vol. 3, p. 395, pl. 33, fig. 1; 1887, Bull. Soc. Zool. France, vol. 12, pp. 523–525. Werner, 1917, Verh. k. k. Zool.-Bot. Ges. Wien, p. 203. Smith, 1935, Fauna British India, vol. 2, pp. 347–348. Werner, 1936, Festschrift Strand, vol. 2, p. 201. Shockley, 1949, Herpetologica, vol. 5, pp. 121–123. Neill, 1958, Bull. Mar. Sci. Gulf and Caribbean, vol. 8, pp. 1–97. Schmidt and Inger, 1957, Living Reptiles of the World, p. 132. Anderson, 1963, Proc. California Acad. Sci., ser. 4, vol. 31, p. 476.

Distribution. Coastal sand dunes of southern Iran and West Pakistan.

Known localities. Southern Iran or West Pakistan (Blanford, 1879). IRAN: *Fars Province* (Werner, 1917); *Baluchistan*: Chah Bahar, 25°18′ N., 60°37′ E. (here designated as type locality). PAKISTAN: Ras Jiunri (=Jiwani), 10 air miles east of Iranian border, on the coast (Shockley, 1949).

Material examined (5). USNM 148660, Iran: Baluchistan: Chah Bahar, collected by Ranck and Herman. CNHM 43437, Pakistan: Ras Jiunri, 10 air miles east of Iranian border, collected by Clarence H. Shockley, October 1–7,

1945. BM 91.9.14.5, Baluchistan?, collected by W. T. Blanford. MUG 83, 85, Iran: Fars Province, collected by Andreas, 1905.

DIAGNOSIS. Snout cuneiform, with angular labial edge; interparietal as long as broad; frontonasal not twice as long as broad. Twenty scales round the middle of the body. Fingers four; toes three.

Cream or pale brown above in preservative, the two median dorsal scale rows with scattered dark spots, forming more or less distinct longitudinal lines; the scale rows immediately lateral to these median dorsal rows without dark markings; the third and fourth rows from the vertebral line with dark brown dots forming well-marked lines which extend forward along sides of head. Top of head with or without a central dark streak.

REMARKS. We have examined two of the three specimens recorded by Werner (1917). They agree in every respect with the specimens from southeastern Iran. The locality on the labels is simply "Persien." Supposedly, all of Prof. Andreas' material was collected in Fars Province. Werner fails to cite any locality for these specimens. Several specimens of other reptiles collected by Andreas were reported by Werner as coming from the vicinity of Bushire, and it seems not unlikely that the specimens of *Ophiomorus blanfordi* also came from this region, probably from the coastal dunes. This form will likely be found in the dunes along the coast between Bushire and the nearest eastern locality, Chah Bahar.

Nikolsky (1899) felt that *O. blanfordi* was probably a variety of *O. brevipes*. While his specimens listed as *O. brevipes* had 22 scales round the body, the "prefrontal" (=frontonasal) was as long as wide, as is the case in *O. blanfordi*. In the material at hand, the frontonasal is approximately as long as broad, or slightly broader than long in *O. blanfordi,* while in *O. brevipes* it is approximately twice as broad as long.

Because *O. blanfordi* differs from *O. brevipes* not only in the number of scale rows, but also in the proportion of the head scales and in the color pattern, its status as a species is here retained. Its nearest ally is *O. brevipes*.

TRIDACTYLUS GROUP

Ophiomorus streeti, Anderson and Leviton, new species.

(Figures 4a, 4b, 5a.)

HOLOTYPE. Chicago Natural History Museum 141551, ♀, Iran: Baluchistan: 11 miles west of Iranshahr; collected by W. S. Street, J. K. Street, and Douglas M. Lay, November 27–December 4, 1962.

PARATYPE. CAS 100024, ♀, same data as holotype.

DIAGNOSIS. Snout cuneiform, with sharp angular labial edge; supranasals broadly in contact medially; prefrontals not in contact with upper labials; frontonasal longer than broad. Twenty scales round the middle of the body. Fingers three; toes three.

Cream above in preservative, each scale of the eight dorsal rows with a dark brown spot, these forming eight longitudinal lines extending from the posterior head shields to the level of insertion of the hind limbs; posteriorly six lines continue onto tail. Venter and sides immaculate white.

Description of holotype. Head depressed; snout cuneiform, with sharp angular labial edge; mouth inferior. Rostral with a triangular, convex, superior portion equal in length to two-thirds the width, the inferior portion slightly concave, lying entirely in front of the mouth, and equal in length to about two-fifths the width; the obtuse posterior angle of the rostral does not partially separate the supranasals; frontonasal septagonal, three-fourths as broad as long, twice as long as the suture formed by the supranasals; frontal ten-sided, broader than long, as long as the distance between its anterior border and the apex of the rostral; interparietal broader than long, longer than the frontal, and as broad as the frontal, its straight anterior border forming a broad suture with the straight posterior border of the frontal; a pair of elongate, curved parietals, about one-third as broad as long, obliquely arranged, meet behind the interparietal to form a short suture; two enlarged nuchal shields on the left, three on the right. Nostril in the suture between the nasal and the supranasal, narrowly separated from the rostral; nasal three-fourths the length of the supranasal, as high as long, and pointed behind; supranasal longer than broad; prefrontals quadrangular, acutely pointed behind, about three-fifths as broad as long, broadly separated from the supralabials by the loreal and the preocular, broadly separated from one another by the suture formed by the frontal and frontonasal; loreal as high as long, higher than the preocular, which is half again as long as high, and longer than the loreal; three small supraoculars, the anterior two larger than the posterior; a small shield interposed between the frontal and the suture formed by the 1st and 2nd supraoculars; two small frontoparietals, widely separated from one another, and slightly larger than the postocular; four elongate supraciliaries; upper eyelid rudimentary; lower lid with a large transparent scale and 13 much smaller scales (the right side of the head is somewhat mutilated, and the exact number of scales in the lower lid cannot be determined); a single postocular, much larger than the posterior suboculars; two large temporals, the anterior higher, the posterior longer, both bordering the parietals. Seven supralabials, the 5th and 6th below the eye, the 5th much the longest, the 1st much the smallest, the 7th much smaller than the 6th, and lying below the anterior temporal. No ear opening.

Mental quadrangular, the posterior border concave; two azygous postmentals, the posterior much the larger; a series of four enlarged shields on either side of the chin, bordering the infralabials. Seven infralabials.

Body very elongate, with distinct ventrolateral edge, which continues the labial angulation to the groin. Length of hind limb goes slightly more than five

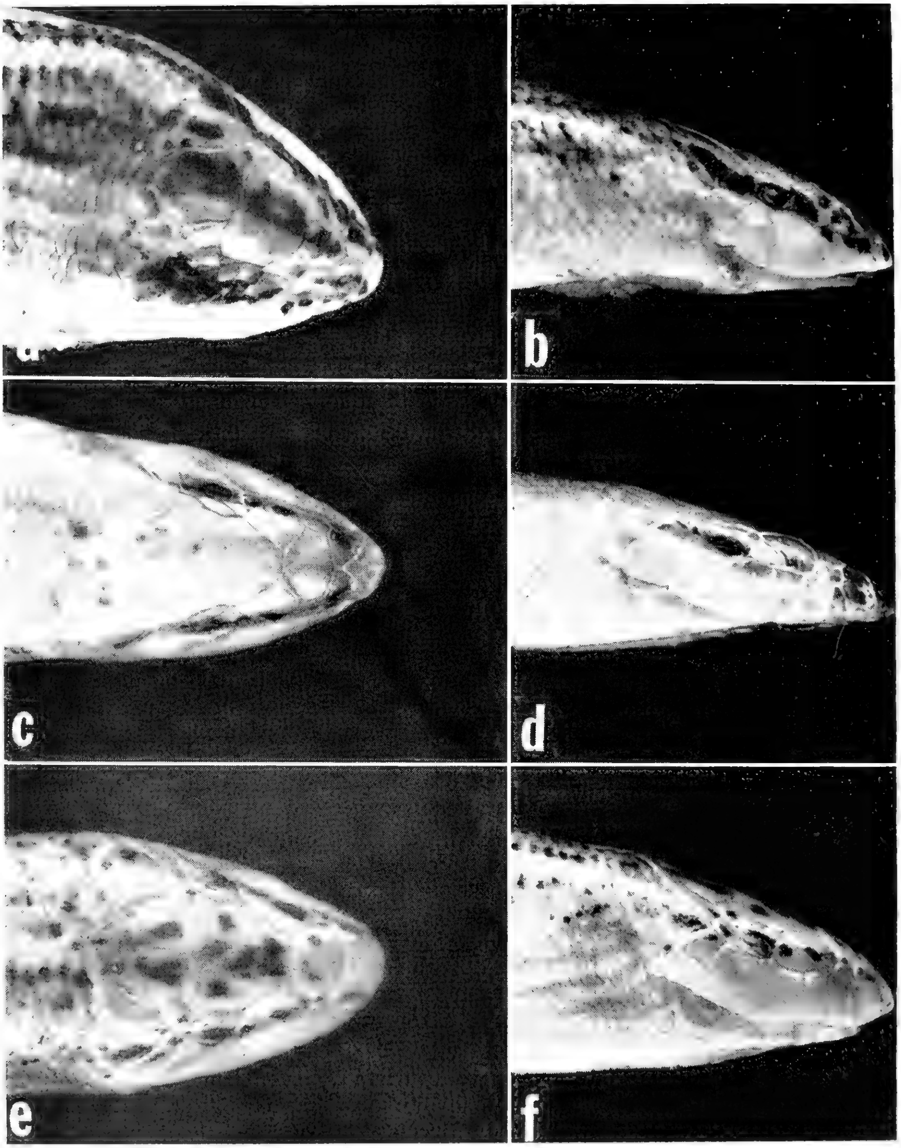

FIGURE 4. "*Tridactylus*" group of the genus *Ophiomorus*; dorsal and lateral views of head: a and b) *O. streeti*; c and d) *O. tridactylus*; e and f) *O. raithmai.*

times into distance between axilla and groin. All scales of body perfectly smooth, imbricate, more than twice as broad as long. Twenty longitudinal, straight series of scales round the body; 109 scales between the parietals and a line drawn at the level of the vent. A pair of enlarged preanal scales.

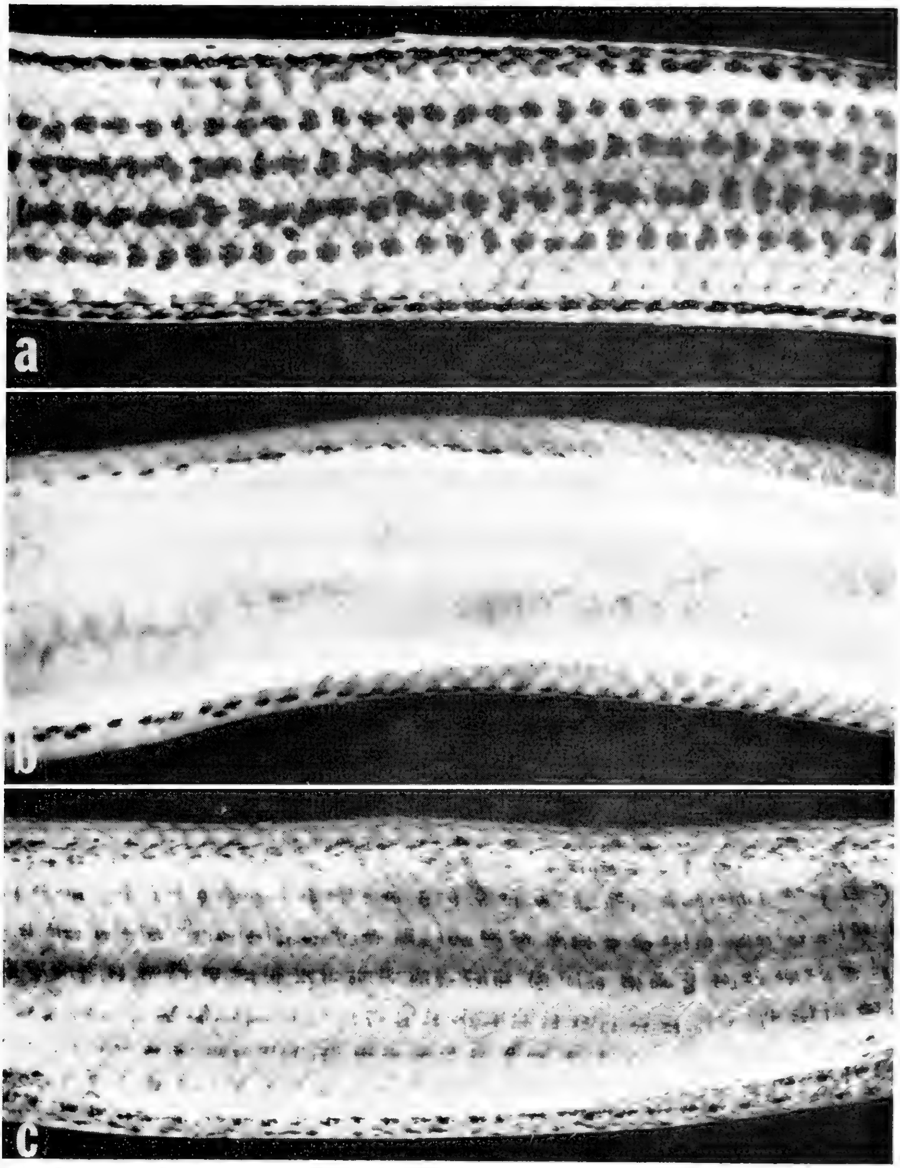

Figure 5. "*Tridactylus*" group of the genus *Ophiomorus*; mid-body sections showing typical color patterns: a) *O. streeti*; b) *O. tridactylus*; c) *O. raithmai.*

Tail slightly depressed, scales subequal to those of body; a median subcaudal series of slightly enlarged scales.

Forelimb less than one-half length of hind limb; three fingers, the one on the radial side shortest, that of the ulnar side very slightly larger than the middle one; six lamellae beneath the longest finger, two beneath the shortest, five beneath the middle finger.

Three toes, the toe of the tibial side the shortest, slightly more than one-half the length of the toe of the fibular side, which is longer than the middle toe. Eleven lamellae under the longest toe, seven scales on lateral aspect, four lamellae under the shortest toe, seven under the middle toe. All fingers and toes clawed.

Color (in alcohol) cream above, each scale of the eight dorsal rows with a dark brown spot, these forming eight longitudinal lines of discrete spots extending from the posterior head shields to the tip of the tail. Venter and sides immaculate white. Upper surface of hind limb with dark brown dots. Dark brown markings on rostral, nasals, upper labials, loreals, postocular, and temporals, forming a line through the eye. Each upper head shield with a rather irregular dark mark.

Measurements (in mm.). *Holotype*: snout–vent: 84; tail: 53 (terminal one-fourth regenerated); head (tip of snout to angle of jaw): 10; hind limb: 14; eye (opening between lids): 1.0; snout (tip of snout to orbit): 4.

Paratype: snout–vent: 91; tail: 52 (terminal one-third regenerated); head: 9; hind limb: 16; eye: 1; snout: 4.

Remarks. The paratype agrees with the holotype in most of the particulars given above, as far as can be determined, the head shields being rather badly mutilated. There is a single pair of nuchals; there are 112 scales between the parietals and a line drawn at the level of the vent; the length of the hind limb goes slightly less than five times into the distance between axilla and groin. Seven lamellae beneath longest finger, two beneath the shortest, six beneath middle finger; 12 lamellae under longest toe, four under shortest, eight under middle toe. Eight scales on lateral aspect of longest toe of right foot, seven on longest toe of left foot.

The habitus of this new form suggests it is a sand-burrowing form, as are *O. tridactylus, O. blanfordi, O. raithmai,* and *O. brevipes.*

It is noteworthy that among the specimens collected by the Street Expedition to Iran are five of *O. brevipes* having the same locality data as the new species. Mr. Douglas M. Lay, a member of the expedition, provided the following information (personal communication):

"I cannot say positively whether or not these [*O. brevipes*] originated from the same habitat. However, there are no major habitat differences in the area west of Iranshahr where the specimens were taken. The widest ecologic variation there was that between an area of sand dunes south of the Bampur River and the rolling pebble desert to the north. Both of these areas were accessible to the kids who collected the specimens, but the sand dunes were between a half mile and a mile across gravel plain from their village, near which we camped."

It would be most curious to find these two related sand-dwelling species in the same area under the same circumstances. This matter warrants investigation by future collectors.

Ophiomorus tridactylus (Blyth).

(Figures 4c, 4d, 5b.)

Sphenocephalus tridactylus Blyth, 1855, J. Asiatic Soc. Bengal, vol. 22, p. 654 (type locality: Afghanistan). Günther, 1864, Rept. British India, p. 98. Jerdon, 1870, Proc. Asiatic Soc. Bengal, p. 74. Blanford, 1876, Eastern Persia, vol. 2, Zool. and Geol., p. 395.

Ophiomorus tridactylus Boulenger, 1887 (in part), Cat. Lizards British Mus., vol. 3, pp. 394–395; 1887, Bull. Soc. Zool. France, vol. 12, pp. 520–523; 1889, *in* Aitchison, Trans. Linnaean Soc. London, Zool., vol. 5, p. 101; 1890 (in part), Fauna British India, p. 222, fig. 59. Alcock and Finn, 1896, J. Asiatic Soc. Bengal, vol. 65, p. 561. Nikolsky, 1899, Ann. Mus. Zool. Acad. Imp. Sci. St. Pétersbourg, vol. 4, p. 402. Annandale, 1906, Mem. Asiatic Soc. Bengal, vol. 1, p. 197. Smith, 1935 (in part), Fauna British India, vol. 2, p. 346, fig. 78. Werner, 1936, Festschrift Strand, vol. 2, p. 201. Constable, 1949, Bull. Mus. Comp. Zool., Harvard, vol. 103, p. 107. Leviton, 1959, Proc. California Acad. Sci., ser. 4, vol. 29, pp. 450–451. Anderson, 1963, Proc. California Acad. Sci., ser. 4, vol. 31, p. 476.

Distribution. The sandy areas of the Helmand basin and adjacent regions of eastern Iran, southern Afghanistan, and northern Baluchistan, Pakistan.

Known localities. AFGHANISTAN (Blyth, 1855, type locality); Chaman, 30°55′ N., 60°30′ E. (Alcock and Finn, 1896); Chah-i-Angir, 31°41′ N., 64°23′ E. (Leviton, 1959); 20 miles southeast of Kandahar [3,500 ft. elevation]; Kandahar (Boulenger, 1887); Helmand (Boulenger, 1887). PAKISTAN: *Baluchistan*: Quetta, 30°12′ N., 67°00′ E. IRAN: *Sistan*: Nasirabad, 31°03′ N., 61°25′ E. (Blanford, 1876); Schile (Nikolsky, 1899); Neizar (Nikolsky, 1899); Perso-Baluch border (Annandale, 1906); 15 miles southwest of Zabol; *Zirkuch*: Chadschi-du-i-Tschagi (Nikolsky, 1899).

Material examined (18). CAS 84669–84675, Afghanistan: Chah-i-Angir, collected by John Gasperetti, March–September, 1950. CAS 97973, Afghanistan: 20 miles southeast of Kandahar, collected by Richard Clark, August 28, 1964. CNHM 141376, Iran: Sistan: 15 miles southwest of Zabol, collected by the Street Expedition to Iran, November 22, 1962. CNHM 731, "Baluchistan." AMNH 74578, 77109, Afghanistan: Dasht-i-Margo, near Chah-i-Angir. AMNH 75607–75611, Pakistan: Baluchistan: Quetta. MCZ 7193, "Baluchistan," collected by F. P. Maynard and A. H. McMahon.

Diagnosis. Snout cuneiform, with sharp angular labial edge; supranasals usually narrowly in contact, partly separated from one another by the apex of the rostral; prefrontals in contact with the upper labials; frontonasal broader than long; parietal in contact with anterior temporal, postocular scale about as large as posterior suboculars. Twenty-two scales round the middle of the body. A distinct ventrolateral edge from snout to groin. Fingers three; toes three; usually seven or eight scales on third (longest) toe.

Cream or pale brown above in preservative, uniform, or with a dorsolateral brown line on either side, from nostril, through the eye, on body, and extending onto tail, composed of more or less confluent dots on one or two rows of scales; occasionally with a few scattered dark spots on dorsum; brown dots arranged in lines on dorsal surface of tail. Dorsal surface of hind limbs with brown dots. A few dark marks on head shields present or absent. Immaculate cream below.

Remarks. In *Ophiomorus tridactylus* the 5th and 6th supralabials are fused, forming a single large shield below the eye. Laterally, the prefrontal projects downward, being interposed between the preocular and the loreal, and forming a suture with the 3rd and 4th supralabials. In *O. brevipes* and *O. streeti* the prefrontals are smaller than in *O. tridactylus,* and do not contact the supralabials. In these two species the preocular and loreal are larger than in *O. tridactylus* and form a vertical suture with one another.

Blyth (1853), in the original description says of the color pattern: "Very pale brown, a little deeper on the upper parts." No mention is made of the lateral dark markings. All of the specimens from Iran and Afghanistan have these markings on the body.

Snout–vent length (mm.): ♂: 71–91; ♀: 76–85; dorsal scales from occipital to a point at the level of the vent: ♂: 101–114 (mean 110.9); ♀: 114–121 (mean 116.7).

The following specimens contain ovarian eggs: CAS 84670, 84672, CNHM 141376, the largest egg slightly less than 2 mm. in diameter. None of the specimens have eggs in the oviducts.

Four additional specimens, none with precise locality data, are worthy of special mention. These are: BM 68.4.3.71, "Punjab," collected by W. Theobald; BM 1936.9.11.1, "Punjab"; CNHM 731, "Baluchistan"; MCZ 7193, "Baluchistan," collected by F. P. Maynard and A. M. McMahon.

These four individuals differ from *O. tridactylus* from Afghanistan and Iran in that they are noticeably heavier bodied (fig. 6a–c) and completely lack color pattern on the body, limbs, and tail. There is a light brown line from the nostril through the eye to the temporal region, and a few faint brown markings on the median head shields.

MCZ 731 has only 20 scales round the middle of the body. Smith (1935) also records a single specimen from the Punjab with 20 scale rows. The fact that one specimen of *O. raithmai* from Las Bela, Pakistan has but 20 scale rows at mid-body, and another from Gizri, Pakistan has but 21, indicates that this character is subject to occasional variation.

These animals suggest that a distinct population, possibly inhabiting

Pakistan east of the Sulaiman Range, may be worthy of recognition when sufficient material is available. We have not been able to locate any specimens with precise or reliable data from Punjab or Rajasthan, although Jerdon (1870) states that they are common in the sandy areas of the southern and western Punjab.

Ophiomorus tridactylus is most closely allied to *O. raithmai* from which it differs in the color pattern, scalation of the temporal region (reflecting a greater dorsoventral compression of the skull), and longer toes (the third toe having seven or eight, rather than five or six scales). It is also related to *O. streeti,* which has fewer scales round the body (20), parietals in contact posteriorly, prefrontals separated from the supralabials, and a lineolate color pattern.

Ophiomorus raithmai Anderson and Leviton, new species.[9]

(Figures 4e, 4f, 5c.)

Sphenocephalus tridactylus Stoliczka, 1872, Proc. Asiatic Soc. Bengal, pp. 76 and 88. Theobald, 1876 (in part), Cat. Rept. British India, p. 70. Blanford, 1879 (in part), J. Asiatic Soc. Bengal, vol. 48, p. 128. Murray, 1884, Vertebrate Zoology of Sind, p. 356.

Ophiomorus tridactylus Boulenger, 1887 (in part), Cat. Lizards British Mus., vol. 3, pp. 394–395; 1887, Bull. Soc. Zool. France, vol. 12, pp. 520–523; 1890 (in part), Fauna British India, p. 222. Smith, 1935 (in part), Fauna British India, vol. 2, p. 346. Minton, 1962, American Mus. Novitates, no. 2081, pp. 11 and 37, fig. 41.

Distribution. The sandy tracts of southern and eastern West Pakistan; northwestern India.

Known localities. INDIA: Kachh, between the eastern branches of the Indus River and Kathiwar (Stoliczka, 1872). PAKISTAN: *Sind*: along right bank of Indus River, between Karachi and Sakkar (Stoliczka, 1872); *Karachi District*: Karachi, 24°52′ N., 67°03′ E.; Ghizri, 24°49′ N., 67°03′ E., near Clifton; Malir Cantonment North, 24°56′ N., 67°12′ E.; *Dadu District*: Canyon of Sari River, 23 miles northeast of Malir; *Sanghar District*: 0.5 miles west of Burra; *Las Bela District*: Sonmiani Beach, 25°26′ N., 66°36′ E.

Holotype. California Academy of Sciences 99834, adult male, Pakistan: Karachi District: Ghizri, collected by Jeromie A. Anderson, March 24, 1965.

Paratypes (26). CAS 99835–99836, 99838, 99840–99846, MCZ 84027, ZIL (catalog number unavailable, formerly CAS 99837), Pakistan: Karachi District: Ghizri, collected by J. A. Anderson, March 24, 1965. AMNH 82205, Pakistan: Karachi District: Karachi, east edge of city, near Hill Park, collected by Mary April and Sherman A. Minton, July 10, 1959. AMNH 86876, Pakistan: Karachi District: Karachi, Jinnah Hospital, collected by Sherman

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[9] From *raith mai*, sand-fish, a term used for this lizard by the Sindhis and some of the neighboring Baluchis in the region in which it occurs (Jeromie A. Anderson, personal communication).

A. Minton, June 29, 1961. AMNH 86877–86879, Pakistan: Karachi District: Ghizri, near Clifton, collected by Jeromie A. Anderson, June 28, 1961. AMNH 86880, Pakistan: Karachi District: Malir Cantonment North, collected by Madge and Sherman Minton, June 22, 1961. AMNH 85843, Pakistan: Dadu District: Canyon of Sari River, 23 miles northeast of Malir, collected by Minton and Feffer, February 19, 1961. AMNH 85844, Pakistan: Sanghar District: 0.5 miles west of Burra, collected by Sid, Mike, and Clarence Gulik and Sherman Minton, March 31, 1961. AMNH 85845–85848, Pakistan: Las Bela District: Sonmiani Beach, collected by Sherman A. Minton and family, February 12, 1961. BM 1934.3.4.3, 1934.3.4.4, Pakistan: Sind (Bombay Natural History Society).

Diagnosis. Snout cuneiform, with sharp angular labial edge; supranasals usually narrowly in contact, partly separated from one another by the apex of the rostral; prefrontals in contact with the upper labials; frontonasal broader than long; parietal not in contact with anterior temporal (posterior temporal intervenes); postocular scale much larger than posterior suboculars. Twenty-two scales round the middle of the body. A distinct ventrolateral edge from snout to groin. Fingers three; toes three. Usually four to six scales on third (longest) toe.

In life the dorsal surfaces are pale brown, many specimens being suffused with yellow ochre. This ochre color is most intense at the upper center of each scale, in the region in which the dark brown spots occur.

Cream or pale brown above in preservative, each of the eight or 10 dorsal and dorsolateral longitudinal scale rows having a dark brown line composed of discrete dots extending from the nape to the level of the hind limbs, reducing to six or eight lines on the tail. Dorsal surface of hind limbs with brown dots. A dark brown line from nostril through eye, across temporal region. Dark brown markings on the median head shields. Immaculate cream or tan below.

Description of holotype. Head depressed, snout cuneiform with a sharp angular labial edge; mouth inferior. Rostral with a triangular, convex, superior portion equal in length to two-thirds the width, the inferior portion flat, lying entirely in front of the mouth, and equal in length to about one-half the width; the posterior angle of the rostral partially separates the supranasals, which are in contact for approximately one-fourth their total length; frontonasal septagonal, about two-thirds as long as broad, as long as the superior portion of the rostral; frontal slightly broader than long, ten-sided, longer than the distance between its anterior border and the apex of the rostral, but shorter than the distance between its anterior border and the tip of the snout; interparietal slightly broader than long, slightly shorter than the frontal, and as broad as the frontal, its straight anterior border forming a broad suture with the straight posterior border of the frontal; the elongate, obliquely situated parietals are about twice as long as broad, and do not meet behind the interparietal; the anterior scales of the first two dorsal scale rows on either side of the midline are fused to form two nuchal shields, just posterior to the interparietal. Nostril in the suture between the nasal and the supranasal, narrowly separated from the rostral; nasal slightly longer than supranasal, twice as long as high; supranasal slightly longer than broad; prefrontals five-sided, acutely pointed behind, longer than broad, interposed between the loreal and the preocular, and broadly in contact with the supralabials (with the 4th supralabial on the right, the 3rd and 4th on the left side), broadly separated from one another by the suture formed by the frontal and frontonasal; loreal higher than long, as high as the preocular, which is slightly longer than high; three small supraoculars, the anterior two larger than the posterior; two small frontoparietals, widely separated from one another, pentagonal, and less than twice as long as the postocular; five small, elongate supraciliaries on the right, four on the left; upper eyelid rudimentary; lower lid with a large transparent scale and seven much smaller scales on the right side, nine on the left side of head; four small suboculars on the right, five on the left; a single postocular, much larger than the posterior suboculars, positioned in such a way that the anterior temporal fails to contact the parietal; two large temporals, the posterior largest, anterior in contact with 5th and 6th upper labials, postsubocular, postocular, posterior temporal, and an enlarged scale lying between the 6th upper labial and posterior temporal; the posterior temporal forms a broad suture with the parietal. Six supralabials, increasing in size from the 1st to the 5th, the 6th much smaller than 5th. No external ear opening.

Mental quadrangular, anterior border convex, posterior border concave; two azygous postmentals, the posterior much the larger; a series of four enlarged shields on either side of the chin, bordering the infralabials. Six infralabials.

Body very elongate, with distinct ventrolateral edge, which continues the labial angulation to the groin (this edge present in living as well as preserved specimens). Length of hind limb goes slightly more than four times into distance between axilla and groin. All scales of body perfectly smooth, imbricate, broader than long, the two midventral rows narrower than adjacent rows. Twenty-two longitudinal, straight series of scales round the middle of the body; 107 dorsal scales between posterior margin of the interparietal and a point at the level of the vent. Four enlarged preanal scales, the mid-ventral pair largest.

Tail slightly depressed, subcircular in cross section, scales about one and one-half times wider than those of body; a median subcaudal series of slightly enlarged scales.

Forelimb less than one-half length of hind limb, three fingers, the one on

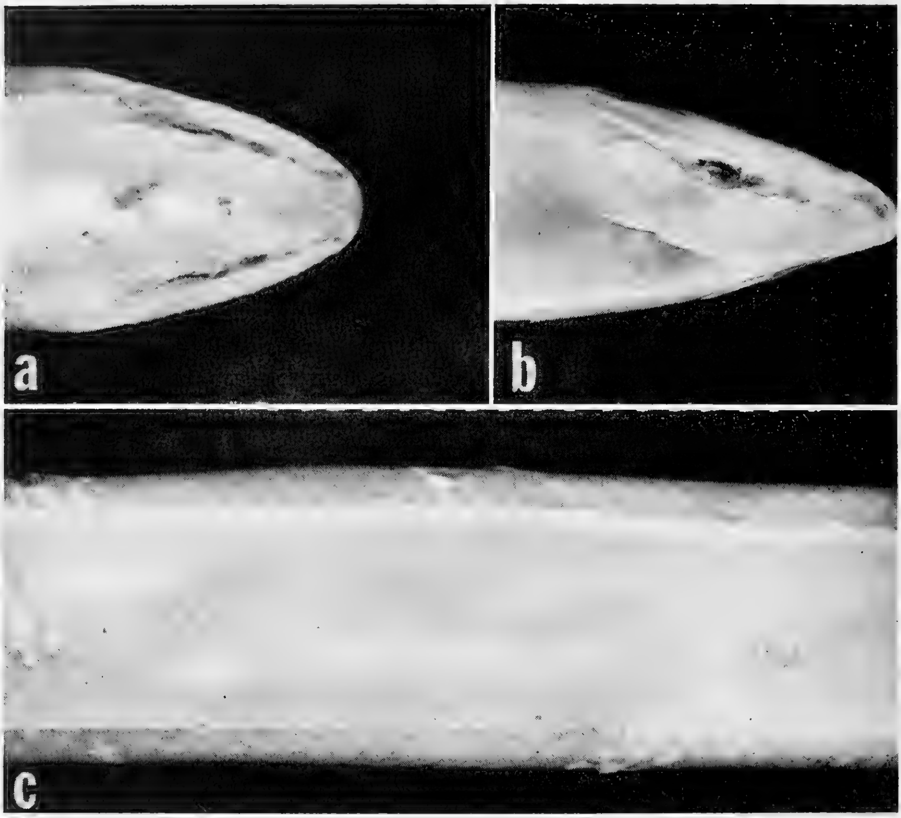

FIGURE 6. *Ophiomorus tridactylus* from the Punjab, India.

the radial side shortest, that of the ulnar side slightly shorter than the middle finger; two scales on the lateral aspect of the two longest fingers, one on the shortest.

Three toes, the toe of the tibial side shortest, about two-thirds the length of the toe of the fibular side, which is longer than the middle toe. Lateral aspect of longest toe with four scales, middle toe with three, shortest toe with two. All fingers and toes clawed.

Hemipenes: In the holotype, both hemipenes are everted, the left more fully than the right. The two organs are mirror images of one another. The everted organ is five mm. in length, or equal to nine subcaudal scales. The hemipenis is bilobed and bulbous, the sulcus spermaticus is simple, with prominent, thick lips, appearing basally on the posterior side of the everted organ, traversing the lateral aspect of the apical portion obliquely, and ascending the apical portion vertically to its termination midway between the termination of the basal portion and the apex of the organ. The hemispherical lobes are

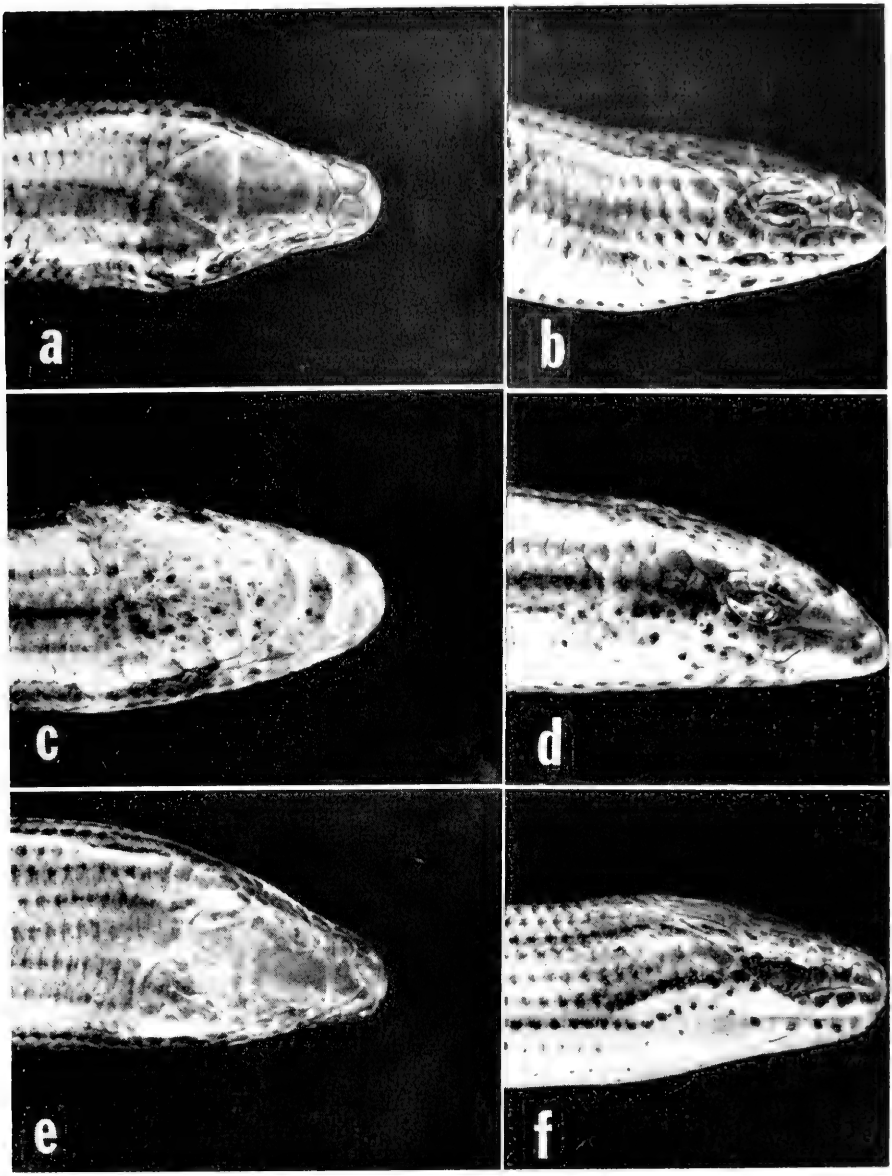

Figure 7. "*Punctatissimus*" group of the genus *Ophiomorus*; dorsal and lateral views of head: a and b) *O. punctatissimus*; c and d) *O. latastii*; e and f) *O. persicus*.

ornamented with smooth, vertically oriented ridges, running from the shallow groove between the lobes to the base of each lobe. The basal portion of the organ is cylindrical and naked, constituting about half the total length of the hemipenis.

Color (in alcohol) light brown above, nearly every scale of the eight dorsal rows with a dark brown spot, those of the mid-dorsal rows largest, forming eight longitudinal lines of discrete spots extending from the posterior head shields to level of groin. Six lines of spots on tail. Venter and sides immaculate white. Upper surface of hind limb with scattered dark brown dots. Forelimbs unspotted. Dark brown markings on supransasals, nasals, loreals, frontonasal, prefrontals, preoculars, frontal, frontoparietals, interparietal, parietals, temporals; a broken dark brown line from nostril through eye, onto temporal region. Dorsum of body and tail suffused with yellow in life, the yellow color concentrated in the areas surrounding the dark spots.

MEASUREMENTS OF HOLOTYPE (in mm.). Snout–vent: 83; tail: 59 (terminal one-fifth regenerated); head (tip of snout to angle of jaw): 8; hind limb: 14; eye (opening between lids): 1; snout (tip of snout to orbit): 5.

REMARKS. Of the 27 examples examined, a single specimen (AM 85847) has 20, rather than 22 scales round the middle of the body and another (CAS 99843) has 21 due to fusion of two lateral rows on one side for a short distance; there is a subsequent reduction to 20 rows in the posterior half of the body. A specimen reported by Stoliczka (1872) from Kachh is stated to have 20 scale rows at mid-body. Stoliczka's description agrees in general with the material at hand. However, he does not mention the prefrontal being in contact with the upper labials, and thus the description would fit *Ophiomorus streeti* equally well. Considering the locality of his material, and in absence of evidence to the contrary, it is assumed that the Kachh specimen (or specimens?) is *O. raithmai.*

Boulenger (1887a, 1887b) and Smith (1935), in discussing *O. tridactylus,* include material from Cutch and Sind, and also from the Punjab. Both workers state that the color pattern may be uniform cream or pale brown, or with longitudinal series of brown dots on the back. It is apparent that the material they examined included *O. raithmai.*

Four specimens in the British Museum (70.11.29.39, 39A, 39B, 39C) collected by T. C. Jerdon and said to come from Punjab agree with *O. raithmai* in scalation of head and body. The longest toe has seven scales on the lateral aspect, however. The dorsal pattern of dark spots linearly arranged is faint and much reduced in these specimens, the spots being scattered on the eight dorsal scale rows. These specimens may represent a distinct population in the sandy regions east of the Indus River. Without precise locality data it is impossible to evaluate these four individuals. The eastern limits of the genus *Ophiomorus* are in much need of investigation.

Snout–vent length (mm.): ♂: 64–85; ♀: 63–99; dorsal scales from occipital to a point at the level of the vent: ♂: 102–110 (mean 105.4; ♀: 110–114 (mean 111.8).

The following specimens contain ovarian eggs: BM 1934.3.4.3, 1934.3.4.4, AMNH 85847, 86876, 86880, the largest egg slightly less than 2 mm. in diameter. None of the specimens have eggs in the oviducts.

There has been some question as to whether the lower eyelid, although not fused with the upper, was movable or immovable (Smith, 1935). In the living animal it is readily observed that the eye can be opened completely.

In retaining the lineolate color pattern and in the scalation of the temporal region, *O. raithmai* appears to be less specialized than *O. tridactylus*, to which it is closely related. The toes are shorter than in *O. tridactylus,* however.

Punctatissimus Group

Ophiomorus punctatissimus (Bibron and Bory de St. Vincent).

(Figures 7a, 7b, 8a.)

Anguis punctatissimus Bibron and Bory de St. Vincent, 1833, Exped. Sci. Morée, Rept., p. 71, pl. 11, fig. 5 (type locality: Greece: Morea). Gervais, 1836, Ann. Sci. Nat., vol. 6, p. 310.

Ophiomorus miliaris Duméril and Bibron, 1839, Erp. Gén., vol. 5, p. 799. Bonaparte, 1841, Faun. Ital., vol. 30. Gray, 1845, Cat. Lizards, p. 121. Strauch, 1862, Mém. Acad. Imp. Sci. St. Pétersbourg, ser. 7, vol. 14, p. 46. De Betta, 1868, Atti Ist. Venice, ser. 3, vol. 13, p. 915. Schreiber, 1875, Herp. Europa, pp. 338–339. Boettger, 1876, Berlin Offenb. Ver. Naturk., vol. 15/16, p. 57. Bedriaga, 1882, Bull. Soc. Nat. Moscou, vol. 61, p. 51.

Ophiomorus punctatissimus Boulenger, 1887, Cat. Lizards British Mus., vol. 3, p. 397; 1887, Bull. Soc. Zool. France, vol. 12, pp. 528–533. Schreiber, 1912, Herp. Europa, p. 329, fig. 65; Nikolsky, 1915, Fauna de la Russie, vol. 1, p. 518. Werner, 1930, Occ. Pap. Mus. Zool. Univ. Michigan, p. 19, pl. 6, fig. 29. Mertens and Müller, 1940, Abh. Senckenberg Naturf. Ges., vol. 451, p. 48. Hellmich, 1956, Die Lurche und Kriechtiere Europas, p. 128. Mertens and Wermuth, 1960, Amph. Rept. Europas, pp. 162–163. Hellmich, 1962, Reptiles and Amphibians of Europe, p. 123.

Distribution. Mainland Greece; southwestern Turkey.

Known localities. GREECE: Morea (Peloponnesus) (Bibron and Bory de St. Vincent, 1883, type locality); Peloponnesus (Schreiber, 1912); Larissa (Werner, 1930); Thessaly (Werner, 1930); Acro-Corinth (Werner, 1930); Peloponnesus: Taygetos. TURKEY: Xanthus (Boulenger, 1887).

Material examined (6). CAS 12752, Greece: Morea. MCZ 25933, and USNM 31956, 37299, Greece: Peloponnesus: Taygetos. AMNH 17819, Turkey: Xanthus. MCZ 38517, Greece: Corinth.

Diagnosis. Snout obtuse, rounded, rostral scarcely projecting beyond lip; prefrontals present; supranasals broadly in contact, not partly separated from one another by the apex of the rostral. Eighteen scales round the middle of the body. Limbs lacking.

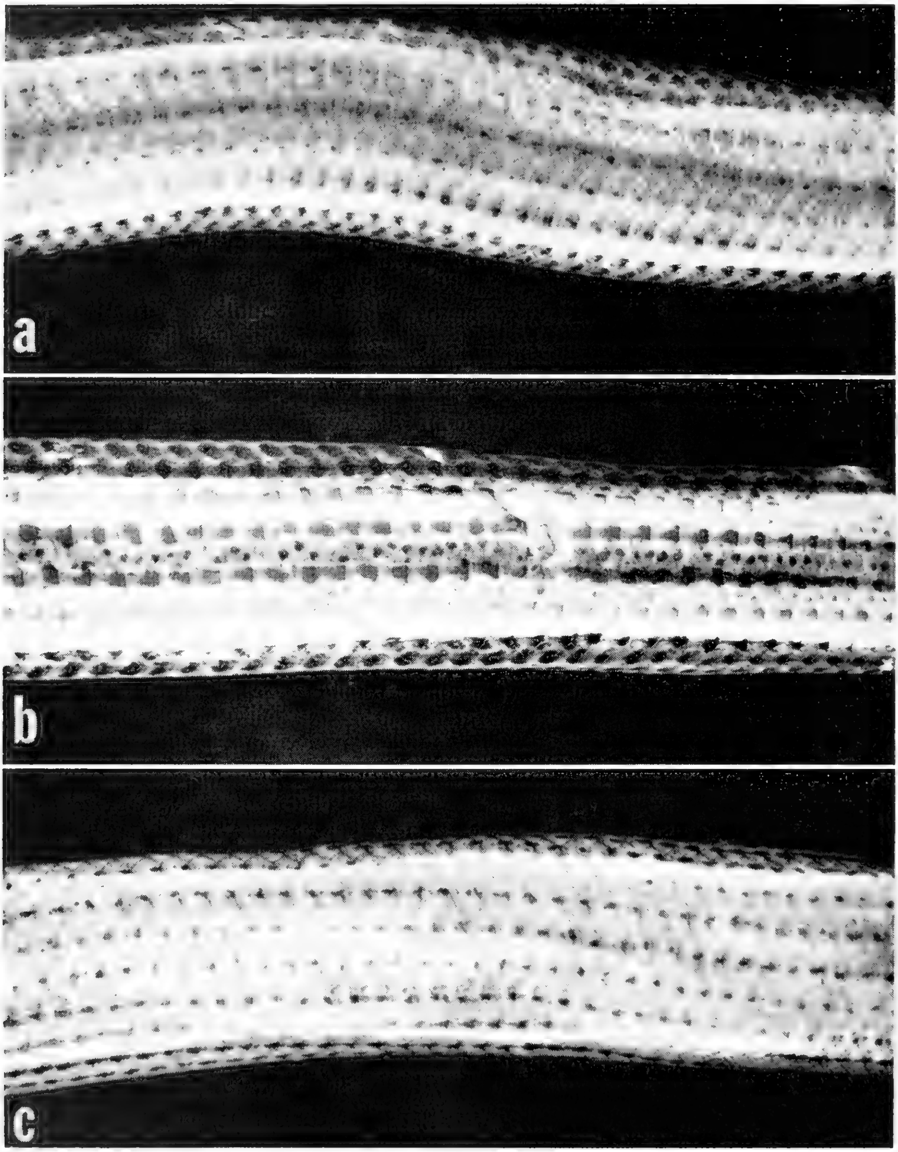

Figure 8. "*Punctatissimus*" group of the genus *Ophiomorus*; mid-body sections showing typical color patterns: a) *O. punctatissimus*; b) *O. latastii*; c) *O. persicus*.

Cream above in preservative, the four median dorsal scale rows of body without dark markings or with four faint dark lines. A broad brown lateral stripe extending from nostril to tip of tail, three scale rows wide on body, and involving four scale rows. Five brown lines on the venter, from chin to end of tail. Dorsum of tail with four narrow brown lines.

Remarks. Xanthus is apparently the only recorded locality for Turkey; all other localities are in mainland Greece. The single specimen examined here from Xanthus is indistinguishable from those from Greece.

MCZ 25933 has 20 scale rows at midbody, the reduction to 18 taking place just posterior to this point.

This species has been collected under rocks (Schreiber, 1912; Werner, 1930; Hellmich, 1956).

Snout–vent length (mm.): ♂: 53–77; ♀: 50; dorsal scale rows from occipital region to a point at the level of the vent: ♂: 102–107 (mean 104); ♀: 113.

CAS 12752 contains ovarian eggs, the largest less than 1 mm. in diameter.

Ophiomorus latastii Boulenger.

(Figures 7c, 7d, 8b.)

Ophiomorus miliaris (*nec* Duméril and Bibron) Günther, 1864, Proc. Zool. Soc. London, p. 488.

Ophiomorus latastii Boulenger, 1887, Cat. Lizards British Mus., vol. 3, p. 398, pl. 33, fig. 2 (type locality: Palestine: Mt. Hermon); 1887, Bull. Soc. Zool. France, vol. 12, pp. 533–534. Haas, 1951, Bull. Res. Council Israel, vol. 1, pp. 75–76.

Distribution. Lebanon; Israel; Jordan. Upper and Lower Galilee and the Jordan Valley (Haas, 1951).

Known localities. LEBANON: Mt. Hermon (Günther, 1864, type locality). ISRAEL: Mt. Carmel (Haas, 1951); Mt. Gilboa (Tirat Zvi) (Haas, 1951); Ein Hamifratz. JORDAN: Waid Heidan, east of the Dead Sea (Haas, 1951).

Material examined (3). CAS 87417, Palestine. CNHM 74419, no data. AMNH 88382, Israel: Ein Hamifratz.

Diagnosis. Snout acutely conical, a slight labial edge; rostral projects beyond lip; no prefrontals; supranasals narrowly in contact, partly separated from one another anteriorly by the apex of the rostral. Sixteen scale rows round the middle of the body. Limbs lacking.

Cream above in preservative, each scale of body and tail with a dark brown spot, these spots being more or less confluent, forming longitudinal dark lines on the dorsum and sides, running the length of body and tail. Two stripes on either side, much broader than those on the dorsum, and narrowly separated. Lines of discrete brown dots on all ventral surfaces. A brown line from rostral through the eye and temporal region, becoming confluent with the two broad lateral stripes. Lips and top of head with scattered brown dots.

Remarks. *Ophiomorus latastii* is the most specialized of the three western species as regards the head shields. The prefrontals are absent, apparently as a result of fusion with the first supraocular. The loreal is larger, and the perocular smaller than in any other species of the genus, and the rostral larger, wider, and more projecting than in either *O. persicus* or *O. punctatissimus.*

The color pattern is the least specialized of any member of the genus, in that each scale of the body has a dark marking, confluent as longitudinal stripes on all scale rows except on the belly, where they form lines of discrete dots.

AMNH 88382 contains ovarian eggs, the largest approximately 2 mm. in diameter.

Ophiomorus persicus (Steindachner).

(Figures 7e, 7f, 8c.)

Hemipodion persicum STEINDACHNER, 1867, Sitzb. Akad. Wiss. Wien, vol. 55, p. 265, pl. 1 (type locality: Persia; here restricted to Iran: Fars Province: 5 kilometers southeast of Pol-i-Abgineh, approximately 29°33′ N., 51°46′ E.[10]). BLANFORD, 1876, Eastern Persia, vol. 2, Zool. and Geol., p. 394.

Ophiomorus persicus BOULENGER, 1887, Cat. Lizards British Mus., vol. 3, pp. 396–397; 1887, Bull. Soc. Zool. France, vol. 12, pp. 526–528. NIKOLSKY, 1915, Faune de la Russie, vol. 1, p. 516. WERNER, 1936, Festschrift Strand, vol. 2, p. 201. ANDERSON, 1963, Proc. California Acad. Sci., ser. 4, vol. 31, p. 476.

DISTRIBUTION. Western slopes of Zagros Mountains in southwestern Iran.

MATERIAL EXAMINED (18). CNHM 141555–141565, 141576–141582, Iran: Fars Province: 5 kilometers southeast of Pol-i-Abgineh, Collected by W. S. Street, J. K. Street, and D. M. Lay, January 1–4, 1963.

DIAGNOSIS. Snout obtuse, rounded, the rostral scarcely projecting beyond lip; 20 scales round the middle of the body. Fingers three; toes two.

Cream or light brown above in preservative, each dorsal and lateral scale with a brown spot, these more or less confluent to form lines the length of the body. These dark lines are distinct on the sides, the four median lines being much paler. The dots are not confluent on the tail. The ventral surface of the body is cream or tan, the four ventral rows of scales free of dark spots. All scales of tail possess a dark spot. A brown line from nostril through eye, onto temporal region; upper surface of head mottled with brown.

REMARKS. In form and color pattern *Ophiomorus persicus* most closely resembles *O. punctatissimus,* undoubtedly its closest living relative. In addition to the presence of small limbs, it differs from *O. punctatissimus* in the absence of any external ear opening, and the snout, which is slightly more

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[10] The specimen in the British Museum from the type series collected by F. Kotschy in 1845 is labeled "Kurdistan." Since the name Kurdistan is applied to several widely separated regions in Iran, the type locality cannot be determined. The specimens collected by the Street Expedition to Iran constitute the second record for the species, and are from one of the regions sometimes referred to as Kurdistan (see United States Board on Geographic Names, 1956, Gazetteer number 19, Iran, pp. 305 and 314).

blunt. As in the other two western members of the genus, there is some dark pigmentation of the peritoneum and the mesenteries investing the digestive tract.

While it is extremely doubtful that *O. persicus* itself could have given rise to any of the other living species of the genus, it occupies the central position in the group geographically, as well as with respect to the adaptive trends observed in these lizards.

In *O. punctatissimus* and *O. latastii* there have been modifications of the skull and head scalation, apparently in relation to burrowing habits, just as the eastern members of the genus have independently undergone even more drastic modification in these structures. *Ophiomorus persicus* shows little specialization in this regard, and most likely is representative of the ancestral skull form. *Ophiomorus persicus* is intermediate in the reduction of the limbs, the sand-inhabiting species having the least limb reduction, while the two westernmost species have lost all external vestiges of limbs. In number of longitudinal scale rows *O. persicus* is also intermediate. It shares the lack of external ear opening with the eastern species, however.

Snout–vent length (mm.): ♂: 56–69; ♀: 73–82; dorsal scales from occipital region to a point at the level of the vent: ♂: 112–117 (mean 114.3); ♀: 118–124 (mean 120.8). Thus there seems to be strong sexual dimorphism in size as well as number of dorsal scale rows in this species.

The following specimens contain ovarian eggs: CNHM 141555, 141557, 141558, 141560, 141561, 141565, 141579. The largest egg is slightly less than 2 mm. in diameter.

Discussion

The genus *Ophiomorus* is composed of nine species as recognized here. The genus is distributed from Greece through southwest Asia to northwestern India. None of the species have been collected in eastern Turkey, Syria, Iraq, or northern Iran. This apparent hiatus in their distribution may be due in part to their secretive habits. Collection records are few for the entire genus.

Ophiomorus chernovi is known from a single locality, Pul-i-Khatun, Turkmen, USSR, several hundred miles north of the nearest Iranian record for the genus. The westernmost record for *O. blanfordi* lies several hundred miles west of the two other known localities for this form. All three localities are either known or presumed to be coastal dune areas.

Ophiomorus punctatissimus is apparently known outside of mainland Greece only from Xanthus, in southwestern Turkey. Obviously, much more collecting is required before the limits of distribution can be established for any of these forms.

While little is known of the habits of these animals, they fall into two groups from the standpoint of habitat selection as well as morphology. The eastern forms, *O. brevipes, O. chernovi, O. blanfordi, O. streeti, O. tridactylus,* and *O. raithmai,* are sand-burrowers, and their morphological adaptation to this mode of life is at once apparent. The least specialized of the sand-dwelling forms is *O. chernovi,* with 24 scale rows, the snout being very slightly less wedge-shaped than any of the others. It has four fingers, as do *O. brevipes* and *O. blanfordi.* The three-fingered species have the most sharply acuminate snouts, *O. tridactylus* and *O. raithmai* having the greatest degree of fusion of the head shields, but retaining 22 scale rows, while *O. streeti* has only 20. From the standpoint of color pattern, *O. streeti* and *O. raithmai* are the least specialized, while *O. tridactylus* has lost the dark pattern almost completely.

The three western species have been collected under rocks, and do not live in areas of wind-blown sand. The tendency to limb reduction finds its extreme in these species. Least specialized of the three is *O. persicus,* also the most central in the distribution of the genus. It has an obtuse, rounded snout, possesses limbs, but with only three fingers and two toes, and has 20 scale rows round the body. The most specialized of this group is *O. latastii,* with only 16 scale rows round the body. In this species the prefrontals have apparently fused with the first supraoculars, and the snout is acutely conical. This form possesses a color pattern that is probably closest to the ancestral type, however, each scale of the body and tail bearing a dark spot, these arranged to form lines the length of body and tail.

Both of the limbless species, *O. latastii* and *O. punctatissimus,* have external ear openings, a curious fact, since *O. persicus,* in many ways the least specialized of the genus, lacks external ear openings, as do the sand-dwelling species.

Dark pigment is present in the peritoneum and the mesenteries investing the digestive tract in all of the three western species. The pigmentation is heaviest in *O. persicus.* In the sand-dwelling species the peritoneum and mesenteries are devoid of dark pigment. If this pigmentation has a role in the animals' thermal relations to the environment, the basic habitat differences are undoubtedly reflected here. Subsurface sand dune temperatures are relatively static, while the microhabitat under rocks, or in burrows where there is air circulation, may exhibit considerable fluctuation of temperature.

Taxonomic recognition of the two major groups of the genus as presently constituted would certainly be justified, placing the dune-dwelling species in the genus or subgenus *Zygnopsis* Blanford. Because *Ophiomorus persicus* appears to link the two groups in some morphological respects, and since a study of the intergeneric relationships of the skinks of southwest Asia is contemplated, we have not separated the two radiations into separate taxa here.

The morphology of these lizards, as well as their distribution, invites speculation as to their evolutionary history. A hypothetical ancestral form would be expected to have 24 scale rows round the body, a rounded, conical snout, external ear openings, at least four fingers and three toes, and a dorsal and lateral pattern of dark brown longitudinal stripes or linearly arranged dots involving all of the scale rows of the elongate body. Such a form might have existed in the area which is now the Central Plateau of Iran and upland areas of Iran and contiguous country at a time when this region had a climate supporting a more or less continuously distributed savannah or grassland vegetation type.

With the breakup in the continuity of this habitat, possibly coincident with increased orogeny in the western portion of the region, one line of specialization resulted in the legless western species occupying an upland, under-rock habitat. With increasing aridity and further fragmentation of the environment of the Central Plateau of Iran, a line of specialization adapted to live in the windblown sand took place.

Wind as an agent of distribution of Ophiomorus. The morphological specialization of the eastern species has been directional, in a geographic sense, from north to south and west to east. The four-fingered forms have not been collected east of the Iranian border (with the exception of a record for *Ophiomorus blanfordi* 10 miles east of the border). The least specialized of these forms is the most northern while the southernmost is the most highly modified. Of the three-fingered forms, *O. streeti,* the least specialized as regards head shields and color pattern, is found farthest west; the other two forms occur to the east of the Iranian Plateau, and there is a suggestion, based on insufficient material, that even more highly modified populations exist to the east of these.

This distribution suggests that the dune-inhabiting forms originated on the northern Iranian Plateau, increasingly modified populations subsequently becoming distributed southward and eastward. Since these animals are obligate dune dwellers, they are dependent on the progressive movement of the sand for their distribution.

We are indebted to Mr. Adrian H. Gordon of the United Nations Technical Assistance Board and Special Fund in Tehran for the following information on surface winds in eastern Iran:

> During the cold months the area is under the influence of the Siberian Anticyclone. A strong northeasterly stream of air moves over parts of the Iranian Plateau in the winter. Frequently, however, relatively warm, moist air masses from the Mediterranean break through the plateau.
>
> In the summer the Iranian winds are dominated by the Indian monsoon system, but since higher pressure prevails to the north at all seasons (northeast in winter and northwest in summer), there is no reversal of wind directions from winter to summer in Iran. The low pressure area of India and Pakistan in summer influences the entire Middle East, and winds generally blow toward this low center in all sections. Over most of the Iranian Plateau the wind direction is more or less from the north or northwest, but the actual direction of local winds is modified by topography. On the eastern borders of Iran, particularly in Seistan, north to northwest winds (the "Bad-i-Sad-o-Bist-Roz" or

> "Wind of 120 days") blow from May to September from the northwest with great regularity, steadiness, and sometimes violence; the direction appears to be fairly constant. These winds are said to reach 40 or 50 knots, with gusts of 60 to 70 knots. This is a powerful erosive force, driving clouds of dust and gravel before it, and in ruined cities of the region, all walls built at right angles to the direction of wind have been demolished. [Adrian H. Gordon, *in litt.*]

The sand-living populations of *Ophiomorus* recognized in this review are apparently isolated from one another by physical barriers to the distribution of the dunes in which they live. *O. tridactylus* is isolated from *O. raithmai* by the Kirthar Range and the rugged broken terrain of Baluchistan. The Sulaiman Range may isolate the Afghanistan population from populations of *O. tridactylus* in the Thar Desert of Rajasthan and the Punjab. *Ophiomorus raithmai*, the coastal Pakistan population, is found west of the Indus River, possibly isolated from recognizably distinct populations east of the Indus.

These populations are somewhat analogous to island populations in their isolation from one another. Contact between populations can be reestablished only as the agency of wind in conjunction with changing landforms brings existing dune areas into contact. Thus, while geographic isolation may be relatively transitory, immediate genetic isolation can be assumed to be complete. Small populations of considerable genetic and phenotypic stability would be expected, and the evidence from the admittedly small amount of material at hand is not inconsistent with this hypothesis.

Ophiomorus and the related genera, *Chalcides* and *Scincus,* may have arisen from a *Eumeces*-like forebear. The relationships among these genera are in need of investigation before any more meaningful speculation can be made. Perhaps worthy of note is the fact that there is little overlap in the distribution of *Ophiomorus* with either *Chalcides* or *Scincus.*

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 17, pp. 535–542; 1 fig. July 8, 1966

THE STRATIOMYIDAE (DIPTERA) OF THE GALÁPAGOS ISLANDS[1]

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The stratiomyid fauna of the Galápagos Islands is, as would be expected, limited but quite interesting. So far as known it consists of five species, at least four of which are endemic though showing close relationships with the other Neotropical fauna, either insular or continental.

Previous studies of the Galápagos Stratiomyidae have been quite scant. The first species to be known from the Archipelago, *Nemotelus albiventris* Thomson (1868), was collected on the expedition of the Swedish frigate *Eugenie*, although at the time of its description it was recorded as coming from the Philippine Islands. Coquillett (1901) recorded three species, and Curran (1932) repeated these records but described as new the species which Coquillett had thought to be the same as his *Pelagomyia albitalus*, from St. Vincent. Johnson (1924) mentioned no Stratiomyidae as represented in the Williams material. Curran (1934) added several records for *Pelagomyia dubia*, including the male but without description of that sex.

The present study is based chiefly on the collections of the 1964 Galápagos International Scientific Project, though a small amount of material has come from another source. Holotypes and allotypes of the new species are in the collection of the California Academy of Sciences. I wish to express my thanks to Dr. Paul H. Arnaud, Jr., and to the California Academy of Sciences for giving me the opportunity to study this interesting collection.

Pelagomyia dubia Curran.
Pelagomyia dubia Curran, 1932, p. 348.

This species was originally recorded from Albemarle Island by Coquillett

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[1] Scientific paper 2699, College of Agriculture, Washington State University. Work was conducted under Project 9043. Contribution no. 41 from the Charles Darwin Foundation.

(1901) as *P. albitalus* Coquillett. Curran (1932) pointed out that *P. albitalus,* as originally described from St. Vincent, is a different species, and he described the Galápagos form as *P. dubia,* the type, a unique female, coming from Charles Island.

The male is similar in appearance to the female and Curran's description applies equally well to both sexes. The amount of black pile on the frons is variable, the sexes showing no difference in this respect. Coloration is not clearly defined; reddish brown may merge into brown and into blackish, and within a series and the same sex color variation may occur; the face, frons, and vertex, for example, may range from light reddish brown to dark brown. Pale abdominal tegumentary fasciae are usually quite evident. The "pollinose" abdominal fasciae described by Curran are composed of tomentum rather than pollen; the tomentum is almost silvery and fairly long. The width of the frons and vertex is approximately the same in both sexes; the ratio of the vertex to head width in two males measured 0.24 and 0.24, that of two females measured 0.23 and 0.26.

An exceptional size range, not associated with sex, was observed, particularly in the Academy Bay series. Extremes in length measured 5.5 and 14 mm. (with ovipositor withdrawn); the usual range was 9 to 12 mm.

NEW RECORDS. 40♀♀, 16♂♂, Academy Bay, Santa Cruz (Indefatigable) Island, January 21 to February 24, 1964, E. G. Linsley, R. O. Schuster, and D. Q. Cavagnero; 8♀♀, 2♂♂, Little (North) Seymour Island, March 10–14, 1946, Dale Jenkins.

Nemotelus albiventris Thomson.

Nemotelus albiventris THOMSON, 1868, p. 462.

This species was described from a unique male with the locality given as "Manilla" (Manila, Philippine Islands). Coquillett (1901) recorded it from a single specimen, sex not stated, from Albemarle Island, with the explanation that the type locality as stated by Thomson was probably erroneous, since the *Eugenie* expedition included collections from the Galápagos as well as from the Philippine Islands and other Pacific areas. Curran (1932) repeated Coquillett's record, without comment.

Coquillett was probably correct in the recognition of the Galápagos form as this species. The genus is, so far as known, foreign to the Oriental and Australasian faunas. The males which I have had for study agree quite well with Thomson's description, though some of his detailed description of the wing venation is hard to interpret. Also, his statement, "thorax . . . parce et tenuiter pallido-pubescens" hardly applies; the pubescence of the thorax is rather dense, though Thomson's specimen may have been somewhat rubbed. *Nemotelus albiventris* is close to *N. albirostris* Macquart from the southeastern United States; the two differ in a number of respects, however, chiefly in the more attenuated facial prominence of *N. albiventris,* the coloration of the facial prominence (wholly whitish above in *N. albirostris,* wholly black or whitish only in front of the base of the antenna in *N. albiventris*), and the pale markings of the female abdomen (paired spots on the intermediate segments in *N. albirostris,* transverse bands in *N. albiventris*). It is reasonable to hypothecate that *N. albirostris* is ancestral to *N. albiventris;* the introduction of the ancestral stock from the coastal mainland, the present-day habitat of *N. albirostris,* to the Galápagos Islands would have been quite natural.

New records. 22♂♂, 10♀♀, Academy Bay, Santa Cruz (Indefatigable) Island, January 23 to February 20, 1964, R. O. Schuster and D. Q. Cavagnero; 1♀, Darwin (Culpepper) Island, January 29, 1964, D. Q. Cavagnero; 5♀♀, Tower (Genovesa) Island, March 25, 1953, Templeton Crocker.

Nemotelus acutirostris Loew.

Nemotelus acutirostris Loew, 1863, p. 8.

This species was recorded from the Galápagos Archipelago by Coquillett (1901) on the basis of one specimen, sex not indicated, and the record was repeated by Curran (1923). It is common in Cuba, the Florida Keys, and Bimini Islands (from which I recorded it erroneously as *N. wheeleri* Melander). I have not seen any material from the Galápagos and the record from those islands may be erroneous; I have seen a closely related, undescribed species from Baja California which may be conspecific with the Galápagos form.

Brachycara digitata James, new species.

Male. Head black, subshining; a pair of triangular ivory spots on the frontal triangle. Eyes subcontiguous for about half the distance from antennal base to anterior ocellus, set with scattered, short, stiff black hairs. Very narrow facial and occipital orbits whitish tomentose, tomentum of facial orbit almost pollen-like; face with silvery, genae with yellowish white appressed hairs. Ocellar triangle prominent, with a few whitish hairs. Antenna brownish yellow on first, second, and basal three segments of flagellum, otherwise black; hairs same color as background; terminal flagellar segment as long as preceding two combined. Proboscis pale yellow.

Thorax including scutellum black; humerus below and postalar callus in part brownish yellow; a narrow yellow line from each humerus to wing base. Mesonotum and scutellum with considerable whitish tomentum and some erect white pile, the latter more abundant posteriorly and on the scutellum; pile of pleura white, mostly semierect on mesopleura and pteropleura. Legs brownish yellow, the front pair, all coxae and trochanters, middle tarsus, and hind basitarsus more nearly clear yellow. Halteres yellow. Wing subhyaline; stigma brown; second basal cell without microtrichia except a few along its anterior margin; anal cell with microtrichia on approximately its apical half. Squamae and hairs yellow.

Abdomen pellucid yellow on disc; first tergum, basal half to two-thirds of fifth, and lateral margins of intermediate terga brownish to brownish black; the infuscation of the intermediate terga suggests anterolateral spots, but these are not clearly defined. Sternal pattern similar but with less well defined lateral margins. Terga with short, appressed black pile and sterna with similar yellow pile; sides of abdomen with erect to semierect black to yellowish pile. Genitalia (fig. 1) brownish to black, ventral plate yellow; dististylus well sclerotized, subshining, slender, with a more slender, digitate process extending ventrad C-like from its base; aedeagus trifid, the lateral processes well separated on apical part and there running almost parallel to the intromittent organ.

Length, 5–6 mm.

Female. Frons broad, 0.4 head width. Frontal callus ivory, broadly interrupted medially and consequently forming a pair of slender, transverse triangles. Pile of head and thorax more uniformly silvery than in the male. Abdomen, dorsally and ventrally, pitchy or brownish black, without any pattern; basal two sterna may be more yellowish medially; pile as in the male. Genitalia brownish black. Otherwise except sexually as in the male.

Types. Holotype, male, Santa Cruz (Indefatigable) Island, Academy Bay, Darwin Research Station, February 1, 1964, R. O. Schuster. Allotype, female, same data but January 26. Paratypes, 6♂♂, 1♀, same data but January 26, February 7, and February 18, R. O. Schuster, and February 20, R. O. Schuster and D. Q. Cavagnero.

In my key to the known species of *Brachycara* (James, 1962, p. 88) this species runs to *B. slossonae* (Johnson); however, it is a much more robust

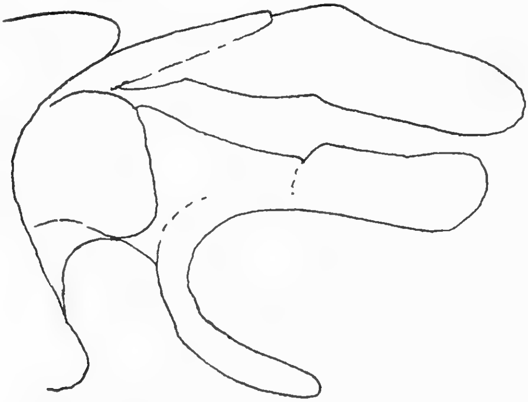

Figure 1. *Brachycara digitata* James, new species. Male genitalia, side view, from holotype. Setation omitted.

species; the antennae in *B. slossonae* are brownish yellow rather than clear yellow at the base and the abdomen of the female is reddish yellow. The male genitalia of the two species are strikingly different; the dististyli of *B. slossonae* are short and oval and completely lack the digitate process of *B. digitata*. *Brachycara maculata* (James), from the Bahama Islands (Bimini), has similar processes but they are filiform rather than digitate; the dististyli are also quite different, being flattened and appearing blade-like when viewed ventrally.

Dactylodeictes insularis James, new species.

Female. Head and body, excluding appendages and ovipositor, wholly black. Head in profile similar to Lindner's illustration of his *D. lopesi;* antennae similar in structure, set at approximately middle of eye height; the ocellar triangle more prominent than that illustrated by Lindner, though not nearly as much so as that of *D. amazonicus* Kertész, according to Kertész' illustration. Frontal callus not well marked; area between callus and ocellar triangle wholly punctate, with appressed whitish pile (or long tomentum); area below callus glossy black and bare medially, receding somewhat into a pit toward antennal bases; a broad lateral orbit beginning at the callus and extending on each side of the depressed area, then continuing laterad and forming the facial orbits, white tomentose and pollinose; these orbits on the front are each a little more than half the greatest transverse diameter of the frontal depression; face aside from orbits with semierect to appressed white pile except for a narrow extension of the glabrous frontal area that extends between the antennae and to the upper part of the oral margin. Ocellar triangle with only a few very short black hairs. Occipital pile appressed, white on the cerebrale, otherwise black above and yellowish below; occipital orbits with white pollen-like tomentum and a fringe of white hairs. Genae shining medially, in some specimens castaneous although usually black like the rest of the head. Eyes bare. Antennae yellow, the basal segments almost whitish, flagellar complex and arista orange-yellow; a crescentric polished brownish black spot on inner margum of flagellum, as in *D. lopesi*. Proboscis brownish black.

Mesonotum with considerable appressed pile, mostly yellowish except laterally. Scutellum forming only a slight angle with the mesonotum; pile yellow on disc, black laterally and on the apical fingerlike projection; the latter bluntly rounded and forming an angle of about 45° with the dorsal surface of the scutellum. Pleura with white appressed pile, contrasting in color with that of the mesonotum except on the supra-alar regions. Coxae black; front tibia except at base and basal two segments of front tarsus brown, legs otherwise yellow. Halteres yellow. Wing hyaline; vein R_1 along approximately length of first basal cell brown, the costa less distinctly so along approximately the same extent; veins otherwise yellow except when concolorous with the membrane. R_{2+3} arising interstitially with or slightly before r-m, the latter very short or punctate. Wing uniformly set with microtrichia beyond its base; bare areas include anterior half or more of anal cell and base of basal cells, but not the alula. Squamae and their pile yellow.

Densely punctate area of abdomen extending dorsally broadly to apex of third tergum but not very clearly discernible, black pilose; first sternum and sides of second quite evidently densely punctate and with short, white microsetulae; abdomen otherwise with white hairs, ground color more shining ventrally. Ovipositor yellow to brown.

Length, 3–3.5 mm.

MALE. Very similar to the female; the frons is narrower, its width not exceding that of the ocellar triangle; consequently it broadens more rapidly toward the callus. Genitalia not exposed in the single male available and not dissected.

TYPES. Holotype ♀, Santa Cruz (Indefatigable) Island, Academy Bay, Darwin Research Station, January 29, 1964, R. O. Schuster. Allotype, male, same data but February 7. Paratypes, 9 ♀ ♀, same data but January 23, January 26, February 7, and February 20, R. O. Schuster, and February 9, February 13, and February 24, D. Q. Cavagnero and R. O. Schuster.

A female was selected as the holotype because of its much better state of preservation than that of the single male of the series.

Two species have been described previously in this genus: *D. amazonicus* Kertész (1914, p. 545), the type, and *D. lopesi* Lindner (1914, p. 15). *Dactylodeictes amazonicus* differs from both *D. insularis* and *D. lopesi* in the highly elevated vertex, particularly of the female, the position of the antennae well below the middle of the head, in the lack of a polished crescent-shaped callus on the antennal flagellum, and in other respects. *Dactylodeictes lopesi* is described by Lindner as having the scutellum set at an angle of 45° with the mesonotum; in contrast the scutellum and mesonotum are described by Kertész as being on the same plane, and this is virtually also true of *D. insularis*. Also, in *D. lopesi* the head from the front is described as shining black with whitish tomentose ocular orbits; this is true of *D. insularis* except that the frons above the callus is almost wholly clothed with appressed pile. I have seen a male from Corozal, Canal Zone, January 21, 1929, C. H. Curran, which agrees with *D. lopesi* in these respects. It is closely related to *D. insularis,* though distinct. If it belongs to *D. lopesi,* the known distribution of that species (southern Brazil, Canal Zone) suggests another mainland migrant to the Galápagos Islands which has there undergone sufficient differentiation to be of specific significance.

ADDENDUM

It appears as though *Chrysochlora fasciata* Thomson, 1868: 460, described from the Galápagos Islands, is a senior synonym of *Pelagomyia dubia* Curran, although there are some discrepancies in the original description of *C. fasciata*. If this is so, that species will take priority as *Pelagomyia fasciata* (Thomson), new combination.

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 18, pp. 543–550; 6 figs. July 8, 1966

CRITICAL NOTES ON THE GENUS *STENOPELMATUS* BURMEISTER IN CALIFORNIA, WITH REDESCRIPTION OF *S. INTERMEDIUS* DAVIS AND SMITH AND A KEY TO THE SPECIES

By
Ernest R. Tinkham

It seems desirable at this time, preparatory to revisionary studies on the Californian species of the genus *Stenopelmatus* and the description of several new species, to present a critique on the present status of that genus in California which would form the foundation for further work. With this in mind, critical notes will be presented on the present valid species, along with a key and redescription of *Stenopelmatus intermedius* Davis and Smith.

California is not only the zoocenter of the genus in North America, but by the same token is also the synonym-center of that genus. The synonyms *S. californicus* Brunner, *S. irregularis* Brunner, *S. oculatus* Scudder, *S. histrio* Saussure, *S. cephalotus* Walker, and *S. hydrocephalus* Brunner have all been reported from California and attest to this fact. The *Stenopelmatus* species generally accepted as valid at the time of this writing include *S. fuscus* Haldeman, *S. longispina* Brunner, and *S. pictus* Scudder. The status of *S. intermedius* Davis and Smith, the last species to be described in 1926, is at present questionable and needs clarification. The taxonomic situation is further complicated by megacephaly, particularly in the male sex.

Summary of Taxonomic Characters

The status of the last named species, *S. intermedius,* must be at present questioned, chiefly because of the nebulous nature of the features used in its description by its authors. Such features as the punctation of the head, the relative length of the three basal segments of the antennae, and the nature of the frontal sutures appear useless in a genus as notoriously difficult as is *Stenopelmatus*. What is needed are prominent characters which can be used to separate the various valid species as well as any newly named species.

Likewise, a study of the prosternal plate, which also exhibits some variability in a species, seems to offer no critical criteria for the separation of the species and is all too often hidden under the backwardly directed head. Similarly, the meso- and metasternites offer little differentiation of worth. The subgenital plates in both males and females are morphologically similar in the various species and thus appear valueless. The ovipositor, without any evidence of teeth, appears likewise to be of no value in the separation of the females of the various species.

With the elimination of the above-mentioned features, we are forced to rely on the chaetotaxy of the legs for the eventual separation of the several species, despite the fact that Davis and Smith stated "as not dependable and varies from one extreme (*S. fuscus*) to the other (*S. longispina*) in the same locality in Berkeley." Those authors also stated "the simplest way out would be to call all specimens of the genus *Stenopelmatus fuscus*, as all our crickets are named *Gryllus assimilis*."

Despite the above statements concerning valueless features as well as those of Davis and Smith, it appears that *S. intermedius* must be considered a biological species or race based on the fact that those authors observed mating in *S. intermedius* and could induce no crossbreeding with the other known Californian species which were considered to be *S. fuscus* and *S. pictus*; *S. longispina* was considered a synonym of *S. fuscus* by Davis and Smith.

The writer firmly believes that a thorough study of any group of animals will reveal valuable characters perhaps overlooked by earlier workers where lack of time and specimens may have been a factor. It is interesting to note that Scudder, in 1899, based his key on the spination of the caudal tibiae and Hebard, 1916, combined these characters with size, form of head, length of limbs, and the calcars or terminal spurs of the caudal tibiae in his key separation of the valid species.

REDESCRIPTION OF *STENOPELMATUS INTERMEDIUS* Davis and Smith

In their description of *S. intermedius*, Davis and Smith failed to mention a single word concerning the chaetotaxy of the legs, which character or feature appears to be the most important of the taxonomic criteria at present available. Those authors devote their rather lengthy description to the punctation of head and frons, antennal segments, and the shape of the prosternal spine or plate, features which seem worthless. On the other hand, their minute description of the stridulating plate has considerable merit; the chief drawback in the use of this organ as a taxonomic character is in the fact that the hind leg has to be removed before an unobstructed view of the plate can be obtained. Since no mention was made by Davis and Smith concerning the leg spination, a complete redescription of the types is presented below.

The writer wishes to thank the authorities of the California Academy of Sciences, particularly Mr. Hugh B. Leech, for permission to study the types. It should be noted here that the holotype is a male and not a female, as stated on page 179 by Davis and Smith; the holotype label I have corrected by changing the ♀ sign to a ♂ sign. Hence, the allotype is a female and interestingly enough, the ink label so states but someone has crossed out the inked "Allotype" in pencil and written in pencil "Holotype."

Stenopelmatus intermedius Davis and Smith.

Form typical of the genus; size medium-small. Appearance of the head moderately slender; its depth from occiput to clypeal suture exactly equaling the breadth of the head at that suture which measures 5.6 mm. in the type male. Eyes inverted–pyriform; viewed in profile slightly subglobose but less so than in *S. fuscus* and *S. longispina.*

Pronotum approximately the same breadth as the maximum width of the head, its length about nine-tenths the pronotal width; in dorsal profile lateral margins parallel in anterior half, very gently rounding in the posterior half and thus only slightly narrowed in the posterior half, a feature distinguishing it from *S. fuscus* and *S. longispina* but closely resembling that observed in *S. pictus*. Anterior margin of pronotum gently emarginate; posterior margin practically straight; inferior margin of the lateral lobes very broadly rounded posteriorly, gently rounded anteriorly with a slight emargination about the anterior third.

Leg spination as follows: legs with tibiae only bearing spines. Foretibiae with four apical acuminate calcars which have their internal faces obliquely truncate to near their bases; the two internal calcars the largest and nearly equal in size, the two external smaller and equal, the smaller bearing the less oblique face. Dorsal internal margin (ventral in folded leg) with one large spur immediately basad of the long dorsointernal calcar. Ventral margin with one apical acuminate spur directly basad of the large ventrointernal calcar which is followed by one similar subapical spur and a third slightly smaller spur situated about the apical third, the three not forming a straight line. Mesotibiae with four long, even, acuminate calcars, with a smaller ventral pair of acuminate spurs (dorsal in folded leg) just basad of the ventral pair of calcars. Externo-dorsal margin (ventral side of folded leg) with one subapical acuminate spur and another similar spur about the apical third; internal dorsal margin with an acuminate spur at the apical three-fourths and a smaller one about the basal third. Caudal tibiae with six apical calcars, a ventral pair of apical small spurs and two external and four internal dorsal spines. Regarding the four internal dorsal spines, the apical (counted number 1) is slightly smaller than number 2, slightly larger than number 3, and considerably larger than number 4 which is quite small in size and located at the basal third. External dorsal spines with number 1 (nearest apex) short and heavy and number 2 smaller; these paired with internal dorsal spines 1 and 2. Apical calcars with the internal dorsal one (no. 1) the largest, acuminate, and with its inner surface flattened near apex. Calcars 2 and 3 equal and slightly shorter than number 1, number 4 shorter than 2 and 3, number 5 shorter than 4, and number 6 equal to number 4 in size. The small pair of ventral spurs is situated just basad of calcars 3 and 4. Tarsi all four-segmented, the first segment twice the length of the second which is, in turn, twice that of the very short third, the fourth segment bearing the claws. First three tarsomeres with their dorsoventral angles bluntly acute, the first with a similar blunt knob about the basal half.

Genitalia. Supra-anal hooks typical of the genus; subgenital plate strongly convex, the posterior margin broadly circularly rounded. Ovipositor typical of the genus.

Coloration. Generally dark, the head dark reddish brown with the center of the head with a black quadrangular patch from which anastomosing veins run upward and also from the upper point of the compound eyes as shown in figures 3 and 4; this character considered of specific value in the diagnosis of this species. Pronotum and legs dark reddish brown. Ventral surfaces of head and pronotum paler and tinged with yellow. Abdominal tergites shining black, each segment irregularly and narrowly edged with yellow on the anterior margin and regularly edged with a pale yellowish line on their posterior margins.

→

Figure 1. External lateral view of caudal tibia of the male holotype of *Stenopelmatus intermedius* Davis and Smith greatly enlarged, from Oakland, California, XII, 1925, L. M. Smith.

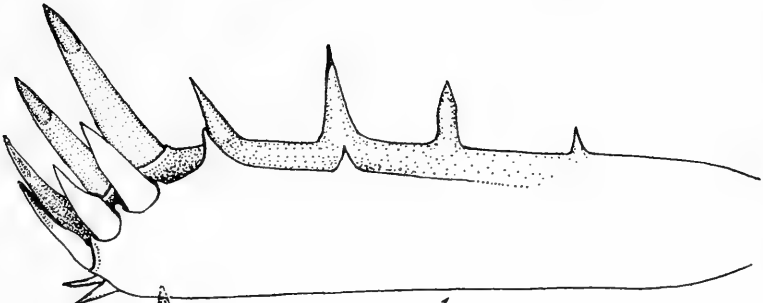
Figure 2. External lateral view of caudal tibia of the female allotype of *S. intermedius* Davis and Smith greatly enlarged, from Oakland, California, XII, 1925, L. M. Smith.

Figure 3. Front view of head of type male drawn eight times natural size and then reduced in printing and showing anastamosing network of veins in occipital half of head.

Figure 4. Front view of head of allotype female drawn eight times natural and reduced in printing.

Figure 5. External lateral view of foretibiae of the male type much enlarged showing calcars and spurs.

Figure 6. External lateral view of foretibiae of allotype female much enlarged showing configuration of calcars and spurs.



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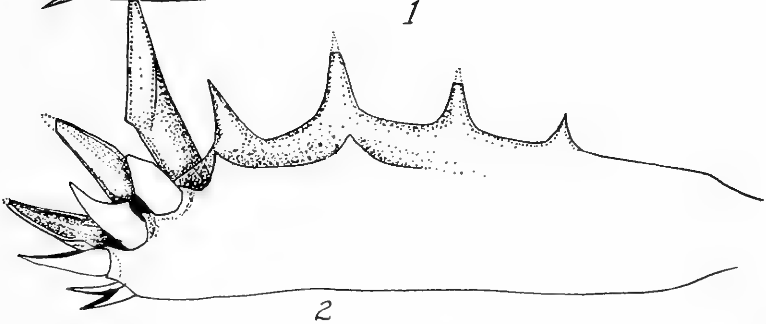

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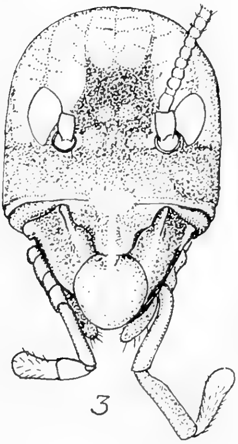

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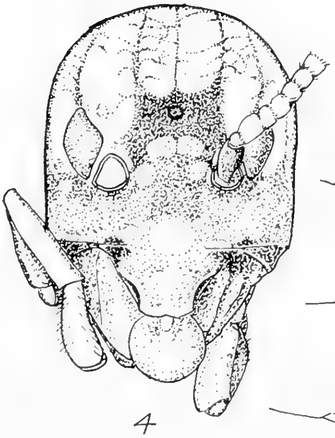

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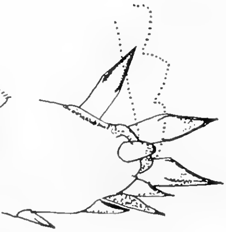

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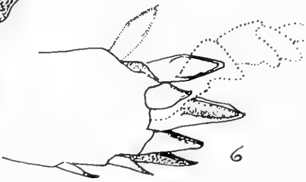

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del. E. R. Tinkham 1964

NOTES ON OTHER CALIFORNIA SPECIES

Stenopelmatus pictus Scudder.

A small, easily recognized species with dark piceous streaks, separated by narrow tan, sutural areas on the upper half of the head and with dark areas of shining black of irregular conformation on the dorsum of the pronotum. Scudder described this rather small species from San Francisco in 1897. Hebard (1916) added Palo Alto, and Davis and Smith (1926) added Suisun to its distribution. Two specimens before me, on loan from the Museum of Zoology, University of Michigan are: one female, Patterson Pass, Alameda County, California, and one male from Antioch, California, March 29, 1956, B. J. Adelson. I have a specimen from Stockton, California, April 15, 1960, collected by Jean Swagerty. It is evident from this brief information that the distribution, habitat, and habits of this interesting cricket are poorly understood at present.

Stenopelmatus longispina Brunner.

Originally described from Vancouver Island; Scudder (1899) added Ft. Boise, Drain, and Roseberg, Oregon, as well as several locations in coastal California to its range. Hebard (1916) indicated that *S. californicus* Brunner and *S. irregularis* Brunner were synonyms and gave a number of places as farther extending its distribution. *Stenopelmatus longispina* is a large reddish brown species characterized by the long, acuminate, conically tapering, internal calcar of the caudal tibia which is much longer than the other five. Much needs to be learned about the distribution, ecological niche, and habits of this interesting creature.

Stenopelmatus fuscus Haldeman.

This large reddish brown species Hebard recorded from many locations in the western United States, extending from Nebraska and New Mexico west to the Pacific Coast and from Montana south to Chihuahua, Mexico. Only a study of extensive collections from this vast area will decide whether there is only the one species or whether several geographic races occur. Hebard indicated that *S. cephalotes* Walker, *S. fasciatus* Thomas, *S. oculatus* Scudder, and *S. hydrocephalus* Brunner were synonyms.

Much still has to be learned about this large, handsome species which is distinguished from *S. longispina* by the more even character of the six calcars of the caudal tibiae, the inner faces of which are obliquely truncate and spatulate.

PROVISIONAL KEY TO KNOWN CALIFORNIA SPECIES

1. Size large; color of head and pronotum orange red 2
   Size medium to small; color of head and pronotum not orange red but piceous to shining black 3

2. Calcars of the caudal tibiae forming a semiringlet of six spurs, the two innermost much the longest and cylindrical in form .... *S. longispina* Brunner

   Calcars of the caudal tibiae forming a semiringlet of six, these spathulate or trowel-shaped on their inner faces, the three inner relatively equal and longer than the three outer spurs .... *S. fuscus* Haldeman

3. Entire body uniformly dark brown with black abdominal tergites. Caudal tibiae with four internal and two external dorsal teeth .... *S. intermedius* Davis and Smith

   Upper half of head shining black with tan sutural areas; pronotum with dorsum bearing irregular areas of shining black. Femora marked with pale brown fasciations .... *S. pictus* Scudder

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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 19, pp. 551–620; 13 figs.; 17 tables July 8, 1966

THE SYSTEMATICS OF THE PACIFIC TREE FROG, *HYLA REGILLA*

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The first review of the western forms of *Hyla* was by F. C. Test in 1898 in which he made some delightful comments on the use of poorly preserved specimens, "meager material collected at points whose precise location and geographical relation to each other were many times but vaguely understood" and "the too ready and free description" of new specimens. This could be taken as a condemnation of some of the practices of the last 65 years of the 19th century. The first 65 years of the 20th century have been characterized by more of the same, including some astounding statements by the senior author. Unfortunately the present work will not offer real solutions to the problem; in fact that is not our intention. If we can kindle the imagination, tease the doubters, and stimulate those who follow, we will have succeeded. We have collected more localities than Test had specimens (512), we have borrowed enough museum material to more than equal our own collections, and we have compared our animals with every North American hyla we could borrow and every hyla we could take the time to look at in our stay at the American Museum of Natural History in the fall of 1963.

With real hesitation we offer the following systematic consideration of a portion of the genus *Hyla* from western North America. The data are too meager, and we have been too ready and free in our descriptions. We would like to wait another 12 years, but we face the fact that, like it or not, this must be done. We have genetic, physiological, and ecological studies which are short on, or completely lacking in, meaning, because the systematic analysis is not available to assist in their interpretation. We have the next round of studies to perform and these require the context of an attempted systematic treatment.

The senior author has long espoused the concept that a subspecies should be described only when to fail to do so would obscure more biological truths than would be lost by describing the subspecies. The reader should be warned that our subspecies is a biological one composed of morphological facts, ecological observations, physiological measurements, genetic approximations, and geological guesses. After reading the paper, some of our colleagues may insist that the subspecies have been drawn from random tables on a malfunctioning computer. Hamming (1962) has stated that "The function of computing is insight, not numbers." The discriminant analyses and factor analyses described here were used to gain information about similarities and differences rather than to establish statistical bases for conclusions. These methods are descriptive rather than statistical; the fact that statistical tests are available once computations are made is useful, but the fact that discontinuous variables in morphology, physiology, ecology, behavior, genetics, and development support the results is of more significance.

NOMENCLATORIAL HISTORY

Hyla regilla was described by Baird and Girard (1852, p. 174) along with several other new species collected by the U. S. Exploring Expedition under the command of Capt. Charles Wilkes, USN. The description is based on "Specimens . . . collected on Sacramento River, in Oregon and Puget Sound." No type specimens were designated.

Yarrow (1882, pp. 171–172) listed a number of specimens of *Hyla regilla* in the U. S. National Museum (USNM), including no. 9182 collected by the C. P. Expedition from "Puget Sound, Alaska," but did not indicate which of these specimens, if any, he considered to be the types.

Cope (1889, pp. 360–363) listed a number of specimens of *Hyla regilla* in the U. S. National Museum, including the Puget Sound specimen listed by Yarrow, but also failed to indicate a type specimen.

Test (1898, pp. 490–491), in his list of *Hyla regilla* in the U. S. National Museum, includes two specimens collected by the C. P. Expedition: no. 9182 from "Puget Sound, Washington" and no. 15409 from "Sacramento River, California." Presumably Test believed that Baird and Girard's description of *Hyla regilla* was based on these specimens for he refers to both of them as type specimens of that species.

Schmidt (1953) restricted the type locality of *Hyla regilla* to Sacramento County, California, for the USNM 15409 and Fort Vancouver, Washington, for the USNM 9182. Cochran (1961, p. 58), in her list of type specimens in the U. S. National Museum, lists the cotypes of *Hyla regilla* as 9182, Puget Sound, Washington, and 15409, Sacramento River, California.

Our examination of USNM 15409, now in very poor condition, indicates that it very probably represents an intergrade of various forms that conjoin in northeastern California. Several characters clearly show this—finger webbing is extensive, extending about one-third the length of the fingers, and ventral granulation appears to stop well before (2.5 mm.) the breast fold. Neither of these characters has been seen in specimens from the Sacramento area or for that matter in any of the *Hyla regilla* examined. At minimum, this specimen, USNM 15409, apparently was not collected in Sacramento County, California. USNM 9182, on the other hand, is in much better condition, and our examination of it indicates that it could very well have come from Fort Vancouver. For these reasons, and for several others, we here designate USNM 9182 as the holotype of *Hyla regilla,* and accept the type locality as Fort Vancouver, Washington, as designated by Schmidt (1953).

Hallowell (1852, p. 183) described *Hyla scapularis* from specimens obtained in Oregon Territory. In the same volume (1852, p. 301) Baird and Girard referred specimens collected by John L. Leconte in San Francisco to *Hyla regilla,* and placed *Hyla scapularis* in the synonymy of *Hyla regilla.* The type specimen of *Hyla scapularis* Academy of Natural Sciences of Philadelphia (ANSP) 1978 is in excellent condition. Unquestionably it may be referred to the race of *Hyla regilla* that now occurs in the vicinity of Vancouver. Thus, *Hyla scapularis* Hallowell is a synonym of the nominate race of *Hyla regilla.*

In 1854 (p. 96) Hallowell described *Hyla nebulosa* on the basis of specimens collected by Dr. Heerman at Tejon Pass (California). This description was immediately followed by a description of *Hyla scapularis* var. *hypochondriaca,* also based on specimens from Tejon Pass collected by Dr. Heerman. Both descriptions were republished in 1859 (pp. 21–22) with slight changes in punctuation and illustrations and the addition of two sentences under "Gen. Obs." following the description of *Hyla nebulosa.*

The specimens on which Hallowell based his description of *Hyla scapularis hypochondriaca* (USNM 3235 (9)) were listed under *Hyla regilla* by Yarrow (1882), Cope (1889), and Test (1898), and were designated as the cotypes of the form by Test. We have examined these specimens and concur with these authors that they may be referred to the race of *Hyla regilla* that occurs in the vicinity of Tejon Pass today.

A number of problems are involved in the identity of *Hyla nebulosa. Hyla scapularis* var. *hypochondriaca* is described (Hallowell, 1854 and 1859) to include the presence of "a narrow, dark colored vitta extending from the anterior margin of the eye to the snout, another much broader from the posterior margin of the eye to the shoulder; margin of upper jaw of same color as the vitta." The description of *Hyla nebulosa* does not mention vitta and includes "dark colored subcircular spots, about a line in diameter, scattered over the upper part of the body, and upon the sides, . . . abdomen and under surface of extremities granulated, terminal disks much flattened"; and a detailed comparison with *Hyla versicolor*. Examination of the illustration of *Hyla nebulosa* shown in the redescription in 1859 (plate X) shows a specimen lacking the characteristic eye stripe and patterns of *Hyla regilla* and possessing the characteristic body form of the canyon toad. These drawings are reported to have been made in the field. The two sentences added to the 1859 description of *Hyla nebulosa* under "Gen. Obs." point out that *Hyla nebulosa* is similar to *Hyla delitescens*. Other authors have not recognized *H. delitescens*. The description by Le Conte (1825) and the description and illustration given by Holbrook would suggest *Hyla versicolor* or *Hyla phaeocrypta*.

We submit that the problem of *Hyla delitescens* is one to be solved by our eastern colleagues, but in any case the beast would be like the *Hyla californiae–arenicolor* group. The characteristics of *Hyla nebulosa* clearly distinguish it from the other species of *Hyla* currently recognized in the Tejon Pass region of southern California. Significantly, both the collectors and Hallowell recognized the existence of the two kinds of animals in southern California. Cope (1866) proposed *Hyla cadaverina* as a substitute name for the preoccupied *Hyla nebulosa*. Yarrow (1882) and Cochran (1961) list the type specimen of *Hyla cadaverina* as USNM 3230. Test (1889) lists USNM 3230 as the type of *Hyla cadaverina,* but this specimen is from Fort Vancouver, Washington. In the previous line Test lists USNM 3230 as the type of *Hyla nebulosa*. A typographical error in Test's paper appears evident. Cope (1889, p. 359) includes a description of the fresh type specimen of *Hyla nebulosa* (=*cadaverina*) and questions the validity of including this form in synonymy with *H. regilla*. The problem is further complicated by the obvious fact that specimen no. 3230 is not one of the animals referred to in Hallowell's original description, nor is it the specimen described by Cope in 1889 (p. 359); (table 1). At the end of his description Cope states "two specimens from Tejon Pass, southern California are located in the Museum Academy of Philadelphia." Hallowell's description refers to "both" specimens. The original cotypes of *Hyla nebulosa* (=*cadaverina*) appear to be lost in the general confusion. Thus, *Hyla nebulosa* Hallowell (=*Hyla cadaverina* Cope) is here considered to be a synonym of *Hyla californiae* Gorman, leaving *Hyla hypochondriaca* as the earliest available name for the race of *Hyla regilla* that occurs in the vicinity of Tejon Pass.

Cope (1866) described *Hyla curta* from 19 "half" adult specimens collected by Jno. Xantus at Cape San Lucas and catalogued under the number 5293. Yarrow (1882) lists these specimens as from Fort Tejon, California. The specimens are now accompanied by a label which indicates they were obtained on August 10, 1859 from Soria, 15 miles north of Cape San Lucas. They are small and faded, the eye mask is still present but the stripes are gone.

Cope (1889, p. 359) described *Hyla regilla laticeps* from eight adult specimens from Cape San Lucas, Baja California, compared it with *Hyla cadaverina,*

Table 1. *Comparative measurements taken on the holotype (USNM 3230) of* Hyla nebulosa *Hallowell (1852) (=* Hyla cadaverina *Cope (1866)) and the largest of eight syntypes of* Hyla scapularis hypochondriaca *Hallowell (USNM 3235).*

	USNM 3230				USNM 3235	
	Hallowell (1852, 1854)	Cope (1889)		Jameson *et al.*	Hallowell (1852, 1854)	Jameson *et al.*
		Lines*	Inches			
Snout–vent	$1\frac{7}{8}''$	19	$1\frac{7}{16}''$	$1\frac{3}{16}''$	$1\frac{1}{2}''$	$1\frac{9}{16}''$
Head width	$\frac{3}{4}''$			$\frac{3}{8}''$	$\frac{5}{8}''$	$\frac{1}{2}''$
Head length		5.9	$\frac{1}{2}''$	$\frac{3}{8}''$	$\frac{5}{8}''$	$\frac{1}{2}''$
Length anterior extremity	$1\frac{5}{8}''$			$1\frac{3}{4}''$	$\frac{7}{8}''$	$1\frac{5}{16}''$
Length posterior extremity	$2\frac{3}{8}''$	32.4^{+}	$2\frac{3}{4}''$	$1\frac{29}{32}''$	$1\frac{7}{8}''$	$2\frac{3}{8}''$

* Twelve lines per inch.

$^{+}$ By addition of femur, 8.7 lines; tibia, 10.6 lines; hind foot, 13.1 lines.

and suggested it was difficult to distinguish from *Hyla curta*. We concur with Cope and determine that the name available for the race of *Hyla regilla* from the Cape region is *Hyla regilla curta*.

Taylor (1938) described *Hyla wrightorum* from Springerville, Apache County, Arizona, and *Hyla cardenasi* from Puebla, Puebla, Mexico. K. P. Schmidt (1953) placed *Hyla wrightorum* in synonymy with *Hyla eximia*. We are of the opinion that this designation is in error. *Hyla lafrentzi* was described by Mertens and Wolterstorff (1929) from the Federal District, Mexico. *Hyla lafrentzi* was placed in synonymy with *Hyla gracilipes* by Kellogg (1932). Taylor (1938) considered *Hyla lafrentzi* a separate species and pointed out that the types of *Hyla gracilipes* differ from *Hyla eximia* by "differences so slight that I regard them as negligible," and he considered *Hyla gracilipes* Cope a synonym of *Hyla eximia* Baird.

We find that *Hyla wrightorum, Hyla lafrentzi, Hyla cardenasi,* and *Hyla regilla* from the northwest Pacific coast are practically indistinguishable; the differences are certainly much less than those distinguishing the other races of *Hyla regilla*. Therefore, we place *Hyla cardenasi* in synonymy with *Hyla lafrentzi* and we consider *Hyla lafrentzi* and *Hyla wrightorum* as races of *Hyla regilla*.

We are indebted to the following museums for the loan of specimens. (Each institution is designated by its abbreviation symbol): The American Museum of Natural History (AMNH), Stanford University Division of Systematic Biology (SU), University of California Museum of Vertebrate Zoology (UCMVZ), Chicago Natural History Museum (CNHM), the University of Texas Natural History Museum (UTNHM), University of Michigan Museum of Zoology (UMMZ), California Academy of Sciences (CAS), San Diego Museum of Natural History (SDMNH), and the San Diego State College (SDSC) research collections. The SDSC research collections are transferred to the San Diego Museum of Natural History on completion of each project.

This report is based in part on work supported by the U. S. Atomic Energy Commission ((AT45-1)-975), National Science Foundation Grant no. G-15558, National Institutes of Health RG-8489, University of Oregon Graduate School, San Diego Museum of Natural History, American Musuem of Natural History, and San Diego State College Foundation.

The senior investigator is indebted to Drs. C. M. Bogert, R. Zweifel, and J. Oliver for their assistance and their permission to use the facilities of the American Museum of Natural History during the fall of 1963. Particular thanks for years of encouragement and assistance go to Dr. R. Storm of Oregon State College, Dr. George Lindsey and Dr. Alan Leviton of the California Academy of Sciences, Dr. Richard Etheridge of San Diego State College, and Dr. R. F. Inger of the Chicago Natural History Museum. Drs. C. Walker and W. Duellman provided us with opinions based on a much broader experience with many different kinds of *Hyla,* and for their assistance we are grateful. Dr. B. E. Lippert and Mr. B. Vallet collected frogs almost yearly for our use.

Professor E. G. Bauer and the San Diego State College computer center staff have been indispensable. Particular credits go to Norman Littell and Richard Bacon. The matrix computations constituting the heart of the computer program are by Walt Davis; the statistical procedures were learned through the patience and assistance of J. Shaul and Dr. C. Bell of the San Diego State College mathematics department.

We are overwhelmed by the thought of naming all those colleagues who have contributed ideas, specimens, and encouragement because of the fear of omitting someone. May we point out that the omissions are, like the omissions of substance and fact in the work itself, the result of our inadequacies and not any attempt to slight either the investigators or the beasts. We stop here not because we have run out of people who helped but because we must leave some room to speak of the frogs.

Methods

Measurements: Seventeen measurements representing various parts of the animal were made on 149 randomly selected male animals of various (those available) species of *Hyla*. The 149 male animals represented 19 species of Hylidae. We were concerned at this stage with discovering the size and shape differences and similarities of some currently recognized species of tree toads. We intentionally did not include forms sometimes considered as different genera (*Pseudacris, Acris*) and intentionally did include animals not necessarily closely related to Pacific tree toads (*Hyla cineria, H. gratiosa, H. loquax*). A discriminant function analysis was performed as described later. The per cent of significant information obtained in each axis is given in table 2 along with the characteristic roots of the discriminant functions. The coefficients of the dis-

Table 2. *Per cent of significant information and the characteristic roots (variance component) of the discriminant functions of 17 measurements and of 10 measurements of 149 male hylids.*

Number of characters measured	Axis	Variance component	Per cent total	Accumulated per cent
	1	1,956.54	46.9	46.9
	2	813.37	19.5	66.4
17	3	349.55	8.4	74.8
	4	260.32	6.2	81.0
	5	216.70	5.2	86.2
	1	1,945.44	64.9	64.9
	2	375.46	12.5	77.4
10	3	266.30	8.9	86.3
	4	140.36	4.7	91.0
	5	97.98	3.3	94.3

criminant functions were standardized by their respective variances. From these standardized coefficients and from a consideration of the cost, time, and accuracy of the measurements, we were able to reduce the number of measurements. We were interested in measurements which contributed the most to the discrimination of the animals into groups; therefore, we selected from those measurements with large standardized coefficients. We were also impressed by the fact that the shape and form of Pacific tree toads from various localities were different and we were concerned with measuring the size and shape variation in the animals. As a primary indicator of size we selected snout–vent. Appendage lengths are represented by shank length, forearm length, and length of fourth finger. Head length is shown as a total measurement and as partitioned into an anterior estimate of the length of the face (eye to nostril) and a posterior estimate of the length of the cranium (tympanum to eye). Face height is represented by the nostril-to-lip measurement. The difficulty of measuring cranial height and obtaining results forced us to abandon this measurement; this is compensated by the apparent correlation between cranial width, height, and length. An estimate of the area of the toe pad is obtained by measuring the width of the toe pad. We then reanalyzed the 149 male animals using only these 10 measurements, and found that we had gained in our ability to discriminate between systematic units of related and currently accepted tree frogs. We plotted the sample means from both the 17-measurement analysis and the 10-measurement analysis, and found that the distribution of the samples on the first and second principal discriminant axes was very similar. With 17 measurements we are able to obtain only 47 per cent of the information in the first principal discriminant axis while with only 10 measurements we are able to obtain 65 per cent of the information in the first principal discriminant axis. The total

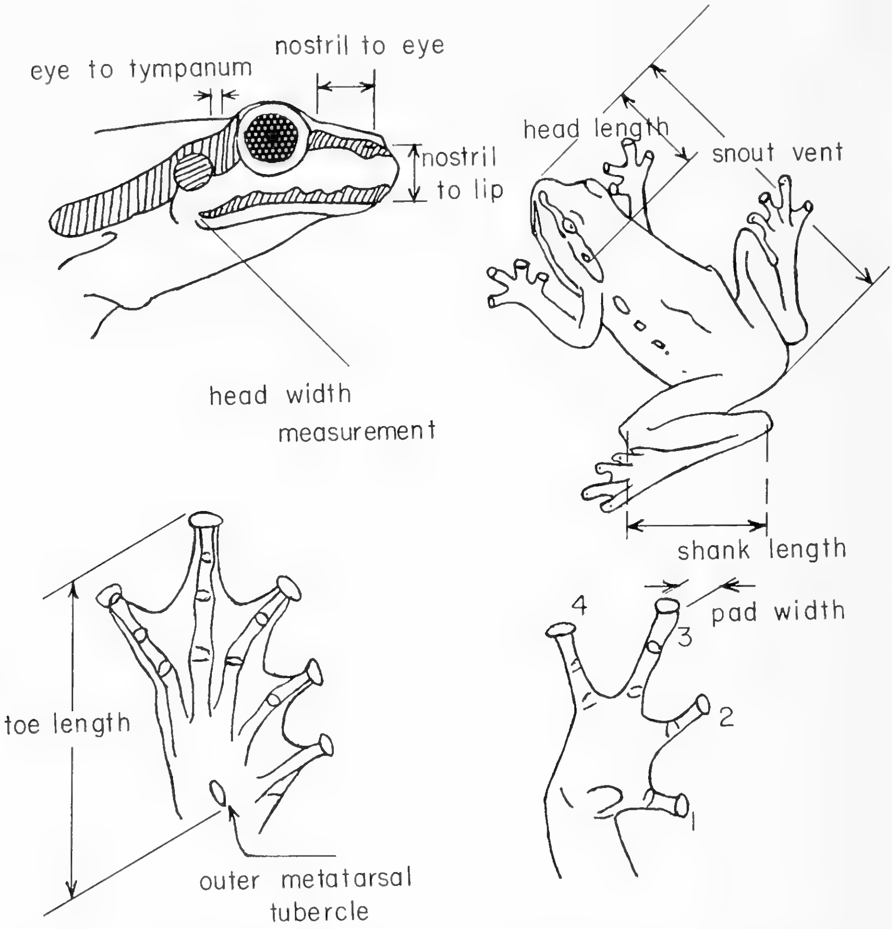

Figure 1. Measurements used in the analysis of size and shape variation within and between the subspecies of *Hyla regilla*.

variance (represented by the sum of the eigenvalues) for the 17 measurements is 4,160 and that for 10 measurements is 3,020; the variance in the first five axes is 3,596 (87%) and 2,825 (94%) for 17 and 10 measurements, respectively. Thus we lose about 25 per cent of our information by discarding seven measurements, but we greatly increase our ability to use (that is, reduce to a single discriminant function) the measurements we retain. We have significantly reduced our cost of measuring by more than half and our cost in computer time by more than two-thirds. We have used computer programs which are available in most installations to predict the usefulness of measurements and to estimate the cost of the study. This is a procedure we highly recommend. The

10 measurements (fig. 1) were obtained as follows: The first four measurements were taken with the aid of a dissecting microscope. The nostril–lip measurement was made perpendicularly from the ventral edge of the nostril to the upper lip, the eye–nostril measurement was made from the anterior edge of the eye to the posterior edge of the nostril, the tympanum–eye measurement was made from the anterior edge of the tympanum to the posterior edge of the eye. Pad width was measured on the third digit at the widest part of the pad. The remainder of the measurements were taken with a pair of vernier calipers (Helios-Braun Chemical Company). Head length was measured from the posterior edge of the tympanum to the end of the snout. Head width was measured at the angle of the jaw. Snout–vent length was from the end of the snout to the anus. Shank length was taken as the length of the left tibio–fibula. The forearm was measured by bending the hand backwards and placing one of the caliper arms on the palm and the other on the elbow. The length of the fourth toe was measured from the posterior edge of the outer metatarsal tubercle to the tip of the fourth toe. Measurements made in 1957 by one of us (J.P.M.) on the Oregon animals were found useful for separate analysis as were measurements made in a different study by G. Schroeder in 1960 and T. Vogt in 1961, 1962, and 1963. With these measurements we were able to test some of our conclusions. We also tested the possibility of grouping measurements made by more than one investigator and found the procedure unsatisfactory. Slight differences in measurements of the same animals (samples) by different investigtaors are (1) not describable in terms of this section, (2) not significantly different in terms of univariant statistics (T tests), and (3) significantly different in terms of multivariate statistics.

The use of discontinuous variables in amphibian studies is plagued by the lack of discrete things to count or identify as clearly present or absent. Many discontinuous variables are actually polygenic characteristics which have passed some threshold. The most useful approach has appeared to be to make some attempt to quantitize continuous variables. Test (1898) considered in detail the colors and stripes of the museum specimens he had at his disposal. He distinguished five categories ranging from little to much pigmentation and concluded (p. 486) "the different styles are so closely connected, and to a great extent actually confluent, that the unity as a species in this respect is very evident." We have studied the development of these patterns and colors and have found that they have geographic variability and that this geographic variability has interest and probably some evolutionary significance, but in terms of museum specimens there are severe limitations to their usefulness. They are subject to seasonal, age, health, background, light, temperature, and excitement modifications. The information given here on color is selected to be useful (in terms of identification of individuals and recognition of systematic groups) rather than comprehensive. A preliminary report on this is available (Resnick and Jameson, 1963) and more comprehensive reports are in progress. The use of characteristics such as amount of wedding, granulation, pigment, and position and shape of teeth and other characters is justified on the basis of tradition and —more practically—they work. While we are certainly convinced that animals from different localities can be distinguished by differences in body form and shape, these are almost impossible to describe convincingly. For this reason we have turned to factor analysis and have found it expressive.

MATHEMATICAL ANALYSIS

Now that we have reduced the number of measurements to 10, we are still faced with the complex task of looking at each set of measurements with respect to each other set of measurements for each of the samples available. To associate one variable with another by the usual bivariate graph would require 45 separate graphs, each with as many groups of data as there are samples. Multivariate discriminant analysis is useful since many characteristics and groups can be considered simultaneously, and an estimate of the amount of the total variation in each discriminant function is available. Further, we have statistical tests to tell us when we have considered the available, significant information with some predetermined degree of accuracy.

Multivariate procedures require that the data be normally distributed, or that normality be obtained by some transformation; in general, the requirement for normality extends to both bivariate and multivariate perspectives. Most metrical biological data is normally distributed or the data is so obviously not normally distributed that the decision is not a problem. In any case reasonable tests are available and were used.

There are a number of relatively straightforward expositions of multivariate procedures available. Cooley and Lohnes (1962) have the advantage of being comprehensive without being overly abstract and have the additional advantage of providing both computation procedures and some examples. The most concise statement we have found is that of Jolicoeur (1959), and we particularly recommend pages 287 and 298 of his paper; this work is additionally useful because it is a study of geographic variation. The two procedures we have used are (1) multivariate discriminant analysis and (2) factor analysis.

Multivariate discriminant analysis: Imagine a universe with 10 separate planes passing through a single point. The 10 planes represent our 10 measurements (X_i; $i = 1–10$). The point is the mean of each measurement. Within this 10-dimensional universe the mean of each sample (population, subspecies, etc.) is plotted with respect to each of the 10 characters. If one now shines a light through this array the position of each population casts a shadow on a screen held opposite the light. We have in effect created a marginal distribution which represents our discriminant function. We can rotate the light and screen in such a way as to maximize the between-group (B) variation and to minimize the within-group (W) variation. Naturally, we have not described all the variation in this one plane (marginal distribution, discriminant function), but we can eliminate (algebraically) the variation we have described and repeat the process to find the marginal distribution (plane) which maximizes B and minimizes W of the remaining variation. The process is repeated until all the variation is accounted for. For each plane there are coefficients (K) of the discriminant function such that $K_1X_1 + K_2X_2 + K_3X_3 + \ldots K_{10}X_{10} = P$ which is the point on the plane represented by the animal with the measurements $X_1 \ldots X_{10}$. The use of the sample means (X_i) will allow us to plot the means of each population. These coefficients (K) are direction cosines and the sum of their squares total 1.00; that is, they total to all the contribution of the measurements to the position of each animal or sample in plane under study. Because we successively account for all the variability, we also note that the sum of the squares of all the K_1's totals to all the contribution of the measurement X_1 to all the discriminant functions. In this way we are able to determine the contribution of a given measurement (X) to the discriminant function by the size of its coefficient (K). Each discriminant axis has a characteristic root (variance component, D) and the sum of these roots can be used to make tests of the significance of the information in the discriminant functions. The ratio of the size of the characteristic root to the sum of all the roots is an estimate of the per cent of the information (variation) described by that discriminant function.

The dispersion of the group means around their grand mean is expressed by the between-group covariance matrix B. The within group variance–covariance matrix W is the set of individual mean squared deviations and cross products. The standardization of matrix B by matrix W ($B \times W^{-1}$) accomplishes two things: (1) it adjusts each measurement by the variance of every other measurement and thus allows the emphasis of factors other than age or size in the determination of the differences between samples; and (2) it allows us to algebraically maximize the between-group variance and at the same time minimize the within-group variation.

At this point we are able to plot two discriminant axes at once (fig. 2), showing the per cent of the variation in each axis, the position of each sample mean, and of the grand mean on each axis. Additionally we can plot the coordinate axes of the original measurements as shown by the arrows emanating from the grand mean on each of our discriminant figures. The length of each vector (arrow) is determined by its variance. We have shown one or two standard deviations depending on visual requirements of the illustrations. The vector shows how the grand mean (and thus the discriminant function) would be changed if the measurement represented by that vector was allowed to vary independently.

Factor analysis. This consists of a detailed analysis of the within-group

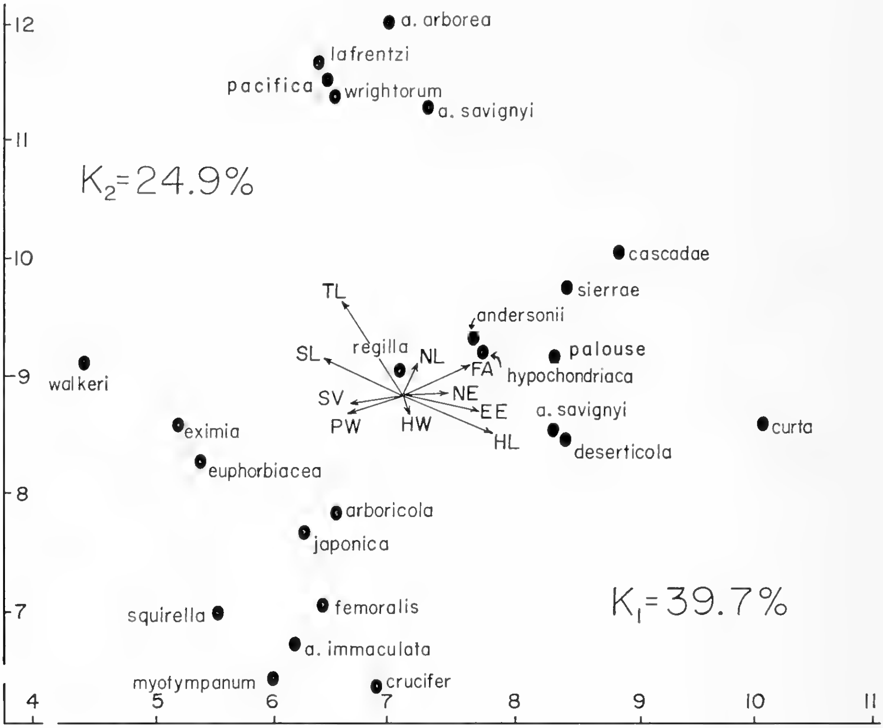

FIGURE 2. Discriminant analysis of 149 male hylids representing various recognized species and subspecies. The mean of each sample is shown on the first ($K_1 = 39.7\%$) and second ($K_2 = 24.9\%$) discriminant axes. The original coordinates are represented by the direction of each vector emanating from the grand mean. The length of the vector is representative of one standard deviation of the measurement. The measurements are labeled as indicated in table 5.

variation (W). A number of methods have been used and are described in Harmon (1960). We used both Hotelling's principal component and the Jacobian method, depending on accuracy and speed of computation required. Consider for a moment a single sample of animals and the 10 measurements plotted on the 10 dimensions of our universe. If we again make use of the light and screen we will find that the points of our sample of animals can be circumscribed by a multidimensional equal-frequency ellipsoid, the principal axis of which is parallel to our screen when we have maximized the variation of the sample about its mean. This principal axis is algebraically obtained from the variance–covariance matrix (W) or the correlation matrix (R) in the same way the discriminant function was obtained from the standardized B matrix. Characteristic roots (D) and coefficients (K) of characteristic vectors (principal component axes) are obtainable and they have comparable characteristics to those described for the discriminant function. In this case we are examining the samples with respect to the principle trends of variation within the sample and we find that the first axis will be essentially a size component. Other axes will represent shape components, and the contribution of the original measurements to these components is discernible by the magnitude of the coefficients (K) since the sum of the squares of the coefficients represents all the variation. Factor analysis is used here to describe systematic units. Its use to determine parameters of growth (see Jolicoeur, 1963) in these frogs will be presented elsewhere.

The roots of the correlation matrix provide a factor solution to the question, "How many unique reference axes are required to explain the variation present in the 10 measurements." Harman (1960, p. 363) has recommended (following Kaiser) the use of those roots greater than 1.0. No more than two roots are greater than 1.0 in any of the subspecific groups we have analyzed here, and we have provided the direction cosines derived from the first two roots with respect to each of the measurements.

A number of rotational schemes are available. One of these (Quartimax) seeks to maximize or at least to emphasize the variation of the measurements; the object in our case would be to provide each measurement with a large direction cosine coefficient on only one or at least a very few factors. This would, in effect, give the amount of adjustment by each other measurement required to explain the variable under consideration. Another solution (Varimax) is to simplify the factors; the result is to rotate the axis so that the smallest number of measurements is responsible for each factor. Both the Quartimax and the Varimax solution are orthogonal. An oblique solution which provides properties of both rotational schemes is also available. For the present study we utilize the unrotated direction cosine matrix because we wish to emphasize the correlations present in the animals.

Selection of specimens and the use of a computer to search: The distribution and abundance of organisms as illustrated by museum collections has a number of built-in biases which prevent or at least make meaningless the use of random techniques. We have made the following assumptions.

(1) Collectors went where they thought the animals would be found.

(2) Collectors tend to collect the rare animal more than the common ones, but large samples are less subject to the error of the intentional collection of a single unusual individual than are small samples.

(3) Detailed maps of distribution based on museum collections tend to show where the collectors have been rather than where the animals are to be found. For this reason we have not attempted to locate every animal in every collection and we have not attempted to map every animal in every collection. We believe that this would be detrimental to the advancement of our understanding of the knowledge of the beasts because it would tend to obscure the problems that need to be solved.

We are providing classical distribution maps, but the type of maps we believe will be most useful are being prepared as parts of other studies.

(4) Rather than attempt to rule out by artificial means the opinions we have developed during the past 12 years about the various kinds of tree toads that may exist, we have attempted to capitalize on and test these opinions. As one of our colleagues has expressed of his own systematic work, "I find in nature what I believe to be a species, then attempt to find the morphological basis for this belief."

(5) A large number of measurements on one animal is better than one measure on a large number of animals.

(6) We cannot possibly measure all the frogs available and poorly preserved animals are generally not worth measuring.

The procedure may be summarized as follows:

I. (1) We selected localities represented by large samples (10 or more animals). (2) We selected localities from many different parts of the range including as parts: states, river drainage patterns, mountain ranges, physiographic provinces, biotic communities, and vacant spots on a map after the above localities were mapped. (3) We selected at least 10 different adult male animals from each locality. (4) We performed a discriminant analysis and plotted the K_1K_2 and the K_3K_4 and sometimes the K_5K_6 axes to see which of these samples was similar morphologically and was contiguous geographically, topologically, or ecologically. (5) From this analysis we made predictions about where we would expect to find samples which were like the samples we had already measured and where we would expect to find samples which were intermediate between samples we had in hand. (6) We searched the collections we had on hand for samples meeting criteria in (5).

II. We repeated 3, 4, 5, and 6 until we had (a) run out of specimens from critical localities or (b) had obtained the same results over and over so that further expenditure of computer time would not appear to be justified.

III. We performed factor analysis on (a) all the animals measured to this point and (b) each group of presumptive races of animals we had in hand. The analysis of each group did in fact show us one locality which we had placed in the "wrong" group and that we had missed the significance of this placement when we had studied the discriminant plots. The displaced locality also showed us the power and significance of the factor analysis; nothing we read and nothing we tried was so convincingly instructional as this mistake.

IV. We then analyzed the groups we had identified on the basis of similarities in size and shape for discontinuous characteristics which would in fact allow us to accept them as systematic categories.

V. Throughout the process we were confronted with cases where previously unexplainable observations were now apparent. Again and again we would review the analysis and see things we had not noticed before; these observations led us back to the animals, field notes, and laboratory experiments where we found confirmation of our results.

We must emphasize that we also found items which do not make sense, and we found items which were in contradiction to all other observations. We even found on one occasion that rarest of events—a computer error so small that it could have been missed. In fact, we would probably miss it today, but at that time we were skeptical of every number.

Again may we emphasize that we used the computer as a tool to search and to discover, not as an end itself. The computer is one more tool to go along with the microscope, the calipers, the typewriter, the sonograph, the slide rule, and the meter stick. The mathematical analysis is one more piece of information to go along with snout–vent length, number of spots, color, temperature, odor of the water, slope of the land, number of people, and our concepts of evolution.

Results

The preliminary analysis of the 149 animals by both the original 17 and by the extensively used 10 measurements (fig. 2) led us to the following conclusions about the size and shape of these frogs: (1) Several forms are so constructed that whatever relation they have to the frogs we are interested in must be found in characteristics other than size and shape. (2) Much the same body form is found in *Hyla eximia, H. euphorbiacea,* and *H. walkeri* and these species can be distinguished from *Hyla squirella, H. femoralis,* and *H. crucifer* which are similar to each other. (3) The Old World *Hyla arborea* can be separated into two morphological groups with respect to size and shape. (4) We were able to recognize the similarity of the body form of *Hyla regilla, H. lafrentzi,* and *H. wrightorum* and to recognize certain differences between them and the *H. eximia* and *H. squirella* "body form group" listed above.

The first discriminant analysis following the procedure outlined in step I above consisted of 41 samples of *Hyla regilla–lafrentzi–wrightorum.* The plots of the sample means suggested that the *H. regilla* populations concentrated in the coastal regions of Oregon, Washington, southern British Columbia, and northern California (fig. 3D) and those recognized as *H. wrightorum* (fig. 3J) from the Great Basin and Arizona and *H. lafrentzi* (fig. 3I) from central Mexico constituted a similar but separate group from all other regillas. Other groupings which appeared justified were the animals from (1) the coast range mountains of California and northern Baja California, (2) high elevations within the Sierras, (3) high elevations within the Cascade Mountains,

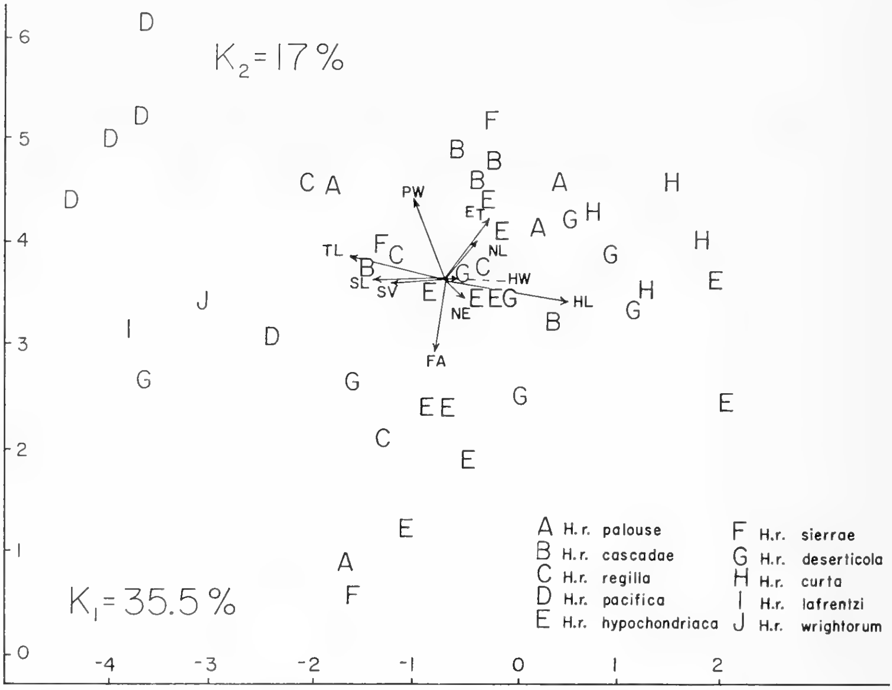

FIGURE 3. Discriminant analysis of 41 samples of *Hyla regilla* from various localities in western North America. The mean of each sample is shown on the first ($K_1 = 35.5\%$) and second ($K_2 = 17\%$) discriminant axes. The symbols are those shown on the map (fig. 11). The original coordinates are represented by the direction of each vector emanating from the grand mean. The length of the vector is representative of one standard deviation of the measurement. The measurements are labeled as indicated in table 5.

(4) the Cape region of Baja California, and (5) isolated desert populations in California, Baja California, and Nevada. Procedure II as given in Methods confirmed the outcome of the previous analysis. We then removed the northwest coastal *H. regilla–wrightorum–lafrentzi* samples and concentrated on the analysis of the remaining populations. Procedure II was repeated. The Puget Sound region and the Willamette Valley form a similar ecological habitat, and animals (and plants, Detling, 1948) from these regions are similar. The animals of the coastal regions of California are very similar to each other, but the analysis at this step left uncertain how far inland this group exists. The Sierra Nevada and the Cascade Mountain animals appeared to be similar to each other and to those from the foothills of the Rockies in Idaho and Montana. The grouping of isolated desert populations, northern Baja California populations, and inland California populations was in doubt. Specific areas were approached dealing with more or less local and discrete problems. Soon we

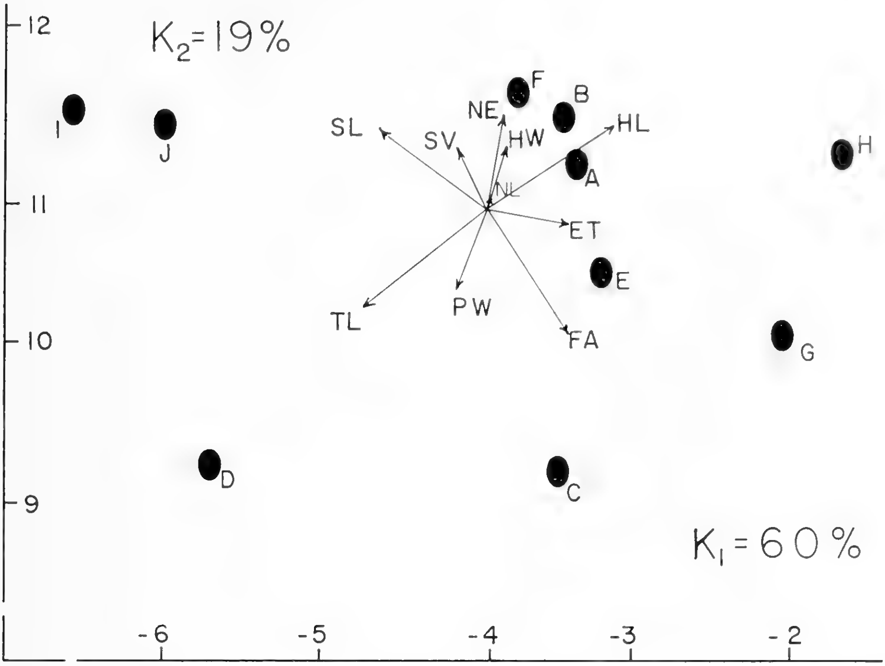

FIGURE 4. Discriminant analysis of the males of the 10 subspecies of *Hyla regilla* recognized in this study (table 3). The mean of each subspecies is shown in the first ($K_1 = 60\%$) and second ($K_2 = 19\%$) discriminant axes. The original coordinates are represented by the direction of each vector emanating from the grand mean. The length of the vector is representative of one standard deviation of the measurement. The measurements are labeled as indicated in table 5.

reached saturation and either ran out of animals or of new information. We then grouped the samples and computed a discriminate analysis on the "presumptive races" giving the results of figures 4, 5, and 6 and table 3.

DISCRIMINATORY ANALYSIS.

The partitioning of the latent roots of the discriminant matrix of 10 measurements of 454 males of *Hyla regilla* when they were grouped into 10 subspecies is shown in table 3. The total variance is 1,712.6, which is highly significant. The amount of variance in the first discriminant function is 1,033.9, which is 60.1 per cent of the total. The second discriminant function has a variance of 328.9 which is 19 per cent of the total. The first two axes have 79 per cent of the total variance of the 10 measurements, and they were plotted in figure 4. The smaller relative shank length and toe length of *H. pacifica* (D), *H. lafrentzi* (I), and *H. wrightorum* (J) set them aside as a separate group. The increased length of the face and head are characteristic of the relation of *H.*

TABLE 3. *Discriminatory analysis of 10 measurements of 454 males of* Hyla regilla *grouped into subspecies. The probability indicates the significance of losing information if that axis and all smaller axes are discarded from the analysis. Only those axes with* P *values smaller than 0.05 are given.*

Discriminant axis	Variance component	Per cent of total	Degrees of freedom	Probability
1	1,033.9	60.3	18	<0.01
2	328.9	19.2	16	<0.01
3	122.9	7.2	14	<0.01
4	79.7	4.7	12	<0.01
5	68.4	4.0	10	<0.01
6	52.8	3.1	8	<0.01
7	19.7	1.2	6	<0.01

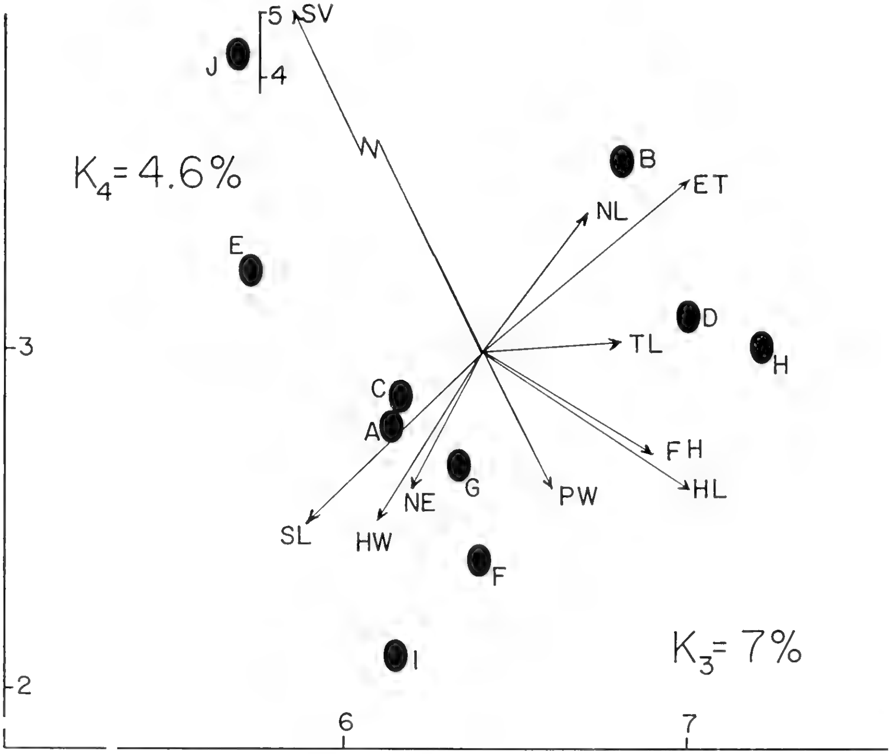

FIGURE 5. The mean of the male samples of each subspecies is shown on the third (K_3 = 7%) and fourth (K_4 = 4.6%) discriminant axes (table 3). Symbol and vector labels are as in figure 4.

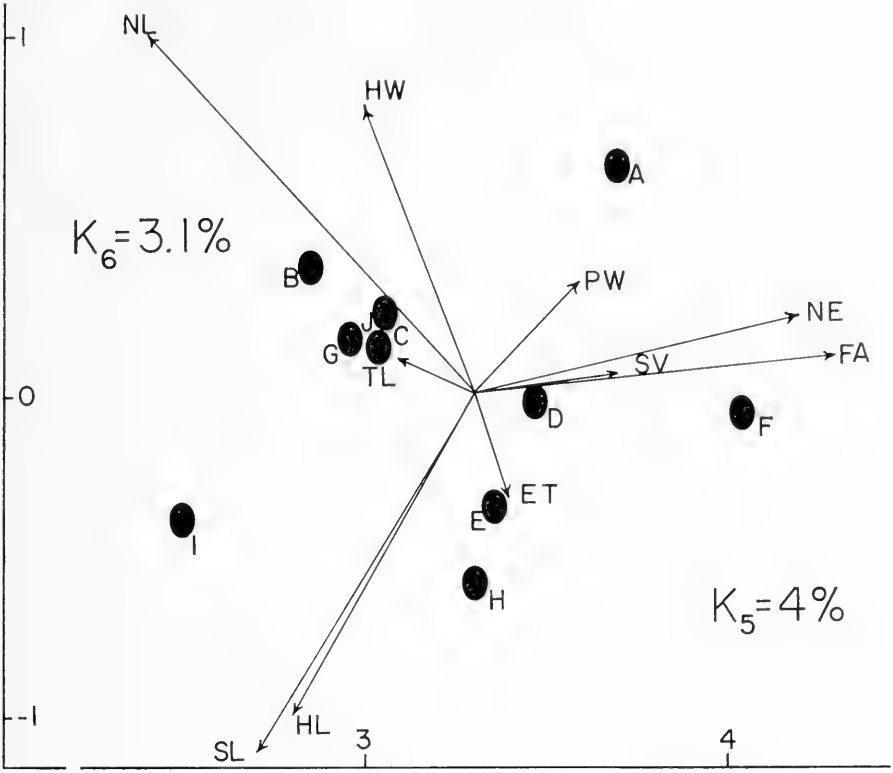

FIGURE 6. The mean of the male samples of each subspecies is shown on the fifth ($K_5 = 4\%$) and sixth ($K_6 = 3.1\%$) discriminant axes (table 3). Symbol and vector labels are as in figure 4.

r. sierra (F), *H. r. cascadae* (B), and *H. r. palouse* (A) to each other and the forearm length and eye–tympanum length indicate their relation to *H. r. hypochondriaca* (E) and *H. regilla* (C). Increase in the relative appendage lengths, eye–tympanum length, and face length distinguish *H. r. curta* (H) and *H. r. deserticola* (G) from other forms.

The plots of the third (variance 122.9, 7.2 per cent) and fourth axes (variance 79.7, 4.7 per cent) indicate the relatively longer snout–vent length in *H. wrightorum* (J), and demonstrate some of the proportions by which *H. r. pacifica* (D) and *H. lafrentzi* (I) differ from *H. wrightorum*. Comparison of the plots of the first four axes with that of the fifth (variance 68.4, 4 per cent) and the sixth axes (variance 52.8, 3.1 per cent) indicates the usefulness of the length of the vectors (determined by their standard deviation) in determining the magnitude and significance of the differences between the groups. Obviously the differences indicated by the plots of the axes with the smaller

TABLE 4. *Discriminatory analysis of 10 measurements of 90 females of* Hyla regilla *grouped into subspecies. The probability indicates the significance of losing information if that axis and all smaller axes are discarded from the analysis. Only those axes with* P *values smaller than 0.05 are given.*

Discriminant axis	Variance component	Per cent of total	Degrees of freedom	Probability
1	495.1	60.9	18	<0.01
2	144.4	17.7	16	<0.01
3	84.8	10.3	14	<0.01
4	53.8	6.6	12	<0.01
5	17.3	2.1	10	<0.01
6	7.9	0.4	8	<0.05

variances have considerably less significance than those indicated by the plots of the first two axes and particularly of the plot of the first axis where 60 per cent of the variance is found.

The available females were separated into the same groups as the males, and a discriminant analysis was performed (figs. 7 and 8; table 4). The groupings and the differences between the groupings in the females are very similar to those indicated in the males. The toe is longer in *H. r. pacifica* (D) than in the others, *H. r. curta* (H) has a longer head, and *H. lafrentzi* (I) is distinguished by its shank length and nostril–lip measurement.

The first two discriminant axes of the males and the females considered at the same time are shown in figure 9. The diagonal separation of the males from the females suggests that the sexes can be distinguished in shape and form by the use of some function of a complex variable which we have not attempted to derive.

FACTOR ANALYSIS OF SIZE AND SHAPE VARIATION.

The use of the correlation matrix (R) to obtain the latent roots and direction cosines (matrix U) allows us to examine the principal sources of variation in size and shape in our animals. The first principal component axis should be essentially a size component. If all parts grow at equal rates (isometry) the coefficients of the direction cosines (U_{1i}) of each of the 10 measurements ($i = 1, 10$) should be $\sqrt{1/10} = 0.316$ because the expected value of the direction cosines is $\sqrt{1/P}$ where P is the number of measurements. The magnitude of the deviation from isometry (i.e., 0°) can be calculated by $\cos \phi = U_1V_1 + U_2V_2 + \ldots . U_{10}V_{10}$ where: v_i = isometric value of 0.316, u_i = observed direction cosine value.

The other axes should represent shape variation in the animals studied. The number of principal component axes preserved for study may be estimated by the Kaiser rule of the thumb (roots larger than 1 accepted), by the per cent of information given by that root and by testing roots to determine if one

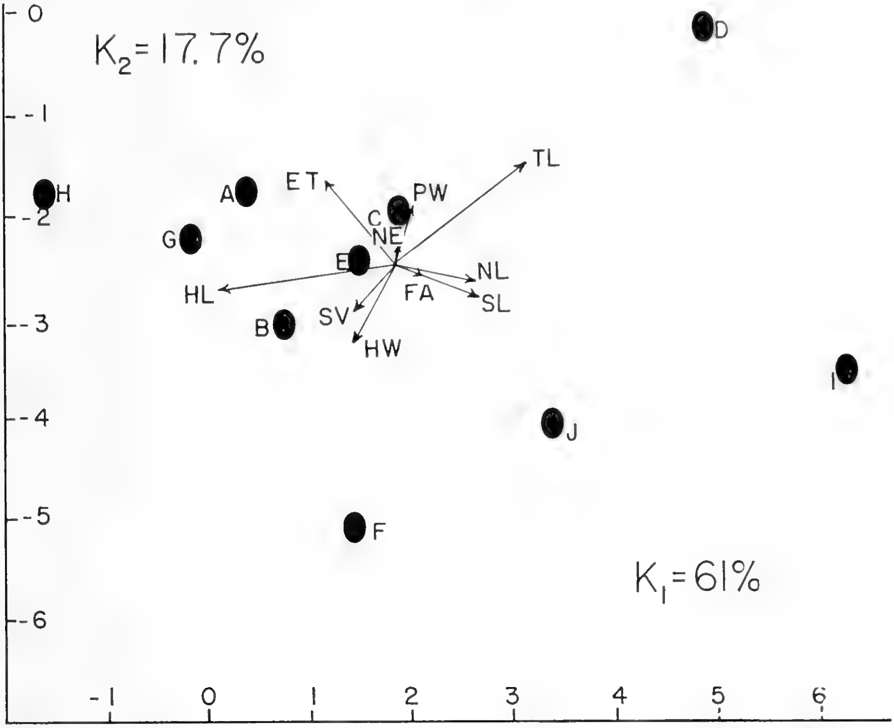

FIGURE 7. The mean of the female samples of each subspecies is shown on the first ($K_1 = 61.0\%$) and second ($K_2 = 17.7\%$) discriminant axes (table 4). Symbol and vector labels are as in figure 4.

successive root is significantly smaller than the next larger. We offer here a detailed summary of the variation in males and females of the total sample with respect to all roots (tables 5–7), and we have used Kaiser's rule of thumb for the comparisons of the subspecies. More complete analyses will be presented elsewhere.

SEXUAL DIMORPHISM.

The roots of the variance–covariance matrix may be compared to provide an estimate of the amount of variation in each group. The females (table 6) are more variable than the males:

$$\Sigma\lambda = 35.62 \text{ in } ♀\, ;\ \Sigma\lambda = 24.80 \text{ in } ♂ \text{ where } i = 1, 10.$$

The per cent variability in each root indicates that the principal factors underlying variation in males and females are similar.

The correlation matrix of males and females is shown in table 5. All the coefficients (r) for the male measurements show a high positive correlation

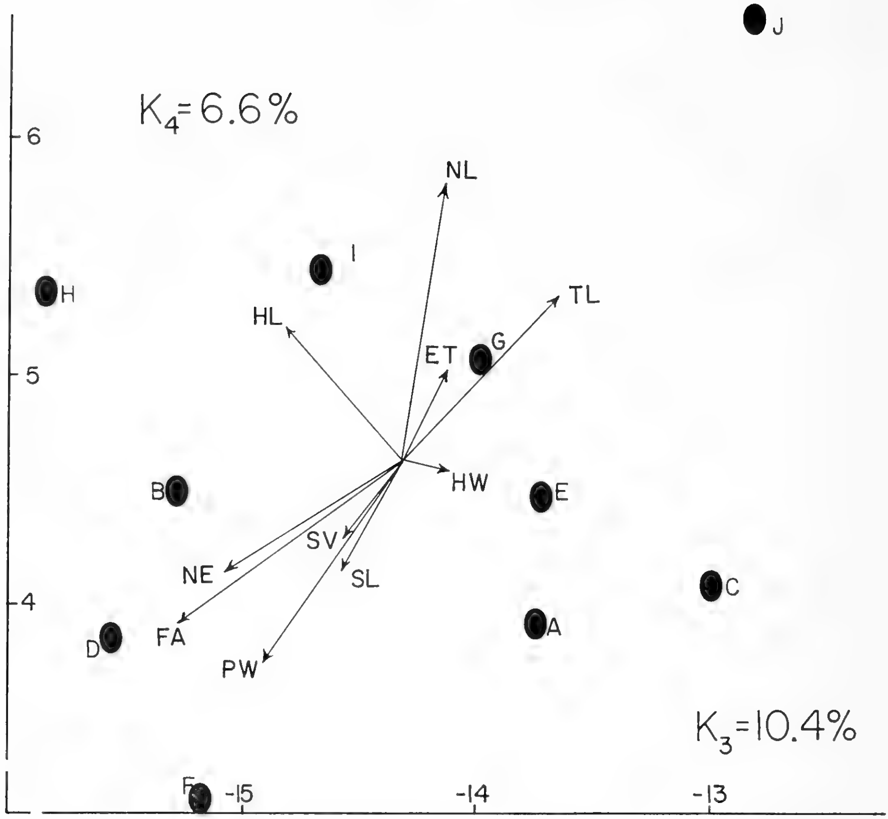

FIGURE 8. The mean of the female samples of each subspecies is shown on the third ($K_3 = 10.4\%$) and fourth ($K_4 = 6.6\%$) discriminant axes (table 4). The symbol and vector labels are as in figure 4.

with each other at $P \leqslant 0.01$. The measurements of females exhibit high values of r except for: shank length—eye–tympanum and toe length—eye–tympanum; these values are not significant at $P = 0.05$. The number of significant r's for both sexes indicates that all parts of an animal tend to increase in size simultaneously. The exceptions involve eye–tympanum and represent the distance between two organs, both of which are increasing in size; one might expect that the distance between the two would decrease, remain constant, or slowly increase. The latter is most probably the case in this instance, resulting in the low values for r.

Males. The head measurements are more highly correlated than expected with each other than with other measurements except that pad width is more correlated with nostril–lip and head length with snout–vent. The former exception is present in both sexes; the latter can be explained by the fact that

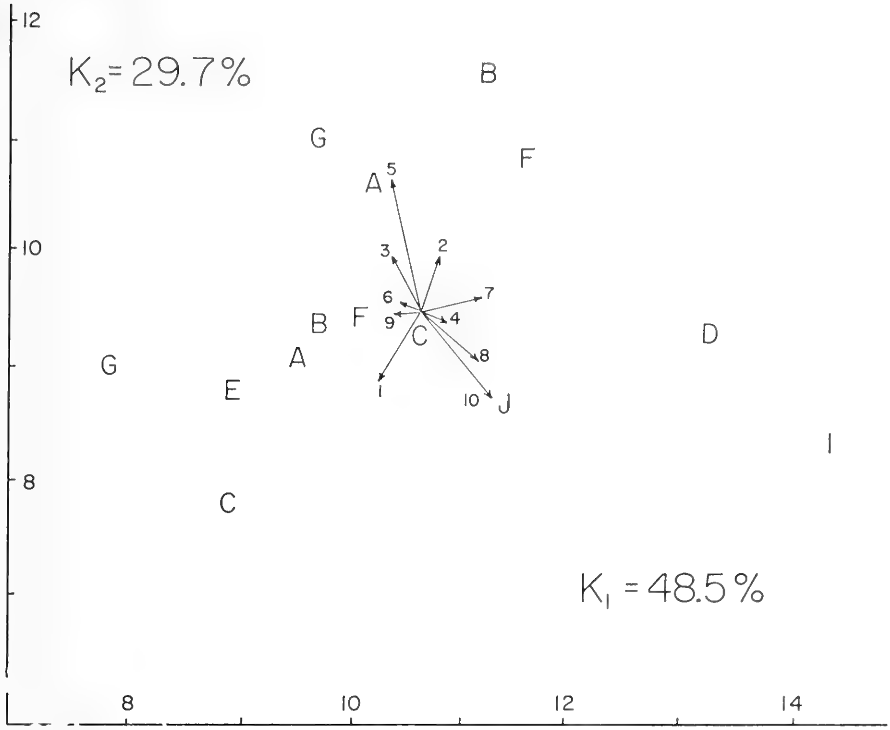

Figure 9. The mean of the male and female samples of each subspecies is shown on the first ($K_1 = 48.5\%$) and second ($K_2 = 29.7\%$) discriminant axes to indicate the simultaneous variation. The vector labels are as in figure 4. The symbols are as in figure 11.

head length is a component of snout–vent and the two vary in proportion to each other.

The appendages and general size (snout–vent) measurements are most highly correlated with each other as expected. The highest correlation coefficient for the male measurements is that of shank length with forearm length indicating that both anterior and posterior appendages are closely related in their relative sizes.

Females. The head measurements are generally highly correlated with other head measurements with two exceptions: nostril–lip with snout–vent and pad width with nostril–lip. The former exception indicates that females tend to have a taller face in relation to their overall length. The latter exception was also present in males.

The appendage measurements are highly correlated with each other and with those measurements which give an indication of general size. The highest correlation coefficients for the female measurements are: head width with head

TABLE 5. *The correlation coefficients of 10 measurements of 90 females of* Hyla regilla *(roman face type) and 454 of* Hyla regilla *(italics). For 88 df,* $P_{0.05} \geqslant 0.205$; $P_{0.01} \geqslant 0.269$. *For 452 df,* $P_{0.05} \geqslant 0.093$; $P_{0.01} \geqslant 0.120$.

		Males									
	Measurement number and letter code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
	Measurement	Nostril–lip	Nostril–eye	Eye–tympanum	Pad width	Head length	Head width	Snout–vent	Shank length	Fore-arm length	Toe length
Females	1–NL		*0.73*	*0.48*	*0.67*	*0.83*	*0.72*	*0.78*	*0.71*	*0.71*	*0.66*
	2–NE	0.66		*0.48*	*0.49*	*0.80*	*0.74*	*0.74*	*0.69*	*0.69*	*0.59*
	3–ET	0.50	0.51		*0.38*	*0.50*	*0.37*	*0.35*	*0.30*	*0.32*	*0.22*
	4–PW	0.62	0.31	0.42		*0.59*	*0.55*	*0.63*	*0.62*	*0.62*	*0.62*
	5–HL	0.82	0.82	0.45	0.47		*0.83*	*0.85*	*0.80*	*0.81*	*0.70*
	6–HW	0.74	0.71	0.33	0.51	0.89		*0.81*	*0.80*	*0.80*	*0.70*
	7–SV	0.85	0.69	0.35	0.56	0.89	0.86		*0.87*	*0.87*	*0.85*
	8–SL	0.72	0.60	0.19	0.47	0.82	0.82	0.85		*0.87*	*0.87*
	9–FA	0.69	0.63	0.28	0.44	0.76	0.70	0.80	0.54		*0.85*
	10–TL	0.77	0.56	0.18	0.61	0.77	0.78	0.89	0.86	0.74	
Sum r →	Males	*7.29*	*6.95*	*4.40*	*6.17*	*7.71*	*7.32*	*7.75*	*7.53*	*7.54*	*7.06*
	Females	7.37	6.49	4.21	5.41	7.69	6.34	6.74	6.87	6.58	6.16

length, head length with snout–vent, and snout–vent with toe length. The value for each of these is 0.89 which is equal to the high value for the males.

Comparison of males and females. If each measurement was exactly correlated with all the other measurements, the sum of the correlation coefficients for a measurement with respect to x measurements should be equal to $(x) \times (1.00)$. With 10 measurements the sum of r for a perfect correlation is 10. Such a sum was calculated for males and females and shown in table 5. As the above analysis of single values for r indicated, males and females differ substantially with respect to the correlation coefficients.

If the values for Σr are arranged in order of magnitude, the largest Σr for both males and females is snout–vent (7.75 males; 7.74 females). This value indicates that the snout–vent measurement is most closely correlated with all the other measurements taken. Head length is second in both males and females (7.71 males; 7.69 females). At this point the numerical order for the sum of r differs between males and females. Those values which fall in the same numerical position for both males and females are: snout–vent [1st], head length [2nd], nostril–eye [8th] (6.95 males; 6.49 females); pad width [9th] (6.15 males; 5.41 females); and eye–tympanum [10th] (4.39 males; 4.21 females). In each of the above cases and, in fact, in seven of the ten measurements the

Table 6. *Factor analysis of 454 males of* Hyla regilla. *For each principal component axis the roots of the variance–covariance* (W) *and the correlation* (R) *matrix and the direction cosines of the 10 measurements are given. The angle of deviation from 0° (isometry) of the first axis is 8°49′. The angle of separation from the female vector in the first axis is 3°26′. The second is 14°10′, and the third and fourth are greater than 40°0′.*

	Principal Component Axis									
	1	2	3	4	5	6	7	8	9	10
Roots of W (λ)	22.07	1.11	0.74	0.41	0.20	0.13	0.06	0.03	0.03	0.02
Per cent of total	89.0	4.5	3.0	1.7	0.8	0.5	0.2	0.1	0.1	0.1
Roots of R	7.12	0.98	0.59	0.37	0.24	0.23	0.14	0.13	0.11	0.09
Direction cosines										
Nostril–lip	0.326	–0.166	0.092	–0.446	0.648	–0.234	0.223	0.264	–0.178	–0.173
Nostril–eye	0.311	–0.218	–0.382	–0.351	–0.206	0.727	0.087	0.078	–0.028	–0.006
Eye–tympanum	0.182	–0.817	0.095	0.530	–0.006	–0.030	0.074	0.039	0.025	–0.040
Pad width	0.272	–0.044	0.831	–0.290	–0.354	0.087	–0.083	–0.085	0.023	0.036
Head length	0.346	–0.125	–0.209	–0.144	0.124	–0.222	–0.434	–0.474	–0.072	0.559
Head width	0.331	0.037	–0.275	–0.108	–0.570	–0.553	0.322	0.243	0.078	0.051
Snout–vent	0.352	0.142	–0.051	0.076	0.158	0.008	–0.141	–0.129	0.817	–0.350
Shank length	0.342	0.237	–0.025	0.245	–0.018	0.032	0.310	–0.587	–0.417	–0.397
Forearm	0.342	0.205	–0.035	0.256	–0.060	0.014	–0.631	0.462	–0.331	–0.227
Toe length	0.321	0.348	0.146	0.387	0.209	0.229	0.352	0.240	0.072	0.567

males have larger correlation coefficients than the females. The value of the summed r's for the eye–tympanum measurement is the smallest value for both males and females, again indicating a low degree of correlation between this measurement and the others.

The first principal axis of the correlation matrix includes 68.7 per cent of the variability for females, 71.2 per cent for males. The magnitude of the deviation of the angle of the sample vector from the isometric or expected vector is 10°14′ in females and 8°49′ in males; the difference is 1°25′. The magnitude of the deviation of the angle between the male sample vector and the female sample vector can be calculated by: $\cos \phi = U_{1,1}U_{2,1} + U_{1,2} + U_{2,2} + \ldots U_{1,10}, U_{2,10}$, where $U_{1,i}$ = male direction cosines ($i = 1, 10$), $U_{2,i}$ = female direction cosines ($i = 1, 10$). This deviation is calculated at 3°26′ in the first axis. The difference between 1°25′ and 3°26′ is surely attributable to further shape differences between males and females. Since all measurements do not increase equally it is apparent that all of the first principal axis is not a size component. The coefficients of the eye-to-tympanum length (0.178 in females, 0.182 in males) and the toe pad width (0.243 in females and 0.272 in males) are certainly less than expected. Both males and females seem to grow longer faster (coefficients of snout–vent (0.366 in males and 0.352 in females) than the other parts. Apparently the head length grows faster in females (0.361)

Table 7. *Factor analysis of 90 females of* Hyla regilla. *For each principal component axis the roots of the variance–covariance* (W) *and correlation* (R) *matrix and the direction cosines of the 10 measurements are given. The angle of deviation from 0° (isometry) of the first axis is 10°14′. The angle of separation from the male vector in the first axis is 3°26′; the second, 14°10′; the third and fourth are greater than 40°0′.*

	Principal Component Axis									
	1	2	3	4	5	6	7	8	9	10
Roots of *W* (λ)	31.69	1.76	0.97	0.61	0.26	0.16	0.08	0.04	0.03	0.02
Per cent of total	89.0	4.9	2.7	1.7	0.7	0.5	0.2	0.1	0.1	0.1
Roots of *R*	6.87	1.05	0.79	0.47	0.26	0.20	0.17	0.08	0.06	0.04
Direction cosines										
Nostril–lip	0.342	–0.117	0.130	0.019	0.502	0.418	–0.605	0.196	0.100	–0.103
Nostril–eye	0.301	–0.222	–0.494	–0.039	–0.451	0.586	0.162	0.139	–0.144	–0.029
Eye–tympanum	0.178	–0.829	–0.013	–0.106	0.261	–0.322	0.293	0.096	0.029	–0.046
Pad width	0.243	–0.197	0.781	0.028	–0.490	0.128	–0.028	–0.180	–0.020	–0.042
Head length	0.361	–0.020	–0.238	–0.076	–0.061	–0.124	–0.174	–0.585	0.452	0.459
Head width	0.345	0.112	–0.122	–0.171	–0.367	–0.552	–0.394	0.473	–0.063	–0.042
Snout–vent	0.366	0.129	0.011	0.050	0.229	–0.094	0.053	–0.252	–0.814	0.239
Shank length	0.328	0.292	0.006	–0.540	0.136	–0.009	0.269	–0.222	0.109	–0.603
Forearm	0.310	0.086	–0.109	0.810	0.004	–0.160	0.116	–0.087	0.135	–0.405
Toe length	0.339	0.299	0.213	0.035	0.166	0.088	0.496	0.464	0.257	0.432

than in males (0.346), while the limbs certainly grow faster in males (shank, 0.342; forearm, 0.342) than in females (shank, 0.327; forearm, 0.310). These deviations from isometry and the amount of variation in axes other than the first suggest that approximately one-third of the variation in *Hyla regilla* is variation in shape.

The second principal axis characteristically represents the differences in shape of males and females, and 10.5 and 9.8 per cent of the variation are present here. Appendage lengths, total lengths, and head width have positive coefficients, while head lengths, face shapes, and toe pad width have negative coefficients. This axis is responsible for 10.5 and 9.8 per cent of the variation in females and males, respectively; a major portion [$(-0.829)^2 = 68.7$ per cent in females; $(-0.817)^2 = 66.7$ per cent in males] of the variability in this axis is the result of the large decrease in growth rate of the eye-to-tympanum measurement. The deviation between the angles of the second principal axes in males and females is 14°10′.

The third principal component represents 7.9 per cent of the variation in females and 5.9 per cent in males; pad width and nostril-to-eye distance are largely responsible for the shape variation in the third axis. The magnitude of the deviation between the male and female third principal axis is 14°7′. The first three axes account for 87.1 per cent of the variation in females and 86.9

per cent of the variation in males, and the differences between males and females are very little.

Considerable differences between the shape of males and females become apparent in the fourth axis where 2.6 per cent of the variability is found in females and 2.4 per cent in males. In males a decrease in the rate of growth of the nostril–lip and the nostril–eye measurements, and an increase in the rate of growth of the eye–tympanum distance and toe length account for 75.3 per cent of the variation in this axis. Decrease in the growth rate of shank length and increase in forearm length account for 91.8 per cent of the variation in the fourth axis in females. The angle of deviation between male and female axes is more than 40° which, to say the least, is enormous.

Less than 10 per cent of the total variation in 10 measurements is found in the last six axes. While these represent little of the total variation, they are of interest in distinguishing components of the total variation between males and females. The differences between the coefficients of growth of the forearm length in males when compared with females in the sixth and seventh principal axes and in shank length in the eighth and ninth axes suggest that additional rotation of both the Quartimax and Varimax type will be of use. Since we are concerned here with differences between subspecific groups rather than a detailed analysis of males and females, we reserve the rotated matrices analysis for future presentation.

Factor Analysis of Subspecies:

Some of the details of these factor analyses are summarized in tables 8–17 and in the discussion of each subspecies. The roots of the covariance matrix (W) may be compared to provide an estimate of the amount of variation in each group and to some extent the nature of that variation. Two sets of latent roots may be compared by Hotelling's T^2 test (1931) or several other tests. When many groups are involved the problem of large beta error arises, and the logical solution is the multivariate discriminate analysis used in figures 3–9 and tables 3 and 4. The obvious similarity between the latent roots of the total males and the total females and the differences between the latent roots of the several subspecies may indicate the usefulness of the latent roots in determining size and shape differences between two adjoining subspecies and in testing the membership of a geographically intermediate population (Rao, p. 308) or of a single individual (Cooley and Lohnes, p. 137).

We have provided the direction cosines for each subspecies for the first two axes following the general rule of Kaiser, who recommends use of those roots greater than 1.0 (the third axis never reaches a value greater than 1.00). From 59.0 per cent of the variance in *H. r. lafrentzi* to 74.6 per cent in *H. r. palouse* can be explained in the first principal component axis and from 6.7 per cent in *H. r. deserticola* to 15.4 per cent in *H. r. lafrentzi* can be explained in the second

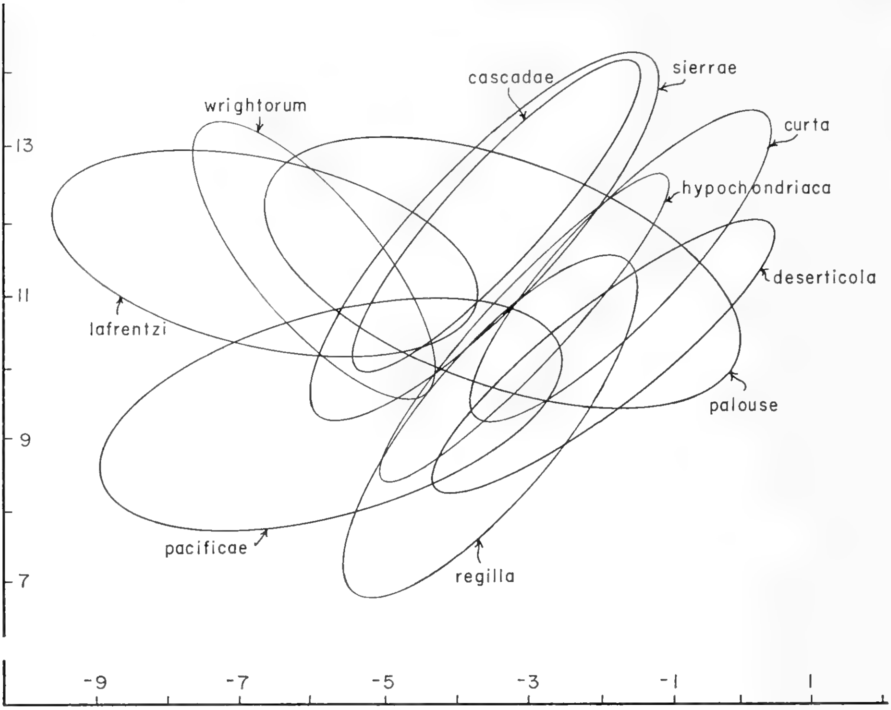

Figure 10. Equal frequency ellipses of 95 per cent of the variation of the male samples of each of the subspecies is shown on the first and second discriminant axes. The axes are the same as those shown in figure 4. The ellipses are not those of the principal axes of the factor analysis.

principal component axis. Combined, the first two principal components contain from 88.5 per cent in *H. r. wrightorum* to 71.0 per cent in *H. r. curta.*

First principal axis:

If all parts of the animal grow at equal rates (isometry), we would expect the value of the direction cosines of the first principal axis would be equal and would be $\sqrt{1/10} = 0.316$. The deviation of each of the direction cosines from 0.316 indicates the direction and amount of allometry in each measurement in each of the subspecies. The total allometry can be estimated by calculating the magnitude of the deviation of the sample from the expected value. The greatest deviation is that of *H. r. lafrentzi* (17°55′), the least is found in *H. r. deserticola* (6°10′). All of these deviations are large enough to suggest that they differ significantly from isometry; the appropriate statistical tools are available and will be used as soon as the computer program can be developed. The coefficient of growth of the eye–tympanum distance is smallest in *H.*

r. lafrentzi (–0.039) and largest in *H. r. wrightorum* (0.288). The pad width growth rate is less than expected (on the basis of isometry) in all forms except *H. r. palouse.* Snout–vent and limb length growth ranges appear to be about equal to each other in *H. r. palouse, H. r. regilla, H. r. pacifica, H. r. wrightorum,* and *H. r. deserticola.* Snout–vent grows faster in *H. r. hypochondriaca* and *H. r. lafrentzi* and slower in *H. r. curta.* Forearm growth is faster in *H. r. lafrentzi* and slower in *H. r. cascadae.* Shank length increases faster in *H. r. sierra, H. r. pacifica,* and *H. r. curta* and slower in *H. r. hypochondriaca.* Toe length increases fastest in *H. r. regilla* and slowest in *H. r. cascadae.* The growth rate of the nostril–lip distance is about equal to that of the nostril–eye distance in *H. r. cascadae, H. r. hypochondriaca,* and *H. r. deserticola* while they are greatly different in *H. r. wrightorum* and *H. r. lafrentzi.*

Second principal axis:

This axis characteristically represents the differences in shape of the different groups. Total males are characterized by positive coefficients with respect to appendage and total lengths, while head lengths and thus face shapes and toe pad width have negative coefficients. Obvious changes in the direction (as shown by change of sign from total males) of growth include: nostril–lip in *H. r. regilla*, nostril–eye in *H. r. cascadae* and *H. r. regilla,* pad width in *H. r. regilla,* head–width in *H. r. regilla* and *H. r. lafrentzi,* snout–vent in *H. r. wrightorum,* shank length in *H. r. regilla* and *H. r. hypochondriaca,* and forearm length in *H. r. palouse* and *H. r. cascadae.* Obvious changes in rate of growth include: nostril–lip in *H. r. pacifica,* nostril–eye in *H. r. regilla, H. r. pacifica, H. r. wrightorum,* and *H. r. lafrentzi,* pad width in *H. r. sierra, H. r. wrightorum,* and *H. r. curta,* head width in *H. r. deserticola* and forearm length in *H. r. pacifica* and *H. r. hypochondriaca.*

Comment. The differences in shape and form of the several subspecies herein described are considerable. Factor analysis provides a method of describing some of these differences as well as describing the differences between males and females. The most stable measurement appears to be the toe length measurement. The most stable factor is, of course, that represented by the first principal component axis (size). The subspecies most similar to the total male population of *Hyla regilla* are *Hyla regilla palouse, H. r. cascadae, H. r. sierrae,* and *H. r. hypochondriaca,* as is illustrated by comparing the tables and by comparing these subspecies to the grand mean in figure 4.

Hyla regilla regilla Baird and Girard.

Hyla regilla (Baird and Girard), 1852. Cotypes (2): 9182, United States National Museum (USNM), Puget Sound, Washington, C. J. Pickering. 15409 (USNHM), Sacramento River (restricted to Sacramento County, California), U. S. Exploring Expedition, 1841.

Hyla scapularis (Hallowell), 1852. Number 1978, Academy of Natural Sciences of Philadelphia, collected in the Oregon Territory, 1852, by Shumard. Restricted to Vancouver, Washington.

Holotype. 9182, U. S. National Museum (USNM), Puget Sound, Washington, C. J. Pickering.

Paratypes. None in existence.

Diagnosis. One of the smallest subspecies of the *Hyla regilla* complex attaining a mean size of 32 mm. head–body length; dorsal skin pustulate; ventral granulation coarse; head narrow; tympanum small, less than one-half the diameter of the eye; minute vestige of web between fingers, toes three-quarters webbed; tibiotarsal articulation to posterior edge of eye or slightly beyond.

Description of the holotype. Adult male. Nostril to edge of lip, 2.3 mm.; nostril to anterior edge of eye, 2.5 mm.; posterior edge of eye to anterior edge of tympanum, 1.0 mm.; width of pad on third digit, 1.1 mm.; length of head, 10.0 mm.; width of head, 10.4 mm.; snout–vent length, 29.5 mm.; tibia, 14.0 mm.; length of forearm, 7.1 mm.; length of fourth toe, 12.2 mm.

Head narrow at angle of jaw, sloping slowly forward to form a rounded snout; in lateral profile snout rounded, extending beyond the mouth; eyes are fairly prominent, protruding beyond outline of jaw; nostrils prominent, surrounded by raised portions of tissue; line between the eye and nostril slightly concave; nostril approximately the same distance from the eye as from the median anterior of lip; tympanum small, approximately equal to one-half the diameter of the eye.

Vomerine teeth small but visible lying between the choanae; tooth groups closer to the choanae than to each other; choanae slightly larger than the size of each tooth group; tongue is generally circular in shape, free posteriorly for about one-third of its length; vocal sac small, folds of skin almost absent because of extreme age of specimen. A moderate to light supratympanic fold extends to the insertion of the forearm; the skin above appears pustulate, becoming granular at the sides; entire abdomen and underside of thigh and arm with granulation; skin granular in anal region; granulation continues into the vocal sac.

Fingers slender with a vestige of web; thickened dermal ridges remain, extending to the termination disks; disks moderately large, the largest being easily greater than one-half the diameter of the tympanum; moderate nuptial callosity exists at the base of the first finger, and each finger has at least one or more tubercles, the total number not being great; a few small palmar tubercles present.

Foot moderately elongate, the part from the tarsometatarsal articulation to the tip of the longest toe extending about three-quarters of the way up the femur; inner metatarsal tubercle small, but easily recognized; the outer tubercle about one-third the size of the inner and may be confused with other foot tubercles; small tubercles distributed on each toe and on the foot; toe webbing extends for about three-quarters of the length of the toes, extended by thickened dermal ridges; toe disk distinctly smaller than finger disks. Legs short, tibiotarsal articulation extending to the posterior edge of the eye; tarsal fold well defined.

Color in alcohol. Above, on limbs and body, a dark brown color (probably green in life). Age has obscured any dorsal markings which might have been present. It appears that an eye stripe may possibly have been present since coloration in this area is lighter, but the preservation medium has successfully removed any other traces of body coloration and pattern.

The original type of *Hyla scapularis* Hallowell is an adult male, 1978, Academy of Natural Sciences of Philadelphia. The following differences are noted between it and the holotype (9182 USNM) of *Hyla regilla regilla* described above: Nostril to edge of lip, 2.8 mm.; nostril to anterior edge of eye, 3.0 mm.; posterior edge of eye to anterior edge of tympanum, 1.6 mm.; width of pad on third digit, 2.0 mm.; length of head, 12.1 mm.; width of head, 13.9 mm.; snout–vent length, 38.0 mm.; tibia, 20.2 mm.; length of forearm, 9.1 mm.; length of fourth toe, 16.4 mm. The vocal sac is slightly more evident in 1978 and only a minute vestige of web is present between the digits; toe webbing is slightly reduced, the toes about one-half webbed.

Variation. The range of variation present in the males comprising the data for the biometrical analysis of this subspecies is shown in table 8. The SDNHM series used for the biometrical analysis of this subspecies follows very closely the description of the holotype. Some variation in the amount of toe webbing present was observed. The SDNHM series showed greater amounts of such webbing. The females of this series show the same characters as the male with the exception of size; the females were generally larger.

Factor analysis of *Hyla regilla regilla*. The primary variation in the first axis accounts for 70.5 per cent of the total and is largely attributable to those measurements which show increases in the size of the animal (table 8). Factors two through five have direction cosines which differ in sign indicating a shape variation. In axes three through five those measurements which show an increase in the size of the head and cranial cavity are responsible for most variation. Factors six through ten show secondary variation in limb and body size. The correlation matrix for this subspecies shows most measurements to be highly correlated, $P < 0.01$. The only nonsignificant correlation is between nostril–eye distance and eye–tympanum distance.

Range. *Hyla regilla regilla* exists in the Rogue, Umpqua, and Willamette valleys and the Puget Trough of Oregon, Washington, and southern British Columbia. The subspecies has its southern limit at Evans Creek, Oregon (just north of Medford); the northern limit appears to be Vernon, British Columbia. The subspecies exists in an easterly direction up into the foothills of the Cascade Mountains; the western limit is the range of mountains along the Pacific Coast.

Material examined. (210): Fort Lawton, Washington: AMNH 299-302,

TABLE 8. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 30 adult males of* Hyla regilla regilla *are listed with the roots (λ) of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nostril–lip	Nostril–eye	Eye–tympanum	Pad width	Head length	Head width	Snout–vent	Shank length	Forearm	Toe length
Female mean	2.71	2.98	1.54	1.53	11.44	12.12	36.49	17.80	8.67	15.34
Male mean	2.54	2.54	1.28	1.40	10.11	10.90	32.13	15.38	7.76	13.23
Standard deviation	0.25	0.24	0.16	0.23	0.82	0.95	2.58	1.49	0.80	1.37
Direction cosines										
First axis	0.288	0.266	0.239	0.262	0.342	0.338	0.347	0.348	0.354	0.350
Second axis	0.169	–0.434	0.622	0.468	–0.128	–0.264	0.113	–0.246	–0.123	0.053
Roots λ	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.05	1.07	0.56	0.50	0.34	0.18	0.15	0.08	0.05	0.03
Variance component	11.50	1.01	0.30	0.13	0.09	0.05	0.03	0.02	0.01	0.01
Per cent of total	87.5	7.7	2.3	1.0	0.7	0.4	0.2	0.2	0.1	0.1

53320. Evans Creek, Oregon: USMVZ 17163, 64, 66-17170. Eugene, Oregon: SDNHM 53171-53264. Corvallis, Oregon: SDNHM 53265-53296. Chilliwack, British Columbia: SDNHM 53297-53326. Portland, Oregon: SDNHM 53327-53344. Abbotsford, British Columbia: SDNHM 53431-53453.

Hyla regilla deserticola Jameson, Mackey, and Richmond, new subspecies.

Hyla regilla (Baird and Girard), 1852. Cotypes (2): 9182 United States National Museum (USNM), Puget Sound (restricted to Fort Vancouver), Washington, C. J. Pickering. 15409 (USNM) Sacramento River (restricted to Sacramento County, California), U. S. Exploring Expedition, 1841.

HOLOTYPE. Adult male, SDNHM 54176, collected San Borjas, Baja California, by D. L. Jameson on November 25, 1961.

PARATYPES. SDNHM series 54166-54175.

DIAGNOSIS. The smallest subspecies of the *Hyla regilla* complex, attaining a mean size of 32 mm. head–body length; dorsal skin pustulate; ventral granulation fine; head narrow; tympanum diameter less than one-half the diameter of eye; minute vestige of web present between fingers; toes three-quarters webbed; tibiotarsal articulation to posterior edge of eye.

DESCRIPTION OF THE HOLOTYPE. Adult male. Nostril to lip, 2.7 mm.; nostril to edge of eye, 2.9 mm.; posterior edge of eye to anterior edge of tympanum, 1.5 mm.; width of pad on second digit, 1.4 mm.; length of head, 11.4 mm.; width of head, 10.9 mm.; snout–vent length, 34.9 mm.; tibia, 15.8 mm.; length of forearm, 8.1 mm.; length of fourth toe, 13.8 mm.

Head moderately narrow at the angle of jaw sloping forward to form a rounded snout; tip of snout rounded in the lateral profile and extending slightly beyond the mouth; eyes moderately prominent but protruding beyond outline of the jaw; nostrils about equally distant from the edge of the upper lip and eye; line between the eye and nostril straight; tympanum small, approximately less than one-half of the diameter of the eye.

Vomerine teeth present, situated wholly between the choanae and lying closer to the choanae than to each other; choanae moderately large and will easily include a tooth group; tongue elliptical in shape, free posteriorly for one-fifth of its length; vocal sac medial, single, evident on the chin by ample folding of skin.

A light supratympanic fold present extending from the posterior edge of the eye to the insertion of the forearm. The skin above pustulate becoming granular at the sides; entire abdomen and underside of thigh and arms finely granular; granulation continues well beyond the breast fold up into the vocal sac; skin granular in anal region.

The fingers moderately elongate with no vestige of web remaining between them; dermal thickening of the edges of the digits extending to the disks is present; disks distinct, small, elliptical in shape but larger than toe disks; width of the largest finger disk approximately equal to the diameter of the tympanum; moderately large nuptial callosity exists on the inside base of the first finger; both the finger and the palm with many tubercles of varying size; foot moderate in length, the part from the tarsometatarsal articulation to the tip of the longest toe extends slightly more than halfway up the tibia; both the inner and outer metatarsal tubercles are small. Toes one-half webbed, webbing continued to the disks in the form of thickened dermal ridges; toe disks small, just slightly wider than the width of the toes; the fourth toe of the left foot has been cut, pad is no longer present; tarsal fold is slight but evident. Legs short, tibiotarsal articulation extending to the posterior edge of the eye.

Color in alcohol. Above, on limbs and body, dark gray (probably a shade of gray or brown in life). A dark line beginning below the nostril and widening rapidly runs through the eye, widens involving the tympanum, becomes discontinuous at the insertion of the forearm, and is continued down the sides as a series of dark spots. A discontinuous line runs around the upper lip bordered above by a thin cream color.

Variation. The ranges of variation present in the males of this subspecies are seen in table 9. The five males and one female of the paratype series show marked similarity to the holotype. Some variation in tibiotarsal articulation is present; it tends to be slightly greater in several paratypes. Dorsal skin also somewhat smoother in the paratype series. The female is similar to the males

TABLE 9. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 133 adult males of* Hyla regilla deserticola *are listed with the roots (λ) of the correlation matrix and the roots and per cent of the total of variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nostril–lip	Nostril–eye	Eye–tympanum	Pad width	Head length	Head width	Snout–vent	Shank length	Forearm	Toe length
Female mean	2.96	3.17	1.79	1.57	12.09	12.62	37.35	17.59	8.87	14.63
Male mean	2.61	2.66	1.39	1.28	10.44	11.12	32.00	15.21	7.64	12.57
Standard deviation	0.27	0.25	0.20	0.24	0.87	1.42	3.18	1.57	0.84	1.42
Direction cosines										
First axis	0.313	0.308	0.229	0.297	0.341	0.287	0.347	0.335	0.343	0.344
Second axis	–0.122	–0.033	–0.915	0.059	0.040	0.310	0.043	0.117	0.116	0.128
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.44	0.67	0.44	0.43	0.37	0.25	0.15	0.11	0.08	0.06
Variance component	16.27	0.95	0.54	0.19	0.14	0.08	0.03	0.02	0.02	0.01
Per cent of total	89.2	5.2	3.0	1.0	0.8	0.4	0.2	0.1	0.1	0.1

in the characters noted with the exception of snout–vent length, the female being larger.

FACTOR ANALYSIS. The first axis shows primary variation in snout–vent, toe length, forearm length, head length, and shank length. The direction cosines for this axis are all positive, indicating size variation or a growth trend responsible for 74.4 per cent of the variation. The second and third factors show primary variation in head size, eye to tympanum, and length of limbs. Factors four and five exhibit variation in body and limb size. The sixth and seventh axes show variation in head height and limb size. Factors eight through ten present variation in limb and body size. The direction cosines of the last nine axes differ in sign and represent a shape variation.

RANGE. *Hyla regilla deserticola* is found in isolated localities in Nevada, Arizona, Baja California Norte, and California. The subspecies is present in the low, somewhat arid regions of Nevada but absent on the high northern plateau of this state. The northern limit of the range in Nevada is Jarbidge, Elko County. The range in Arizona seems to be limited to the border areas near the Lake Mead National Recreation area. The distribution in California includes the great inland valley; the northern limit exists near Corning, California. The subspecies is found south of the Tehachapi Mountains near Willow Springs Road in the Mojave Desert and sporadically along the east face of the coast range in southern California and in the north central region of Baja California and on the Pacific coastal islands. On the western coast of Baja California some intergradation of *Hyla regilla deserticola* and *Hyla regilla hypochondriaca* has occurred, specifically at San Quintín and Rosario.

Material examined. (589): Tehachapi Mountains, California: CAS 39003-39078. Las Vegas, Nevada: CAS 33434, 33440, 36856-36958. Santa Cruz Island, California: CAS 36137-36148, 45233-45302. Santa Catalina Island, California: CAS 3550-35566, 39125-39166, 39855. Santa Rosa Island, California: CAS 36103-36119. Panamint Mountains, California: CAS 65342-65377. Coalinga, California: SU 7521-7526. Wheeler Ridge, California: SU 20309-20322. Cottonwood Creek, California: SU 6452-6457. Fort Mojave, California: SU 14081-14122. Willow Springs, California: SU 18375-18387. San Quintín, Baja California: SU 9693-9703. Saratoga Hot Springs, California: SU 13074-13081 (intergrade between *Hyla regilla deserticola* and *Hyla regilla sierrae*). Pahrump Slough, Nevada: SU 7527-7536. Afton Station, California: SU 9413-9416 (intergrade between *Hyla regilla deserticola* and *Hyla regilla sierrae*). Corning, California: SDNHM 53770-53781. Calamajue, Baja California: SDNHM 54087-54165. San Borjas, Baja California: SDNHM 54166-54176. Carrizo, California: SDNHM 54948-54960. Scissors Crossing, California: SDNHM 54961-54982 (intergrade between *Hyla r. deserticola* and *Hyla r. hypochondriaca*). Las Vegas, Nevada: UCMVZ 8924, 8927, 19509-19512, 19515, 19518, 19538, 19541, 19543. Beatty, Nevada: UCMVZ 12975, 12984, 12988-12989, 12998. Jarbridge, Nevada: UCMVZ 65565, 11956.

Hyla regilla curta Cope, new combination.

Hyla curta (Cope), 1867. Cotypes (19) 5293(19), United States National Museum (USNM). In a spring at Soria, 15 miles north of Cape San Lucas, Baja California, Mexico, J. Xantus, August 10, 1859.

Hyla regilla laticeps (Cope), 1889. Cotypes (7) 5308(7), United States National Museum (USNM). Cape San Lucas, Baja California, Mexico. J. Xantus.

Cotypes. (19) Subadults, number 5293 USNM, collected in a spring at Soria, 15 miles north of Cape San Lucas, Baja California, Mexico, by J. Xantus, August 10, 1859.

Paratypes. None designated.

Diagnosis. A moderate to small-sized subspecies of the *Hyla regilla* complex, attaining an average size of 34 mm. head–body length; dorsal skin smooth, head narrow, tympanum diameter less than one-half the diameter of the eye; no vestige of web present between fingers; large, flattened nuptial callosity on base of first finger; foot three-quarters to fully webbed; tibiotarsal articulation to within or beyond eye.

Description of the cotypes. All cotype specimens subadult, the largest having a snout–vent length of 24.0 mm. Head fairly narrow at the angle of the jaw sloping abruptly to give a rounded snout, in lateral profile snout appears very rounded and extends well beyond the mouth; eyes fairly prominent protruding beyond the outline of the jaw, nostril nearer to median anterior edge of mouth than to the eye; tympanum small, its diameter being less than one-half the diameter of the eye; the line between the eye and nostril slightly concave.

Vomerine teeth groups moderately large lying wholly between the choanae, being slightly closer to each other than to the choanae; choanae are fairly large and easily capable of including two tooth groups; tongue broadly elliptical, free posteriorly for about one-third of its length; vocal sac not present due to subadult status of specimen.

A light to moderate supratympanic fold extends from the posterior edge of the eye to the insertion of the forearm. The skin above is practically smooth (minutely corrugate), becoming finely granular well down on the sides; entire abdomen and underside of thigh with small but distinct granules; granulation generally lacking on skin of breast fold and underarm; skin granular in anal region.

No vestige of web present between the fingers; very slight evidence of dermal thickening on the edges of digits extending to the disks. Disks distinct, elliptical, that on the third finger largest, its length being one-half the diameter of the tympanum; a large but flattened nuptial callosity on the base of the first finger; remainder of finger and palm contain moderate-sized tubercles; foot moderate in length, the part from the tarsometatarsal articulation to the tip of the longest toe reaching one-half of the way up the tibia; inner metatarsal tubercle small, the outer one not present. Toes one-half webbed, clearly defined tarsal fold; foot generally smooth; a tibiotarsal articulation to the posterior edge of the eye or beyond.

Color in alcohol. Above and on limbs gray to light brown, dorsal markings present but fading. A dark stripe beginning slightly beyond the nostril runs through the eye, widens involving the tympanum, and ends at the insertion of the forearm. A thin dark line bordered above in cream runs around the upper lip.

Variation. For the range of variation present in the males comprising the data for the biometric analysis of this subspecies see table 10. The animals used for biometrical analysis of this subspecies follow closely the description of the cotypes with the following exceptions. The vocal sac is present, these animals being adult males. The toes may be webbed to three-quarters of their length. The females of the subspecies show the same characters as the male counterparts and generally vary only in size; females are larger.

Factor analysis. This subspecies exhibits similar trends of growth and shape variation to the desert subspecies. Primary variation (60.0 per cent) in the first axis is based on a general increase of all characters with the limbs and head having the greatest rate of increase. Elongation of the limbs and in-

Table 10. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 38 adult males of* Hyla regilla curta *are listed with the roots (λ) of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nostril–lip	Nostril–eye	Eye–tympanum	Pad width	Head length	Head width	Snout–vent	Shank length	Forearm	Toe length
Female mean	3.18	3.61	2.19	1.73	13.60	14.24	41.00	19.61	9.84	16.03
Male mean	2.76	2.92	1.65	1.33	11.27	11.70	33.36	16.17	8.03	13.04
Standard deviation	0.22	0.21	0.20	0.14	0.67	0.85	1.71	1.13	0.69	1.00
Direction cosines										
First axis	0.335	0.324	0.176	0.180	0.373	0.346	0.322	0.367	0.347	0.318
Second axis	0.077	–0.027	–0.565	–0.728	–0.001	0.104	–0.068	0.106	0.223	0.262
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	6.00	1.10	0.87	0.71	0.43	0.31	0.23	0.17	0.12	0.09
Variance component	5.07	1.14	0.37	0.16	0.11	0.09	0.03	0.02	0.01	0.01
Per cent of total	72.3	16.3	5.3	2.3	1.6	1.3	0.4	0.3	0.1	0.1

crease in size of the cranial cavity accounts for the significant variation in the growth rates of the limbs and body while axes eight and nine indicate increased rates of growth for the cranial cavity.

The correlation matrix for this subspecies shows most measurements to be highly correlated at greater than 0.01 per cent level of significance. Measurements three and four, eye to tympanum and pad width, are responsible for those coefficients which are not highly significant at $P = 0.01$.

Remarks. The choice of a subspecific title for this variant of *Hyla regilla* was limited to two descriptions of specimens from the cape of Baja California made by Cope (1866, p. 313; 1889, p. 359). Cope designated the former, *Hyla curta* (1866), as a new species of *Hyla* and the latter, *Hyla regilla laticeps* (1889), as a variant of *Hyla regilla*. Examination of the specimens used to make these descriptions reveals no essential differences, even though the cotypes of *Hyla regilla laticeps* are fully grown adult males. The age difference in these specimens may account for Cope's placing them in different taxonomic categories.

Range. The lower half of the Baja California peninsula comprises the range of this subspecies. The northern limit appears to be near San Ignacio, the southern limit is the bounds of the peninsula itself. Most localities yielding animals of this subspecies were concentrated south of La Paz.

Material examined. (402): San Ignacio, Baja California: USMVZ 73355-73363, 73365-73367. El Triumpho, Baja California: CAS 91471-91472. Sierra Laguna, Baja California: CAS 47255-47256. La Trinchera, Baja California: CAS 91059-91071. San Ignacio, Baja California: CAS 90343-90351, 90912-90927. Boca de la Sierra, Baja California: CAS 91462. La Purissima, Baja California: CAS 91277. Puerto Escondido, Baja California: CAS 53662-53669. La Laguna, Baja California: CAS 87892-87895. Palmarito, Baja California: CAS 101162-101201; SDNHM 53960-54077. Los Marteles, Baja California: SDNHM 54078. Todos Santos, Baja California: SDNHM 54079-54086. San Ignacio, Baja California: SDNHM 54177-54191. Las Parras, Baja California: SDNHM 54879-54914. San Jose Comondu, Baja California: SDNHM 55016-55037. Comondu, Baja California: SDNHM 55038-55105. La Laguna, Baja California: SDNHM 55106-55142. Las Lagunas, Baja California: SDNHM 55143-55149.

Hyla regilla hypochondriaca Hallowell, new combination.

Hyla scapularis var. *hypochondriaca* Hallowell, 1854. Cotypes (8): 3235 United States National Museum. Tejon Pass, California, collected by Dr. A. L. Heerman.

Cotypes (8). USNM 3235. Two small adult males, two adult females, four very small juveniles.

Paratypes. None in existence.

Diagnosis. A moderate to small-sized subspecies of the *Hyla regilla* complex, attaining an average size of 33.5 mm. head–body length; dorsal skin smooth, head wide, tympanum diameter less than one-half the diameter of eye; no vestige of web present between fingers; granulation not visible on breast fold; small nuptial callosity at the base of the first finger; toes one-half webbed; tibiotarsal articulation to anterior edge of eye or beyond.

Description of the male cotypes (2). The following measurements were made on the larger of the two male cotypes: Nostril to lip, 2.0 mm.; nostril to anterior edge of eye, 2.4 mm.; posterior edge of eye to anterior edge of tympanum, 1.3 mm.; width of pad on third digit, 0.9 mm.; length of head, 9.3 mm.; width of head, 10.0 mm.; snout–vent length, 26.9 mm.; tibia, 13.0 mm.; forearm length, 6.1 mm.; toe length, 10.4 mm. Head wide at the angle of the jaw rounding quickly forward to form a blunt snout; snout appears squared off in the lateral profile but extends slightly beyond the mouth; eyes prominent, protruding beyond jaw; nostrils prominent surrounded by raised tissue, nostril closer to median anterior edge of upper lip than to the eye; tympanum moderate in size being less than one-half the diameter of the eye; line between the eye and nostril slightly concave.

Vomerine teeth small, lying completely between the choanae, being closer to each other than to the choanae; choanae easily larger than one tooth group; tongue generally circular in shape, free posteriorly for about two-fifths of its length; vocal sac medial, single, evident on chin by ample folding of skin.

The supratympanic fold very light but visible from the posterior edge of the eye to the insertion of the forearm. The skin above smooth, minutely pustulate becoming granular at the sides, entire abdomen granular, thigh and arm with patches of fine granulation; granulation continues until the breast fold on which it is absent; minute granules are present on the distended membranes of the throat; skin granular in anal region.

Fingers moderate in size, no vestige of web visible, small amount of dermal thickening on the edges of the digits extending to the disks; disks circular in shape, the largest being easily greater than one-half the diameter of the tympanum; small nuptial callosity on the base of the first finger; all remaining fingers and palm with a few tubercles. The foot only moderate in length, the part from the tarsometatarsal articulation to the tip of the longest toe extends about halfway up the tibia; both the inner and outer metatarsal tubercles are small, the former located well down on the base of the first toe; remainder of the foot and toes dotted with small tubercles. Toes about one-half webbed with a minute amount of dermal thickening of the toes extending beyond the webbing. Tibiotarsal articulation extends to within the eye.

Color in alcohol. The skin above and on the limbs blue–gray (probably a shade of green in life). A dark stripe runs from beyond the nostril through the eye, widens, involves the tympanum, and terminates at the insertion of the forearm. A dark stripe runs around the upper lip bordered by a cream color. Dorsal markings are evident as darker stripes and spots.

Variation. The animals used for biometrical analysis (table 11) follow very closely the description of the cotypes above with the following exceptions: the amount of the tongue free posteriorly is less, about one-third; no vestige of web is present between the fingers; tibiotarsal articulation generally extends beyond the eye. These noted exceptions from the cotype appear to be the case throughout the range of this subspecies. The females of this species show the same morphological characters with the exception of size, the female being larger.

Factor analysis of *Hyla regilla hypochondriaca*. The first factor shows that primary variation in the size of the animal accounts for 65.5 per cent of the variation. Shank length shows a smaller contribution to variation than its corresponding measurements on the first (size component) axis. This can perhaps be explained by consulting table 11 which shows that *Hyla regilla hypochondriaca* has one of the smallest mean shank lengths. Factors two through ten have differing signs for the direction cosines, and, therefore, correspond to a change in shape, specifically in reduced limb size and increased length of the cranial cavity. Factors eight through ten show secondary variation in the size of the limbs and width of the head.

Table 11. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 40 adult males of* Hyla regilla hypochondriaca *are listed with the roots (λ) of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nostril–lip	Nostril–eye	Eye–tympanum	Pad width	Head length	Head width	Snout–vent	Shank length	Forearm	Toe length
Female mean	2.96	3.12	1.65	1.61	12.13	12.88	38.92	18.00	9.71	15.75
Male mean	2.50	2.73	1.26	1.14	10.40	11.11	33.49	15.83	7.93	13.22
Standard deviation	0.23	0.23	0.20	0.19	0.73	0.99	2.51	1.92	0.63	1.29
Direction cosines										
First axis	0.321	0.324	0.269	0.198	0.370	0.363	0.363	0.254	0.339	0.317
Second axis	0.027	0.119	–0.212	–0.781	0.026	0.046	0.132	–0.380	0.334	0.232
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	6.55	0.91	0.71	0.59	0.44	0.24	0.22	0.15	0.12	0.08
Variance component	10.30	2.30	0.62	0.25	0.09	0.06	0.03	0.02	0.02	0.01
Per cent of total	75.2	16.8	4.5	1.8	0.7	0.4	0.2	0.1	0.1	0.1

Remarks. Hallowell (1854) described *Hyla scapularis,* variation *hypochondriaca,* from Tejon Pass, California, from specimens obtained by Dr. A. L. Heerman. Both Yarrow (1882, Bull. of the U. S. Natl. Mus., vol. 24, p. 172) and Test (1898, Proc. U. S. Natl. Mus., vol. 21, p. 490) list USNM number 3255 as the cotype of *Hyla scapularis,* variation *hypochondriaca.* The cotype series consists of two adult males, two adult females, and five juveniles.

Range. *Hyla regilla hypochondriaca* has been collected primarily at localities along the coast of California and part of the western coast of Baja California. The northern limit of the subspecies is near Clear Lake, California, and the southern limit is near Rosario in Baja California. The animals are not found in an easterly direction beyond the coast range of mountains.

Material examined. (882): Kernville, California: SU 8937-8942. La Grulla, Baja California: SU 12949-12955. Banner, California: SU 20200-20255 (intergrade between *Hyla r. hypochondriaca* and *H. r. sierrae*). Cedros Island, Baja California: CAS 42049-42056, 56276-56352, 59626-59677. San Telmo, Baja California: CAS 57520-57523. El Rosario, Baja California: CAS 90863-90872. Clear Lake, California: SDNHM 53576-53608. Russian River, California: SDNHM 53609-53642. San Luis Obispo, California: SDNHM 53654-53677. Osoflaco, California: SDNHM 53678-53685. Long Beach, California:

CAS 101110-101133. Salinas, California: SDNHM 53758-53764. Healdsburg, California: SDNHM 53765-53769. French Gulch, California: SDNHM 53782-53806 (intergrade between *Hyla r. hypochondriaca, H. r. deserticola, H. r. pacifica*, and *H. r. sierrae*). Crescent, California: SDNHM 53889-53919 (intergrade between *Hyla r. hypochondriaca, H. r. sierrae*, and *H. r. wrightorum*). Boulder, California: SDNHM 54275-54343. Lake Henshaw, California: SDNHM 54373-54417. Lake Arrowhead, California: SDNHM 54418-54441 (intergrade between *Hyla r. hypochondriaca* and *H. r. sierrae*). Mount Helix, California: SDNHM 54442-54477. Fuerte Farms, California: SDNHM 54478-54491. Presidio, California: SDNHM 54492-54501. Lakeside, California: SDNHM 54502-54560. Jacks, California: SDNHM 54561-54602. Guadalupe, Baja California: SDNHM 54603-54611. Santa Monica, California: SDNHM 54612-54614. Rancho Santa Fe, California: SDNHM 54615-54618. Miramar, California: SDNHM 54622-54624. Kearney Mesa, California: SDNHM 54625. College Drain, California: SDNHM 54626-54633. Bass Lake, California: CAS 101134-101161. White Water Canyon, California: SDNHM 54863-54896. Earthquake Valley, California: SDNHM 54915-54947 (intergrade between *Hyla r. hypochondriaca* and *H. r. sierrae*). Scissors Crossing, California: SDNHM 54961-54982 (intergrade between *Hyla r. hypochondriaca* and *H. r. deserticola*). Banner, California: SDNHM 54985-55002. Barkers, California: SDNHM 555003-55011 (intergrade between *Hyla r. hypochondriaca* and *H. r. sierrae*).

Hyla regilla pacifica Jameson, Mackey, and Richmond, new subspecies.

Holotype. Adult male, number 101007, California Academy of Sciences (CAS). One of a series collected February 27, 1957, at Big Creek State Park, 4 miles S. of Waldport, Lincoln County, Oregon; R11W, T133, S2, NW. 25 feet, by James P. Mackey.

Paratypes. Sixty adult males CAS 101008-10103F; AMNH F4466-F4483; CNHM 154671-154688; SDNHM 53514-53529; USNM 157836-15F851; MCZ 51857-51873; collected at the type locality.

Diagnosis. One of the largest of the subspecies of the *Hyla regilla* complex attaining a mean size of 36.5 mm. head–body length; dorsal skin smooth, ventral granulation visible on breast fold; small vestige of web between inner fingers; toes about one-half webbed; head coloration present; tibiotarsal articulation to anterior edge of eye or beyond.

Description of the holotype. Nostril to edge of lip, 3.2 mm.; nostril to anterior edge of eye, 3.2 mm.; posterior edge of eye to anterior edge of tympanum, 1.7 mm.; width of pad on third digit, 2.0 mm.; length of head, 12.4 mm.; width of head, 13.3 mm.; snout–vent length, 38.0 mm.; tibia, 19.2 mm.; length of forearm, 8.9 mm.; length of fourth toe, 18.3 mm.

Head widened at angle of the jaw sloping slowly to form a blunt snout; tip of snout appears flattened in lateral profile, extending almost perpendicularly up from the mouth; the line from the eye to the nostril slightly concave; eyes prominent but not protruding greatly beyond the jaw; nostril about equally distant from the eye and median anterior edge of upper lip; tympanum moderately large about equal to one-half the diameter of the eye.

Vomerine teeth readily visible located wholly between choanae and lying approximately equally spaced from each other and the choanae; choanae about equal in size to two tooth groups; tongue broadly elliptical in shape and free posteriorly for about two-fifths of its length; vocal sac medial, single, evident on the chin by ample folding of skin.

Light to moderate supratympanic fold extending well to insertion of the forearm. The skin above smooth, becoming granular at the sides; entire abdomen and underside of thigh and arm with a small amount of granulation; granulation below continues until the breast fold where it rapidly diminishes as the vocal sac is formed; skin granular in anal region.

Fingers rather elongated; small vestige of web remains between the inner fingers, but the outer finger has almost none remaining; the third and fourth digits of the left hand are short, having been cut in a marking procedure; there is little evidence of dermal thickening on the margins of the digits; disks on the fingers moderate, circular in shape, being a little larger than the toe disks; width of the widest pad is easily greater than one-half the diameter of the tympanum; nuptial callosity can be distinguished on the base of the first finger, the palm is not heavily covered with large tubercles as in some variants; the foot is extremely elongate, the part from the tarsometatarsal articulation to the tip of the longest toe extending three-quarters of the way up the tibia; the inner and outer metatarsal tubercles are moderately small. The inner toe is webbed at the base, the rest smaller than the finger disks; a well-defined tarsal fold is in evidence. The legs are elongate, the tibiotarsal articulation reaching to well within the eye.

COLOR IN ALCOHOL. Above, on limbs and body, blue–gray color (most probably a shade of green in life). A dark line beginning below the nostril runs through the eye, widens, and continues through the tympanum ending at about the insertion of the forearm. A thin dark line runs around the lip and is bordered by a light cream color. All dorsal markings have been obscured by the preservation medium, but pattern data taken shortly after the animals were collected shows them to have both head and body markings similar to other variants of *H. regilla.*

VARIATION. The range of variation present in the male comprising the data for the biometrical analysis of this subspecies is shown in table 12. The male paratypes of this subspecies follow closely the description of the holotype. The only variation noted is in the extent of tibiotarsal articulation; the holotype specimen appears to be atypical for this character, tibiotarsal articulation extending easily beyond the eye in most animals of this variant.

Table 12. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 50 adult males of* Hyla regilla pacifica *are listed with the roots* (λ) *of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nostril–lip	Nostril–eye	Eye–tympanum	Pad width	Head length	Head width	Snout–vent	Shank length	Forearm	Toe length
Female mean	3.36	3.44	1.89	2.37	13.16	14.42	43.44	21.30	10.48	19.20
Male mean	2.85	2.81	1.41	1.65	11.06	12.04	36.46	18.34	9.00	16.35
Standard deviation	0.30	0.25	0.19	0.31	0.75	0.80	2.73	1.70	0.71	1.70
Direction cosines										
First axis	0.296	0.281	0.228	0.306	0.334	0.332	0.343	0.350	0.331	0.342
Second axis	–0.320	–0.403	–0.572	–0.305	0.144	0.209	0.215	0.107	0.373	0.232
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.23	0.99	0.58	0.39	0.29	0.20	0.10	0.10	0.07	0.05
Variance component	13.75	0.71	0.30	0.17	0.12	0.06	0.05	0.03	0.02	0.01
Per cent of total	90.3	4.7	2.0	1.1	0.8	0.4	0.3	0.2	0.1	0.1

The females of the subspecies show the same characteristics as the males with the exception that the females are generally larger.

Factor analysis of *Hyla regilla pacifica*. The first axis (table 12) shows the primary variation occurring is the size of the animal. Size variation in *Hyla regilla pacifica* accounts for more than 72 per cent of all variation while change in shape is responsible for the remaining variations. Shank length, snout–vent, and toe length have the largest direction cosines. The signs of all the direction cosines for the first axis are positive, indicating a growth trend or size variation. The remaining factors have a difference in sign indicating shape variation. Factors three through six show the growth of the cranial cavity and enlargement of the limbs. Factors seven to ten exhibit secondary variation primarily in the growth of the limbs.

Remarks. The subspecific title for this variant was chosen with an eye to geographic location. Since the range of this subspecies is the Washington and Oregon Pacific Coast, the name *Hyla regilla pacifica* was applied. This subspecies has been collected at locations (below) from a southern limit near Cannibal Road, California, to the northern limit near Wenberg, Washington. The subspecies is not found east of the coastal range of mountains.

Material examined. (165): Ophir, Oregon: UCMVZ 64538-64545. Tillamook, Oregon: UCMVZ 69538-69588. Alvadore, Oregon: UCMVZ 52421-52426. Reedsport, Oregon: UCMVZ 61751-61755. Cathlamet, Washington: UCMVZ 46430-46433. Wenberg, Washington: SDNHM 53345-53430. Waldport, Oregon: CAS 101008-101037, AMNH 74466-74483, CNHM 154671-154688, SDNHM 53514-53529, USNM 157836-157851, MCZ 51857-51873. Lees Camp, Washington: SDNHM 53562-53575. Cannibal Road, California: SDNHM 53643-53653. French Gulch, California: SDNHM 53782-53806 (intergrade between *Hyla r. pacifica, H. r. deserticola*, and *H. r. hypochondriaca*). Greyback, Oregon: SDNHM 55012-55013.

Hyla regilla wrightorum Taylor, new combination.

Hyla eximia wrightorum Taylor (Schmidt, 1953).

Hyla wrightorum Taylor, 1939 Univ. Kansas Sci. Bull., vol. 25, p. 436. Holotype 79141, Museum of Zoology, University of Michigan. Eleven miles south of Springerville, Apache County, Arizona.

HOLOTYPE. Museum of Zoology, University of Michigan 79141. See above.

PARATYPES. USNM 26605-26609, Meadow Valley, Chihuahua, Mexico. USNM 9338 (2 specimens), Santa Fe, New Mexico. UMMZ 79141 (3 specimens), 11 miles south of Springerville, Apache County, Arizona. UMMZ 79143 (4 specimens), David Lee Lake, southwest of Luna, Catron County, New Mexico [8,000 ft.]. UMMZ 79142 (3 specimens), 26 miles north of Luna, Catron County, New Mexico [8,100 ft.]. UMMZ 75734, 1½ miles northwest of Miller's Peak, Huachuca Mountains, Arizona.

DESCRIPTION OF THE HOLOTYPE. An excellent description of this animal is given by Edward H. Taylor (1938). The largest subspecies of the *Hyla regilla* complex, attaining a mean size of 38.47 mm. head–body length; dorsal skin smooth; fine granulation on breast fold and vocal sac; head wide; tympanum diameter greater than diameter of eye; vestige of web between fingers; foot one-third webbed; tibiotarsal articulation to the anterior edge of the eye or beyond; heels distinctly overlap; anterior edge of tibia spotted with brown; no dorsal head markings present.

DESCRIPTION OF THE PARATYPE SERIES. Head widened at the angle of the jaw sloping slowly to give a slightly rounded snout; in lateral profile snout appears blunt, but slightly rounded, extending a short way beyond the mouth; eye moderately prominent, not protruding beyond jaw; the line between the eye and nostril generally straight or very slightly concave; nostril closer to edge of upper lip than to anterior edge of eye.

Vomerine teeth groups large, lying wholly between the choanae; choanae moderate about the size of one tooth group; tongue broadly elliptical, free posteriorly for two-fifths of its length; tongue papillae visible but not prominent; vocal sac medial, single, evident on chin by ample folding of skin.

Skin above smooth, becoming granular on the sides; entire abdomen and underside of thigh and arm with granules; granulation sparse but visible on breast fold and vocal sac; skin granular in anal region.

A vestige of web present between the fingers; thickened dermal ridge on the edges of the digits extending to the disks; disks on fingers moderate, the width of the widest being equal to or greater than one-half the diameter of the tympanum; nuptial callosity present on the base of the first finger; fingers and palm covered with tubercles of various size; foot moderate in length, the part from the tarsometatarsal articulation to the tip of the longest toe reaching one-half the way up the tibia; inner and outer metatarsal tubercles moderate; toes one-third webbed; clearly defined tarsal fold. Tibiotarsal articulation to beyond the eye, when limbs are folded at right angles to body, heels have distinct overlap. A light to moderate supratympanic fold extends from the posterior edge of the eye to the insertion of the forearm.

Color in alcohol. Above, on limbs and body, gray to lavender (probably a shade of green in life). A dark stripe beginning slightly anterior to the nostril runs to the eye, widens, involves the tympanum, continues to low on the sides where it breaks up into irregular patches of coloration. A thin dark line bordered above in cream runs around the upper lip. No dorsal markings are present.

Variation. The paratypes and other specimens examined of this subspecies (table 13) follow very closely the description given by Taylor (1938) and the above description of part of the paratype series. Taylor (1938) did not make any mention of the absence of dorsal head markings in his description of the holotype; a photograph (p. 443) shows the holotype to have no visible dorsal head markings. The females of this subspecies show the same characters as the males with the exception that females are generally larger.

Factor analysis of *Hyla regilla wrightorum*. The direction cosines for the first axis are all positive, indicating a general growth trend or size variation. Those measurements which show general body size have direction cosines of about the same magnitude. Measurements which show the size of the cranial cavity have direction cosines of smaller magnitude corresponding to slower rates of growth. Factors two through four show variation in shape through differences in sign of the direction cosines. Increase in the size of the limbs and cranial cavity are responsible for this variance. The remaining factors show increases in the size of the cranial cavity and the limbs.

Range. *Hyla regilla wrightorum* has been collected at locations in Nevada, Arizona, New Mexico, and Mexico. Its range may have been restricted to mountain regions until the advent of men (Funk, 1964; Martin, 1963). The northern limit of collection is near Flagstaff, Arizona; the southern limit near Majarachic, Chihuahua, Mexico.

Material examined. (12): Fort Verde, Arizona: AMNH 419. Garden Canon Road, Cochise County, Arizona: AMNH 55073-55074. Alpine, Arizona: AMNH untagged. Majarachic, Chihuahua, Mexico: CNHM 105189-105190.

TABLE 13. *The mean of one adult female and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 10 adult males of* Hyla regilla wrightorum *are listed with the roots (λ) of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nos-tril–lip	Nos-tril–eye	Eye–tym-panum	Pad width	Head length	Head width	Snout–vent	Shank length	Fore-arm	Toe length
Female mean	3.20	3.10	1.50	1.40	12.30	13.90	40.20	19.70	9.00	16.70
Male mean	2.98	3.02	1.31	1.46	11.38	12.46	38.47	18.70	8.65	16.11
Standard deviation	0.22	0.23	0.21	0.22	0.65	1.02	3.27	1.24	0.62	1.08
Direction cosines										
First axis	0.344	0.301	0.288	0.208	0.300	0.347	0.333	0.340	0.347	0.329
Second axis	−0.040	−0.398	−0.311	−0.611	0.300	0.225	−0.209	0.278	0.227	0.240
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.39	1.46	0.46	0.32	0.20	0.11	0.06	0.02	0.00	0.00
Variance component	13.73	1.35	0.20	0.08	0.05	0.02	0.01	0.00	0.00	0.00
Per cent of total	88.9	8.7	1.3	0.5	0.3	0.1	0.1	0.0	0.0	0.0

Flagstaff, Arizona: SU 2084 (3). Springerville, Arizona: UMMZ 79141 (2). Luna, New Mexico: UMMZ 79142 (2).

Hyla regilla lafrentzi Mertens and Walterstorff, new combination.

Hyla lafrentzi Mertens and Walterstorff, 1929, Zool. Anz., B. 84, no. 9/10. Type 49/27 Magdeburg Museum. Desierto de los Leones, in mountain forest near Mexico City, Distrito Federal, 3,000 meters, L. Lafrentz, collector, December 18, 1927. Type not now in existence; destroyed during World War II.

NEOTYPE. Natur-Museum Und Forschungs-Institut "Senckenberg" SMF 30997. Collected Desierto de los Leones (3,000 m.), Mexico, by K. Lafrentz, 1927.

PARATYPES. None in existence.

DIAGNOSIS. One of the largest subspecies of the *Hyla regilla* complex, attaining a mean size of 37.71 mm. head–body length; dorsal skin smooth, granulation over entire ventral portion; head wide, vestige of web between first three fingers only, toes one-half to three-quarters webbed; tibiotarsal articulation to beyond eye.

DESCRIPTION OF THE NEOTYPE. Adult male. Nostril to upper edge of lip, 3.0 mm.; nostril to anterior edge of eye, 2.7 mm.; posterior edge of eye to anterior edge of tympanum, 1.2 mm.; width of pad on third finger, 1.4 mm.; length of head, 12.0 mm.; width of head, 13.3 mm.; snout–vent length, 36.9 mm.; tibia, 20.8 mm.; forearm length, 10.0 mm.; length of fourth toe, 16.6 mm.

Head widened at angle of the jaw sloping to give a rounded snout, in lateral profile snout blunt but slightly rounded and extends beyond the mouth; eye moderately prominent protruding slightly beyond the outline of the jaw; tympanum moderate, its diameter being about equal to one-half the diameter of the eye; the line between the eye and the nostril slightly concave.

Vomerine teeth groups moderate lying wholly between the choanae, being slightly closer to each other than to the choanae; choanae about the size of a tooth group; tongue broadly elliptical free posteriorly for about one-third of its length; vocal sac medial, single, evident on chin by folds of skin; sac appears smaller with fewer folds than in some subspecies.

A light supratympanic fold; extends from the posterior edge of the eye to the insertion of the forearm. Skin above smooth becoming granular well down on the sides; entire underside of body including arms, thighs, and vocal sac with granulation.

A vestige of web present between the fingers, slight dermal thickening of the edges of the digits extending to the disks; disks moderate, that of the third finger being the largest, its width easily greater than one-half the diameter of the tympanum; a large nuptial callosity on the base of the first finger; fingers and palm with tubercles of various size; foot moderate in length, the part from the tarsometatarsal articulation to the tip of the longest toe reaching one-half of the way up the tibia; inner and outer metatarsal tubercles small, the latter being hardly visible. Toes one-half to three-quarters webbed, the webs continued to the disks as thickened dermal ridges. Tibiotarsal articulation to beyond eye.

Color in alcohol. Above, on limbs and body, blue (probably a shade of green in life). A dark stripe beginning anterior to the nostril runs through the eye, widens, involves the tympanum, and continues well beyond the insertion of the forearm. A thin dark line bordered above in cream runs around the upper lip. Dorsal marking evident as dark spots, two such small spots on the head at the edges of the eyes. Legs and feet spotted; a thin dark line bordered very slightly in cream runs along the anterior edge of the tibia.

Variation. The series of specimens used for biometrical analysis of this subspecies (table 14) follows very closely the above description of the neotype with the following deviation. The eyes do not generally protrude beyond the outline of the jaw; the supratympanic fold is usually well defined, and markings on the head are absent. The females of this subspecies show the same characters as the males with the exception that the female is generally larger.

Factor analysis of *Hyla regilla lafrentzi*. Factor analysis of *Hyla regilla lafrentzi* gave the following results. (See table 14.)

TABLE 14. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 15 adult males of* Hyla regilla lafrentzi *are listed with the roots* (λ) *of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nostril–lip	Nostril–eye	Eye–tympanum	Pad width	Head length	Head width	Snout–vent	Shank length	Forearm	Toe length
Female mean	3.45	3.43	1.55	1.86	13.82	15.54	45.37	23.80	10.66	20.30
Male mean	3.00	3.05	1.19	1.63	11.82	13.60	37.71	20.29	9.17	16.96
Standard deviation	0.20	0.18	0.25	0.10	0.50	0.81	2.04	0.94	0.58	0.62
Direction cosines										
First axis	0.326	0.273	–0.039	0.244	0.380	0.319	0.375	0.352	0.379	0.322
Second axis	0.112	–0.320	–0.771	–0.197	–0.009	–0.289	0.144	0.124	–0.117	0.345
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	5.90	1.54	0.83	0.62	0.48	0.31	0.19	0.08	0.04	0.01
Variance component	5.73	0.52	0.27	0.12	0.07	0.04	0.02	0.01	0.00	0.00
Per cent of total	84.5	7.7	4.0	1.8	1.0	0.6	0.3	0.2	0.0	0.0

The first axis (table 14) shows that general size variation with the limbs, body, and head account for 59.0 per cent of the primary variation. The direction cosines are all positive for this axis with the exception of a small negative value for measurement of the eye to tympanum. The second factor shows general shape variation in body length and limb size. Axes three through six exhibit general shape variation in both the limbs and head. Factors seven through ten account for the primary variation or growth in the cranial cavity and elongation of the limbs.

The correlation matrix (table 14) for this subspecies gives the correlation coefficients of all different combinations of measurements. The number of coefficients not significant at 0.1 per cent level has reached a peak in this analysis. Eye-to-tympanum and pad width measurements appear to be responsible for the insignificant values. As the first axis of the factor analysis shows both pad width and eye-to-tympanum measurements have the smallest rates of increase of all measurements. The slow rate of growth for these characters accounts for both the negative and insignificant values calculated for the correlation coefficients.

Hyla regilla lafrentzi is characterized as varying primarily in size or growth of the body. Secondary variation is responsible for the elongation of the limbs and growth of the head and cranial cavity and can be interpreted as shape variation.

Remarks. The holotype and paratype specimens of *Hyla lafrentzi* (Mertens and Walterstorff), deposited in the Museum of Magdeburg, Berlin, Germany, were destroyed at the end of World War II. Dr. Robert Mertens has asked that we declare the remaining paratype as the neotype of *Hyla lafrentzi* (Mertens and Walterstorff). The neotype (SMF 30997) is deposited in the Natur-Museum Und Forschungs-Institut "Senckenberg," Frankfurt, Germany.

Range. The central plateau of Mexico.

Material examined (24). Velasco, Hidalgo, Mexico: AMNH 57824-57829. Lagunas de Zempoala, Morelos, Mexico: AMNH 57692-57699. Llano Grande, Mexico, Mexico: CNHM 107182, 107112, 107184, 107297, 107310, 107167, 107189, 107124, 107174.

Hyla regilla palouse Jameson, Mackey, and Richmond, new subspecies.

Holotype. Adult male, number 100982, California Academy of Sciences (CAS), one of a series collected June 8, 1957, 6 miles SE. of La Grande, Oregon, at the junction of highways US 30 and Oregon 203, 2,800 feet, by Byron E. Lippert.

Paratypes. CAS 100983-100990, 101345, AMNH 74443-74448, CNHM 154666-154670, USNM 157854-157857, SDNHM 44715-44718, MCZ 51853-51856; collected at the type locality.

Diagnosis. One of the larger subspecies of the *Hyla regilla* complex, attaining a mean size of 34.3 mm. head–body length; dorsal skin pustulate, ventral granulation coarse, heels have a slight overlap; head wide; vestige of web between fingers; toes about one-half webbed; tibiotarsal articulation to the posterior edge of eye.

Description of the holotype. Nostril to edge of lip, 3.0 mm.; nostril to anterior edge of eye, 3.0 mm.; posterior edge of eye to anterior edge of tympanum, 1.6 mm.; width of pad on third digit, 1.5 mm.; length of head, 11.2 mm.; width of head, 12.2 mm.; snout–vent length, 26.2 mm.; tibia, 26.2 mm.; length of forearm, 8.3 mm.; length of fourth toe, 14.5 mm. Head widened at the angle of the jaw, sloping quickly forward to the nostril and abruptly to the mouth forming a somewhat rounded snout; in lateral profile snout rounded, extending slightly beyond the mouth; eyes moderately prominent, not protruding beyond outline of jaw; nostril a little closer to the edge of lip than to eye; tympanum small, its diameter a little less than that of the eye.

Vomerine teeth small but visible, lying completely between the choanae, with a space of approximately one tooth group between them; choanae a little larger than one tooth group; tongue generally elliptical in shape, free posteriorly for about one-half its length; vocal sac medial, single, evident on chin by ample folding of skin. Moderately heavy supratympanic fold extending to the insertion of the forearm; skin above pustulate becoming granular at the sides; entire abdomen and underside of arm and thigh granular with remainder of the underside of the legs smooth; granulation becomes smaller on the breast, disappearing in vocal sac; skin granular in anal region. A vestige of web present between the fingers with a thickened dermal ridge extending the length of the digits to the pads; disks distinctly oval in shape, that of the third finger being the largest with a length greater than one-half of the diameter of the tympanum; nuptial callosity present extending from the wrist to slightly beyond the base of the first finger, medial and outer palmar tubercles confluent posteriorly; each finger with many tubercles with exception of the second, which has but one or two; the first and fourth fingers have the largest tubercles situated slightly above the base of the fingers; surface of the palm contains many irregular tubercles which appear to be extensions of the finger tubercles; the second finger of the left hand missing; foot rather elongate, the part from the tarsometatarsal articulation to the tip of the longest toe extends halfway up the tibia; two large metatarsal tubercles are located at the base of the first and fourth toes with the inner tubercle being the largest. Toes somewhat more than one-half webbed, thickened dermal ridges extend to the disks as extensions of webbing; foot and toes contain numerous small tubercles. Tibiotarsal articulation extends to the posterior edge of eye.

Color in alcohol. Upper parts blue–gray with dark dorsal markings; definite eye stripe present, running from the insertion of the forearm, quickly widening to about the diameter of the eye, narrowing at exit from eye, and curving slightly to the nostril where it slopes abruptly and stops approximately one-half the distance down the snout; dark thin stripe runs around the upper lip, edged above in cream color; back of femur is cream yellow with brown reticulation.

Variation. The range of variation present in the males providing the data for the biometric analysis of this subspecies is shown in table 15. The 27 male paratypes of this subspecies follow the description of the holotype with the exception that the nostril is generally slightly closer to the edge of the lip. The tongue may be more circular in shape than present in the holotype specimen. The dorsal markings of the paratype series are in most cases generally faded and in some cases appear to be absent. The two female paratypes designated appear small and were probably collected during their first mating season. The females show no dorsal markings, but this is not assumed to be a subspecific characteristic since females from other localities within the range of this variant have obvious dorsal markings similar to the males.

Remarks. The subspecific name was chosen to correspond to the geographic and ecologic range of this variant which is similar to that of the "Palouse prairie."

Factor analysis. The first factor (table 15) emphasizes that the overall

Table 15. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 30 adult males of* Hyla regilla palouse *are listed with the roots (λ) of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nostril lip	Nostril–eye	Eye–tympanum	Pad width	Head length	Head width	Snout–vent	Shank length	Forearm	Toe length
Female mean	2.77	3.08	1.78	1.68	11.91	13.01	37.13	17.97	8.98	15.17
Male mean	2.80	2.95	1.46	1.49	10.87	12.06	34.26	16.30	8.03	13.68
Standard deviation	0.20	0.19	0.15	0.18	0.72	0.94	2.64	1.55	0.67	1.39
Direction cosines										
First axis	0.303	0.289	0.114	0.313	0.338	0.352	0.349	0.349	0.337	0.345
Second axis	–0.098	–0.023	–0.911	0.134	–0.202	0.120	0.128	0.130	–0.108	0.204
Roots *W*(λ)	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.46	1.06	0.49	0.36	0.26	0.14	0.10	0.06	0.05	0.04
Variance component	12.43	0.38	0.19	0.10	0.09	0.04	0.02	0.01	0.01	0.01
Per cent of total	93.6	2.9	1.4	0.8	0.7	0.3	0.2	0.1	0.1	0.1

growth of the animal accounts for the largest amount of variation (74.6 per cent) on any subspecies. The greatest relative rate of growth occurs in the following body areas: head width, snout–vent length, shank length, and toe length, closely followed by head length and forearm length. Pad width and head height (represented by a nostril-to-lip measurement) show intermediate to slow rates of growth. Nostril-to-eye and eye-to-tympanum measurements show the slowest rate of growth relative to other measurements.

The second factor for *H. r. palouse* shows the greatest rate of growth in the toe length, pad width, shank length, snout–vent, and head width measurements. Those measurements which indicate the growth of the cranial cavity still show a slow growth rate.

The third factor shows the greatest rate of growth in the forearm, pad width, shank length, and toe length measurements. The remaining measurements exhibit slower rates of growth.

The fourth factor shows a marked increase in the growth rates of the following measurements: pad width, nostril to eye, eye to tympanum. The remainder of the measurements show a greatly decreased rate of growth over other previous factors.

Factors five through ten represent a little more than 6 per cent of the variation.

RANGE. *Hyla regilla palouse* has been collected at locations in eastern Washington and Oregon, southern Idaho, and on the border of west central Montana. Its range is thought, therefore, to be confined to low and middle elevations of the foothills and mountain valleys of the northern Rocky Mountains.

MATERIAL EXAMINED (306). Pullman, Washington: CAS 5997-60000. Boise, Idaho: CAS 41536-41539, 43532, 455527-45538, 64138-64150. Lake Como, Montana: USMVZ 31848-31851. Smith's Ferry, Idaho: CNHM 6933-6938. Anthony Lake, Oregon: SDNHM 44685-44695. La Grande, Oregon: CAS 100983-100990, 101345; AMNH 74443-74448; CNHM 154666-154670; USNM 157854-157857; SDNHM 44715-44718; MCZ 51853-51856.

Hyla regilla cascadae Jameson, Mackey, and Richmond, new subspecies.

HOLOTYPE. Adult male, number 101038, California Academy of Sciences (CAS), one of a series collected June 15, 1957 at Bend, Oregon, Deschutes County, one-half mile south of Bend; R12E, T18, S9NW, 3,750 feet, by Abert Minasco.

PARATYPES. CAS 101039-101067; AMNH 74449-74465; CNHM 154696-154713; SDNHM 44971-44987; USNM 157821-157835; MCZ 51874-51889 collected at the type locality.

DIAGNOSIS. One of the largest subspecies of the *Hyla regilla* complex, attaining an average size of 35 mm. head–body length; dorsal skin pustulate, head wide at the angle of the jaw, well-defined supratympanic fold; vestige of web present between fingers; toes fully webbed.

DESCRIPTION OF THE HOLOTYPE. Nostril to edge of lip, 3.5 mm.; nostril to anterior edge of eye, 3.1 mm.; posterior edge of eye to anterior edge of tympanum, 1.5 mm.; width of pad, third digit, 1.7 mm.; length of head, 12.9 mm.; width of head, 14.5 mm.; snout–vent length, 39.9 mm.; tibia, 19.1 mm.; length of forearm, 1.4 mm.; length of fourth toe, 16.7 mm. Head widened at the angle of the jaw sloping slowly to the eyes, forming a slightly rounded snout; in later profile snout appears rounded, extending only slightly beyond mouth giving the appearance of a slightly blunted snout; eyes prominent but not protruding beyond the outline of the jaw; nostril about the same distance from median anterior edge of upper lip as from the eye; line from the nostril to eye slightly concave; tympanum relatively small, its diameter being less than one-half the diameter of the eye.

Vomerine teeth groups visible lying close together with less than the width of a tooth group between them; choanae about the size of a tooth group; tongue generally circular in shape, free posteriorly for only two-fifths of its length; vocal sac medial, single, evident under chin by ample folding of skin.

A moderately heavy supratympanic fold present extending from slightly posterior to the eye to the insertion of the forearm. The skin above pustulate becoming granular on the sides; entire abdomen and underside of thigh and arm granular; granulation extends to the breast fold where it begins to diminish but it is still evident until the colored portion of the vocal sac; skin granular in anal region.

An easily perceivable vestige of web is present between the fingers and a thickened dermal ridge extends to the finger disks; disks distinct, elliptical, only slightly wider than the digits, but greater than half the diameter of the tympanum; a large nuptial callosity is found on the base of the first finger, many tubercles both large and small on the palm and fingers; the fourth digit on the right hand is short and appears to have been cut in marking; foot moderate in length, the part from the tarsometatarsal articulation to the tip of the longest toe extending one-half the way up the tibia; inner and outer metatarsal tubercles readily evident, foot is dotted with numerous other small tubercles, webbing generally extends the full length of the toes, becoming narrow at the tips; tibiotarsal articulation extends to the posterior edge of the eye.

Color in alcohol. Above and on limbs a blue–gray color (probably green in life); dorsal markings dark and distinct. A dark stripe beginning slightly beyond the nostril runs to the eye, and widening, involves the tympanum, and becomes discontinuous at the insertion of the forearm continuing in a series of patches down the side of the animal. A dark stripe bordered above in cream runs around the upper lip.

Variation. The ranges of variation present in the males comprising the data for the biometric analysis of this subspecies are given in table 16. The male paratypes of the type series follow closely the definition of the holotype. The females designated as paratypes show the same characters as the males except in respect to size, the female being generally larger.

Factor analysis of *Hyla regilla cascadae*. The first factor emphasizes increase in size (73.6 per cent) and shows about equal rates of increase for snout–vent, shank length, head width, nostril to eye, nostril to lip, and forearm; somewhat slower growth rates are exhibited by toe length, eye-to-tympanum, and pad width measurements.

The second factor emphasizes primarily the growth of the eye-to-tympanum measurement. Slower rates of increase are indicated by nostril to eye, toe length, shank length, and head length. The remaining measurements show greatly decreased rates of growth. The first two factors have accounted for 95.17 per cent of all variation present.

Factors three through ten primarily indicate a secondary increase in the growth rates of the foot and cranial regions.

The correlation matrix for this subspecies (table 16) shows high positive correlation between all different combinations of measurements. Since correlation coefficients involving measurement three do not result in insignificant values as previously, one must assume that either the tympanum and eye are

TABLE 16. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 46 adult males of* Hyla regilla cascadae *are listed with the roots (λ) of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nos-tril–lip	Nos-tril–eye	Eye–tym-panum	Pad width	Head length	Head width	Snout-vent	Shank length	Fore-arm	Toe length
Female mean	3.14	3.47	1.86	1.73	13.10	14.42	41.54	20.03	9.90	16.36
Male mean	3.03	2.97	1.55	1.48	11.70	12.78	36.82	17.69	8.62	14.62
Standard deviation	0.35	0.32	0.24	0.25	1.09	1.28	3.36	1.80	0.88	1.84
Direction cosines										
First axis	0.337	0.334	0.267	0.247	0.344	0.343	0.348	0.343	0.329	0.243
Second axis	–0.041	0.199	0.501	–0.736	0.119	0.040	–0.126	0.136	–0.302	0.156
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.36	0.78	0.69	0.43	0.20	0.17	0.15	0.10	0.08	0.05
Variance component	18.19	2.06	0.93	0.21	0.19	0.16	0.03	0.02	0.01	0.00
Per cent of total	83.4	9.5	4.3	1.0	0.9	0.7	0.1	0.1	0.0	0.0

small or the growth of the head and cranial cavity results in a wider separation of the eye and tympanum.

Primary variation in this subspecies occurs in the growth of the body and limbs. The growth of the cranial cavity matches the growth rate of general body size and in the second factor accounts for a very significant amount of variation. The remaining variation is accounted for by the growth of the foot and secondary enlargement of the head and cranial cavity.

RANGE. *Hyla regilla cascadae* is found in the Cascade Mountains of central Oregon, Washington, and southern British Columbia. The subspecies has its northern limit in Vernon, British Columbia; its southern limit is Klamath Falls, Oregon.

MATERIAL EXAMINED (377). Fort Klamath, Oregon: UCMVZ 35105-35125. Okanagan Lake, British Columbia: UCMVZ 24783-24787, 24791. Mitchell, Oregon: UCMVZ 26719, 26720, 26722, 26723. Twin Buttes, Washington: UCMVZ 29132-29135, 29138. Klamath Falls, Oregon: CAS 20428-20473. West Fir, Oregon: CAS 101068-101803, SDNHM 44744-44794. Hand Lake, Oregon: CAS 101084-101103, SDNHM 44815-44836. Madras, Oregon: SDNHM 44837-44842. East Lake, Oregon: CAS 101104-101115, SDNHM 44843-44848, 44860-44898. Horse Lake, Oregon: SDNHM 44899-44907. Bend, Oregon:

CAS 101038-101067, AMNH 74449-74465, CNHM 154696-154713, SDNHM 44971-44987, USNM 157821-157835, MCZ 51874-51889.

Hyla regilla sierra, new subspecies.

Holotype. Adult male, number 100991, California Academy of Sciences (CAS), one of a series collected June 26, 1964, 1¼ miles SSE. of Tioga Pass Ranger Station (east of entrance to Yosemite National Park); R25E, T1N, S31, 9,600 feet, by Timothy A. Lyerla.

Paratypes. CAS 100992-101006, AMNH 74484-74490, CNHM 154689-154695, SDNHM 53835-53841, USNM 157858-157864, MCZ 51890-51896; collected at the type locality.

Diagnosis. One of the largest subspecies of the *Hyla regilla* complex, attaining an average size of 36.4 mm. head–body measurement; dorsal skin smooth; head wide at jaw angle, tympanum greater than or about equal to one-half the diameter of eye; vestige of hand web present; toes one-half to three-quarters webbed; tibiotarsal articulation to the anterior edge of the eye or beyond.

Description of the holotype. Nostril to edge of lip, 3.5 mm.; nostril to anterior edge of eye, 3.4 mm.; posterior edge of eye to anterior edge of tympanum, 1.5 mm.; width of pad, third digit, 1.9 mm.; length of head, 13.6 mm.; width of head, 14.5 mm.; snout–vent length, 38.2 mm.; length of forearm, 9.5 mm.; length of fourth toe, 16.0 mm. Head widened at the angle of the jaw sloping slowly to the eyes, then more quickly to give a slightly rounded snout; in lateral profile snout appears blunt but extends slightly beyond the mouth; eyes prominent but do not protrude beyond jaw; nostrils prominent, being closer to the edge of the upper lip than to the eye; the line between the eye and the tympanum concave; tympanum moderate in size being equal to or greater than one-half the diameter of the eye.

Vomerine teeth groups moderate in size, lying completely between the choanae; teeth groups are closer to each other than to the choanae; choanae larger than a tooth group, possibly as large as two, tongue large, generally circular in shape; tongue papillae easily seen; tongue free posteriorly for about one-third of its length; vocal sac medial, single, evident in the chin by ample folding of skin, its elongate openings lying lateral to the posterior part of the tongue. A heavy supratympanic fold is evident extending from the posterior edge of the eye to the insertion of the forearm.

The skin above is essentially smooth becoming finely granular at the sides; entire abdomen with moderate-sized granules; undersides of the femurs and arms are spotted with fine granules; the skin of the breast fold smooth; fine granulation continues well into the vocal sac; skin granular in anal region.

Fingers moderately elongate with a vestige of web remaining; average dermal thickening of the edges of the digits is seen; finger disks larger than one-half the diameter of tympanum; rather large nuptial callosity on the base of the first finger; remainder of the fingers covered with various sizes of tubercles; three large outer tubercles on palm; foot elongate, the part from the tarsometatarsal articulation reaching one-half of the way up the tibia; inner and outer metatarsal tubercles easily seen and are moderately large, toes with several large tubercles, the foot with only a few small ones. Toes one-half to three-quarters webbed with obvious dermal thickening of toe disks; toe disks much smaller than the finger disks and former are not much broader than width of the toes. Tibiotarsal articulation extends beyond the eye but not the nostril.

COLOR IN ALCOHOL. Above and on limbs a light blue–gray (a shade of gray to green in life); dorsal markings, dark, distinct. A dark eye stripe beginning slightly below the nostrils running through the eye, widening, involves the tympanum, becomes discontinuous at the insertion of the forearm, and continues down the side as patches of coloration. The animal lacks a dark line above the upper lip.

VARIATION. The ranges of variation present in the animals comprising the data for the biometrical analysis of this subspecies are shown in table 17. The females of this subspecies are generally similar to males but larger in size. Color variation in this subspecies is low but present, with gray being the dominant hue seen. Red, green, and brown animals have been collected, however.

FACTOR ANALYSIS OF *Hyla regilla sierrae*. The direction cosines for the first axis (table 17) indicate relatively equal rates of growth for shank length, head length, snout–vent, head width, and nostril to eye; toe length, forearm, and nostril to lip exhibit intermediate growth rates, and eye-to-tympanum and pad width show the slowest rates of growth. Again the direction cosines are all positive, indicating the primary size variation or a growth trend of 70.5 per cent.

The second factor shows the greatest rate of growth in the forearm and toe length measurements. Snout–vent, shank length, and head width exhibit intermediate rates of growth. The direction cosines for this and the remaining axes differ in sign, indicating a shape variation.

Factors four, five, and six show shape variation to be occurring primarily in those measurements showing the size of the cranial cavity.

Factors seven through ten show secondary variation in growth of body size, the limbs, and the head. The correlation matrix for this subspecies shows a high positive correlation for all different combinations of measurements. *Hyla regilla sierrae* shows variation similar to the other subspecies of this group. The greatest amount of variation is accounted for by a growth trend or change in size; the remaining variation indicates a change in shape. Enlargement of the cranial cavity is responsible only for secondary variation.

RANGE. *Hyla regilla sierrae* is found in the mountains of the Sierra Nevada range primarily at high elevations and has not moved extensively in an east–west direction. The northern limit is the Pine Forest Mountains of northwestern

Table 17. *The mean of nine adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 39 adult males of* Hyla regilla sierrae *are listed with the roots* (λ) *of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nostril–lip	Nostril–eye	Eye–tympanum	Pad width	Head length	Head width	Snout–vent	Shank length	Forearm	Toe length
Female mean	2.88	3.40	1.39	1.56	12.98	14.44	40.41	20.18	9.82	16.10
Male mean	2.74	2.98	1.37	1.36	11.22	12.46	35.23	17.37	8.63	14.07
Standard deviation	0.30	0.26	0.25	0.43	0.91	1.20	2.93	1.77	0.84	1.42
Direction cosines										
First axis	0.311	0.332	0.237	0.230	0.351	0.340	0.342	0.357	0.315	0.319
Second axis	–0.239	–0.005	–0.523	–0.606	–0.082	0.133	0.190	0.126	0.351	0.320
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.28	1.17	0.54	0.25	0.22	0.20	0.14	0.09	0.08	0.05
Variance component	15.41	0.74	0.41	0.19	0.16	0.12	0.06	0.03	0.02	0.01
Per cent of total	89.9	4.3	2.4	1.1	0.9	0.7	0.4	0.2	0.1	0.1

Nevada and its southern limit is Lake Gorman, California. More southerly populations exist (Lake Arrowhead, California; Julian, California) but the animals show intergradation with *H. r. hypochondriaca* and *H. r. deserticola.*

Material examined (531). Paradise Valley, Nevada: UCMVZ 1256, 1258, 1570, 1572, 1574. Flanigan, Nevada: UCMVZ 21404-21406, 21409-21410, 21414, 21417, 21419, 35006-35009. Incline, Nevada: UCMVZ 14619-14642. Strawberry Lake, California: SU 7294, 7296-7311. Saratoga Hot Springs, California: SU 13074-13081 (intergrade between *Hyla r. sierrae* and *H. r. deserticola*). Afton Station, California: SU 9413-9416 (intergrade between *Hyla r. sierrae* and *H. r. deserticola*). Banner, California: SU 20200-20225 (intergrade between *Hyla r. sierrae* and *H. r. hypochondriaca*). Yosemite, California: CAS 100991-101006, AMNH 74484-74490, CNHM 154689-154695, SDNHM 53835-53841, USNM 157859-157864, MCZ 51890-51896. Lake Van Norden, California: SDNHM 53870-53888. Crescent, California: SDNHM 53889-53919. Julian, California: SDNHM 54192-54274. Lake Gorman, California: SDNHM 54344-54372. Lake Arrowhead, California: SDNHM 54418-54441 (intergrade between *Hyla r. sierrae* and *H. r. hypochondriaca*). East end of Lake Van Norden, California: CAS 101278-101317. Willows, California: CAS 101202-101277. Earthquake Valley, California: SDNHM

54915-54947 (intergrade between *Hyla r. sierrae* and *H. r. hypochondriaca*). Barkers, California: SDNHM 55043-55011 (intergrade between *Hyla r. sierrae* and *H. r. hypochondriaca*). Doerfler, California: SDNHM 55014-55015.

MORPHOLOGICAL COMPARISON OF THE SUBSPECIES OF *Hyla regilla*

The subspecies of *Hyla regilla* appear to fall into three divisions on the basis of similar morphological characters. These groups are: *Hyla regilla regilla, H. r. deserticola, H. r. curta, H. r. hypochondriaca,* "thermal forms"; *Hyla regilla pacifica, H. r. wrightorum, H. r. lafrentzi,* "pluvial forms"; and *Hyla regilla palouse, H. r. cascadae,* and *H. r. sierrae,* "mountain forms."

Separation of *Hyla regilla regilla* from *Hyla regilla deserticola* is accomplished in the following way: *H. r. deserticola*—tongue one-half free posteriorly, *H. r. regilla*—tongue two-fifths free posteriorly; *H. r. deserticola*—no vestige of hand webbing, *H. r. regilla*—shows vestige of hand webbing; *H. r. deserticola*—ventral granulation extends into vocal sac, *H. r. regilla*—ventral granulation does not extend into vocal sac.

Hyla regilla regilla can be distinguished from *Hyla regilla curta* as follows: *H. r. curta*—usually shows greater amount of toe webbing than *H. r. regilla; H. r. curta*—no vestige of hand webbing, *H. r. regilla*—vestige of hand web present; *H. r. regilla*—dorsal skin generally smooth, *H. r. curta*—dorsal skin pustulate; *H. r. regilla*—ventral granulation does not extend into vocal sac, *H. r. curta*—scattered ventral granulation into vocal sac.

Separation of *Hyla regilla regilla* from *Hyla regilla hypochondriaca* is accomplished in the following way: *H. r. regilla*—nostril equally distant from edge of upper lip and anterior edge of eye, *H. r. hypochondriaca*—nostril closer to edge of upper lip than to anterior edge of eye; *H. r. regilla*—skin above pustulate, *H. r. hypochondriaca*—skin above smooth; *H. r. regilla*—nuptial callosity on the base of the first finger large, *H. r. hypochondriaca*—nuptial callosity on the base of the first finger small; *H. r. regilla*—toes three-quarters webbed, *H. r. hypochondriaca*—toes one-half webbed; *H. r. regilla*—tibiotarsal articulation to posterior edge of eye, *H. r. hypochondriaca*—tibiotarsal articulation to within or beyond eye.

Hyla regilla deserticola can be separated from *Hyla regilla curta* in the following way: *H. r. curta*—nostril generally closer to edge of lip than eye, *H. r. deserticola*—nostril about equally distant from anterior edge of eye and edge of upper lip; *H. r. deserticola*—tongue free posteriorly for about one-half of its length, *H. r. curta*—tongue free posteriorly for about one-third of its length; *H. r. deserticola*—dorsal skin pustulate, *H. r. curta*—dorsal skin smooth; *H. r. curta* generally shows greater amount of toe webbing than *H. r. deserticola.*

Hyla regilla deserticola can be distinguished from *Hyla regilla hypochondriaca* as follows: *H. r. deserticola*—nostril equally distant from edge of upper lip and anterior edge of eye, *H. r. hypochondriaca*—nostril closer to edge of upper lip than to anterior edge of eye; *H. r. deserticola*—tongue free posteriorly for one-half of its length, *H. r. hypochondriaca*—tongue free posteriorly for two-fifths of its length; *H. r. deserticola*—nuptial callosity on the base of the first finger moderately small, *H. r. hypochondriaca*—nuptial callosity on the base of the first finger small; *H. r. deserticola*—toes three-quarters webbed, *H. r. hypochondriaca*—toes one-half webbed; *H. r. deserticola*—tibiotarsal articulation to posterior edge of eye, *H. r. hypochondriaca*—tibiotarsal articulation to within or beyond eye.

Separation of *Hyla regilla curta* from *Hyla regilla hypochondriaca* is accomplished in the following way: *H. r. curta*—nuptial callosity on the base of the first finger large, *H. r. hypochondriaca*—nuptial callosity on the base of the first finger small; *H. r. curta*—toes three-quarters to fully webbed, *H. r. hypochondriaca*—toes one-half webbed; *H. r. curta*—tibiotarsal articulation to posterior edge of eye, *H. r. hypochondriaca*—tibiotarsal articulation to within or beyond eye.

The tibiotarsal articulation of the pluvial forms of *Hyla regilla* extend beyond the eye. *Hyla regilla pacifica* can be distinguished from *Hyla regilla wrightorum* in the following manner: *H. r. pacifica*—tympanum size greater than one-half the diameter of the eye, *H. r. wrightorum*—tympanum size less than one-half the diameter of the eye; vomerine teeth groups generally larger in *H. r. wrightorum; H. r. pacifica*—granulation not visible on vocal sac; *H. r. wrightorum*—granulation over entire vocal sac; *H. r. pacifica* generally has a lesser amount of finger webbing; *H. r. wrightorum* has a lesser amount of toe webbing than *H. r. pacifica.*

Hyla regilla lafrentzi and *Hyla regilla pacifica* can be differentiated in the following manner: *H. r. lafrentzi* shows larger vomerine teeth groups; *H. r. lafrentzi* has granulation over the entire vocal sac, *H. r. pacifica* has little or no granulation on the vocal sac; *H. r. pacifica* exhibits finger pads which are less than or equal to one-half the diameter of the tympanum, *H. r. lafrentzi* has finger pads which are easily greater than one-half the diameter of the tympanum; *H. r. pacifica* shows distant dorsal head markings whereas such marking is absent in *H. r. lafrentzi.*

Hyla regilla wrightorum can be separated from *Hyla regilla lafrentzi* by a comparison of these characters: nostril closer to edge of upper lip in *H. r. wrightorum,* nostril closer to anterior edge of eye in *H. r. lafrentzi;* tympanum is less than one-half the diameter of the eye in *H. r. wrightorum,* tympanum greater than one-half the diameter of the eye for *H. r. lafrentzi; H. r. wrightorum* generally exhibits greater choanae size than *H. r. lafrentzi; H. r. lafrentzi* has a greater amount of toe webbing than *H. r. wrightorum.*

The mountain forms of *Hyla regilla* have a vestige of finger webbing, the nostril generally closer to (equal for *H. r. sierrae*) upper lip than to the eye, and the tibiotarsal articulation generally to anterior edge of eye or into eye for *H. r. sierrae.*

Separation of *Hyla regilla palouse* from *Hyla regilla sierrae* is accomplished by observing that *H. r. palouse* exhibits a rounded snout in contrast to the blunt snout of the *H. r. sierra.* The larger tympanum size, more toe webbing, and longer tibiotarsal articulation separate *H. r. sierrae* from *H. r. palouse.*

Hyla regilla cascadae can be separated from *Hyla regilla palouse* by comparing ventral granulation, finer in *H. r. cascadae*; amount of heel overlap, greater in *H. r. palouse;* kind of supratympanic fold, heavier in *H. r. cascadae;* overall size of the animal; *H. r. cascadae* usually larger.

Hyla regilla cascadae can be distinguished from *Hyla regilla sierrae* by comparing the following characters: relative position of nostril closer to lip in *H. r. sierrae,* equally distant from lip and eye in *H. r. cascadae*; tympanum size, *H. r. sierrae* larger; size of choanae, larger in *H. r. sierrae*; skin texture, slightly pustulate in *H. r. cascadae,* smooth in *H. r. sierrae*; amount of ventral granulation, present in vocal sac for *H. r. sierrae,* not for *H. r. cascadae*; toe webbing, *H. r. cascadae* fully webbed, *H. r. sierrae* less; tibiotarsal articulation, beyond eye in *H. r. sierrae* only, to anterior edge of eye in *H. r. cascadae.*

Key to the Subspecies of *HYLA REGILLA*

1a. Dorsal skin smooth or minutely corrugate 5
1b. Dorsal skin pustulate 2
2a. (1) Ventral granulation very fine; tongue smaller, less free posteriorly; no vestige of web between fingers .... *Hyla regilla deserticola*
2b. (2) Ventral granulation coarse; tongue larger, more free posteriorly; vestige of web between fingers 3
3a. (2) Head narrow, eyes protrude beyond jaw; toes three-quarters webbed; choanae small .... *Hyla regilla regilla*
3b. (2) Head wide, eyes do not protrude beyond jaw; toes one-half to fully webbed; choanae size variable 4
4a. (3) Ventral granulation fine; toes fully webbed; heels with slight overlap; heavier supratympanic fold; generally a larger animal .... *Hyla regilla cascadae*
4b. (3) Ventral granulation coarse; toes one-half webbed; heels easily overlap; light supratympanic fold; generally a smaller animal .... *Hyla regilla palouse*
5a. (1) Tibiotarsal articulation to posterior edge of eye or less; head narrow, eyes protrude beyond jaw; no vestige of web between fingers .... *Hyla regilla curta*
5b. (1) Tibiotarsal articulation to well within or beyond eye; head width variable, eyes may or may not protrude beyond jaw; vestige of hand webbing may or may not be present 6
6a. (5) Head markings present 7
6b. (5) Head markings absent 9
7a. (6) Vestige of hand web present; tympanum diameter greater than one-half the diameter of the eyes; choanae larger than a vomerine tooth group; head wide, eyes do not protrude beyond jaw; nuptial callosity on base of first finger moderate to large 8
7b. (6) No vestige of hand web present; tympanum less than one-half the diameter of the eye; choanae are small, less than size of a vomerine tooth group; head narrow, eyes protrude beyond jaw; nuptial callosity on base of first finger small .... *Hyla regilla hypochondriaca*

8a. (7) Granulation fine into vocal sac; vestige of web between fingers; toes one-half to three-quarters webbed; tibiotarsal articulation to within but not beyond eye *Hyla regilla sierrae*

8b. (7) Granulation absent in colored portion of vocal sac; small vestige of web between inner fingers, none present between outer fingers; toes one-half webbed; tibiotarsal articulation to beyond eye, may extend to nostril .... *Hyla regilla pacifica*

9a. (6) Choanae about the size of a vomerine tooth group; toes one-third webbed; top of femur, anterior edge of tibia spotted with brown .... *Hyla regilla wrightorum*

9b. (6) Choanae less than the size of a vomerine tooth group; toes one-half to three-quarters webbed; a dark line bordered above in cream runs down the anterior edge of the tibia to the foot .... *Hyla regilla lafrentzi*

Discussion

A taxonomic study is essentially a study of the morphology of the animals being investigated. Studies of the ecology, genetics, and physiology provide powerful aids to the analysis of the morphological characteristics, but the critical explanation must involve the presence, absence, or magnitude of this or that character.

Closely related forms will evolve in the same direction as the result of the same or similar mutations and the same or similar adaptive requirements, even when genetic isolation is complete. Some of the populations we are considering here exchange genes along a large portion of the geographic continuity. Still others are subject to differences in breeding season, topography, and environmental barriers which seriously limit the gene flow between the populations. Genetic tests among animals from several of the populations do not appear to provide the essential clue to the systematic analysis—the animals interbreed with varying amounts of reduced viability which reinforces our conclusions concerning the morphological relationships. A premature discussion or summary of the results of the genetic, developmental, physiological, and ecological problems involved is not warranted since these studies must be understood in light of the morphological analysis and of the historical interpretation of this analysis.

These animals have been faced with a changing, and perhaps what one could consider a rapidly changing environment, for at least the last dozen centuries. The glacial, or more properly, pluvial maximum of 11,000 years ago was followed by an increase in temperature and decrease in surface moisture terminating in a thermal maximum about 6,000 years ago. The thermal maximum was followed by a return to less extreme conditions. The nature of these secular changes is well documented by extensive pollen profiles (Hansen, Sears, *etc.*). The presence of brief periods of extremely warm or cold cycles superimposed on the general trends is supported by tree ring analysis and even by available historical records. While tree toads are adapted to take advantage of available habitats (ponds, trees) in the presence of conditions which are limiting to either survival or reproduction, a large portion of their distribution and abundance must be dependent on the abilities to avoid extremes. The mountain forms live in the mountains in spite of the necessity to hibernate to escape winter, storms, and glacial movements. The desert animals live where they are by adapting to warm summers, limited and sporadic water, and frequent necessity to aestivate. In the face of secular changes in the environment the animal has three choices: (1) evolve, (2) move, (3) become extinct. In western tree toads a great deal of all three has occurred and is occurring. Certainly these amphibians had a wide distribution during the pluvial maximum (fig. 11) and they were undoubtedly distributed from the edge of the continental glaciers south into Mexico. Their southern distribution may be assumed to have been at higher elevations. In the east they must have extended to the Rockies (perhaps beyond, if the relation to *Hyla andersoni* is demonstrated), and in the west they appeared to have inhabited all areas to the Pacific. The environment of the pluvial maximum was wet and cooler than now; more important, it was variable, and this variability leads us to suggest that some differentiation of animals would be expected at that time. Certainly there appears to have been a prevailing westerly flow of air masses and a rain shadow in this area is to be expected even during pluvial periods.

We suggest that the animals were differentiated into the groups recognizable today: (1) *H. r. palouse, H. r. sierrae,* and *H. r. cascadae* lived near and reproduced in the melting snow surrounding the glacial borders; (2) *H. r. pacifica, H. r. wrightorum,* and *H. r. lafrentzi* were adapted to the wet conditions *H. r. pacifica* occupies today (along the northwest coast and throughout the pluvial lakes and basins and mountains of western North America); (3) *H. r. hypochondriaca* and *H. r. regilla* occupied the coastal regions of California south of the San Francisco region and the rain shadow area of the inland valleys, north to near the glacial borders; (4) *H. r. deserticola* and *H. r. curta* were animals of the interior and lower latitudes, along the coast of Baja California.

Certainly some geographic variation is to be expected within the above four groups, but we suggest that it is reasonable to think of these groups as recognizably different from each other and perhaps not much differentiated within each group.

There is an abundant literature on the location of glacial refuges. Amphibians appear to require refuges from thermal maxima. The distribution of these animals during the thermal maximum is suggested by figure 12. The "mountain group" (*H. r. palouse, H. r. sierrae,* and *H. r. cascadae*) used the remains of glaciers just as they do today. The "pluvial group" refuged along the northwest coast (*H. r. pacifica*), in the mountains of western North America (*H. r. wrightorum*), and in the mountains of central Mexico (*H. r. lafrentzi*). The coastal mountains of southern California must have provided refuge for *H. r. hypochondriaca*. We suggest that *H. r. regilla* survived in springs, meander

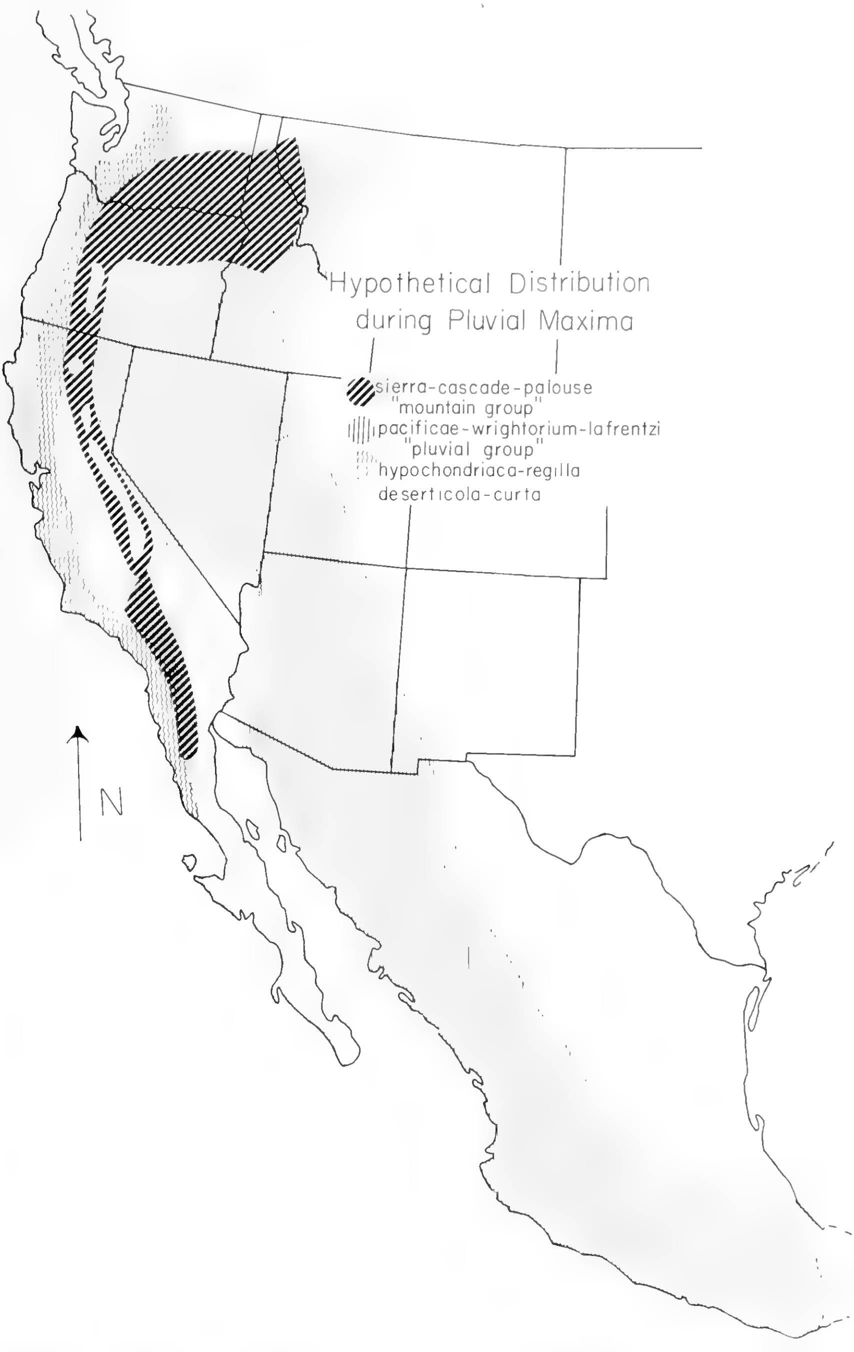

Figure 11. Map of the theoretical distribution of the populations of *Hyla regilla* during the pluvial maximum. To the north and within the distribution of the amphibian the white spaces are glaciers. To the east the distribution is unknown.

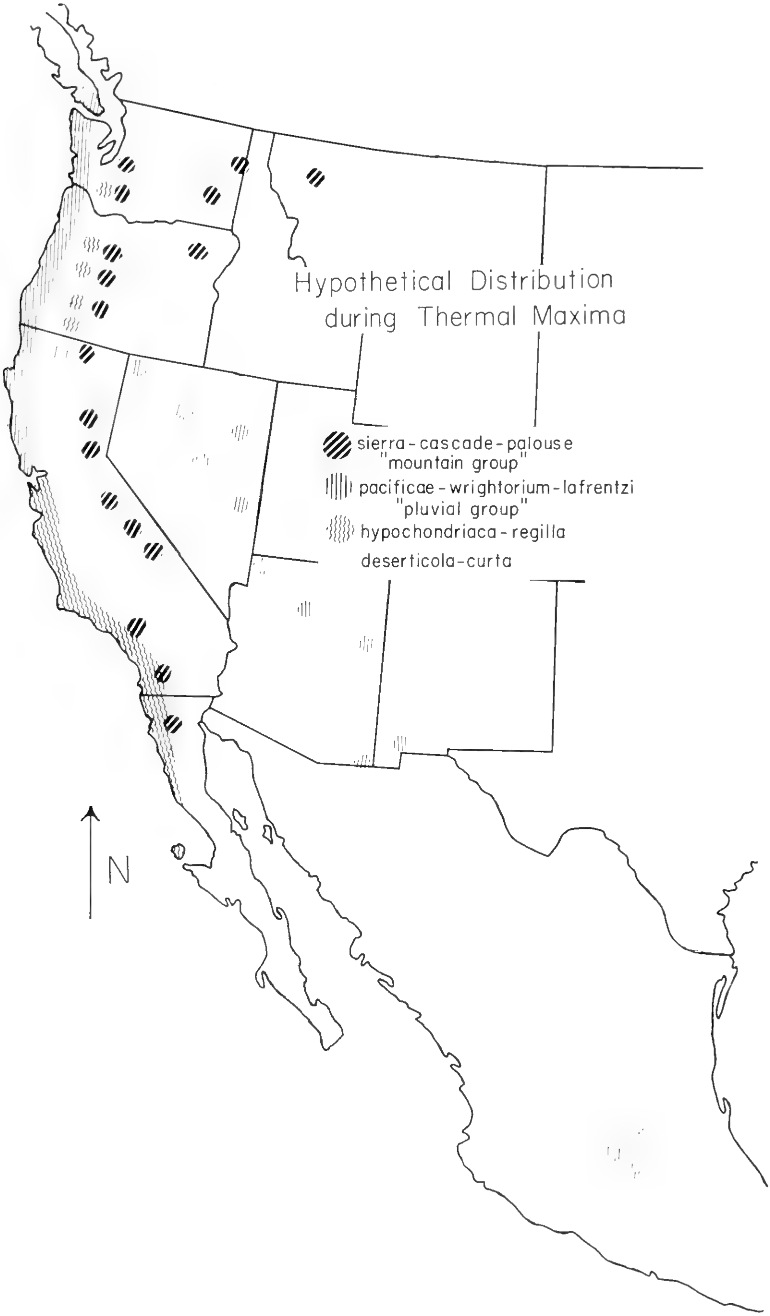

FIGURE 12. Map of the theoretical distribution of the populations of *Hyla regilla* during the thermal maximum.

scars of rivers, and at least partially at lower elevation west of the volcanic peaks in the area known geologically as the "Old Cascades." The distribution of *H. r. deserticola* during the thermal maximum may be very similar to that of today where it is limited to springs, watering holes, and a few meander scars of the Colorado, San Joaquin, and lower Sacramento rivers. The distribution of *H. r. deserticola* is surely less now than it was four or five hundred years ago when the water table was supported by beaver dams and more extensive vegetation. The mountains of the southern Baja California peninsula provide the logical refuge for *H. r. curta*. The migratory rates are sufficient to explain the range expansions of the animals (fig. 13) following the restrictions of the thermal maximum.

At some point we must come to grips with the problem of phylogenetic relationship in the classic sense (geographic speciation) versus adaptive convergence. This problem was apparent with almost every population we studied and was certainly true of our attempts to group subspecies into related forms. Our data seemed to fit an intermediate position between the accumulation of more and more facts leading in one and only one direction and the position of counting characters to assure repeatable results suggested by some approaches to computer systematics. The counting of characters is not satisfactory for us because of the limited number of things to count and because of the problems of identifying their significance. We are unable to accept the position of complete genetic continuity required by proponents of geographic speciation. We feel that most investigators today are inclined to those portions of all methods available which are useful to explain the results obtained.

Perhaps the most complex problem is that of the relationship within the "pluvial group" of *H. r. wrightorum*, *H. r. lafrentzi*, and *H. r. pacifica*. The only consistent morphological difference we have been able to find between *H. r. pacifica* and *H. r. lafrentzi–wrightorum* is the absence of head markings in museum specimens of *H. r. lafrentzi* and *H. r. wrightorum*, while almost all other individuals examined have head markings if you examine the specimen carefully. Slight differences in size of vomerine teeth groups, amount of webbing between toes, and amount and kind of coloring can be used in combination to distinguish *H. r. wrightorum* from *H. r. lafrentzi*. From the standpoint of the practicing taxonomist they can be distinguished by their localities. However, a large distance between two localities is not suggestive of adaptive convergence, and nonadaptive convergence of three forms is a little difficult to accept. The relation between *H. r. pacifica* and *H. r. regilla* or *H. r. hypochondriaca* is fully apparent from intergrades and ecological, genetic, and developmental compatibility. The discovery of *H. r. wrightorum* in northern Nevada (at least it was there in 1910) provides further evidence of historical and prehistorical distributions.

If our opinions concerning the influence of the pluvial and thermal maxima on the distribution of these animals is to have meaning, we must consider the

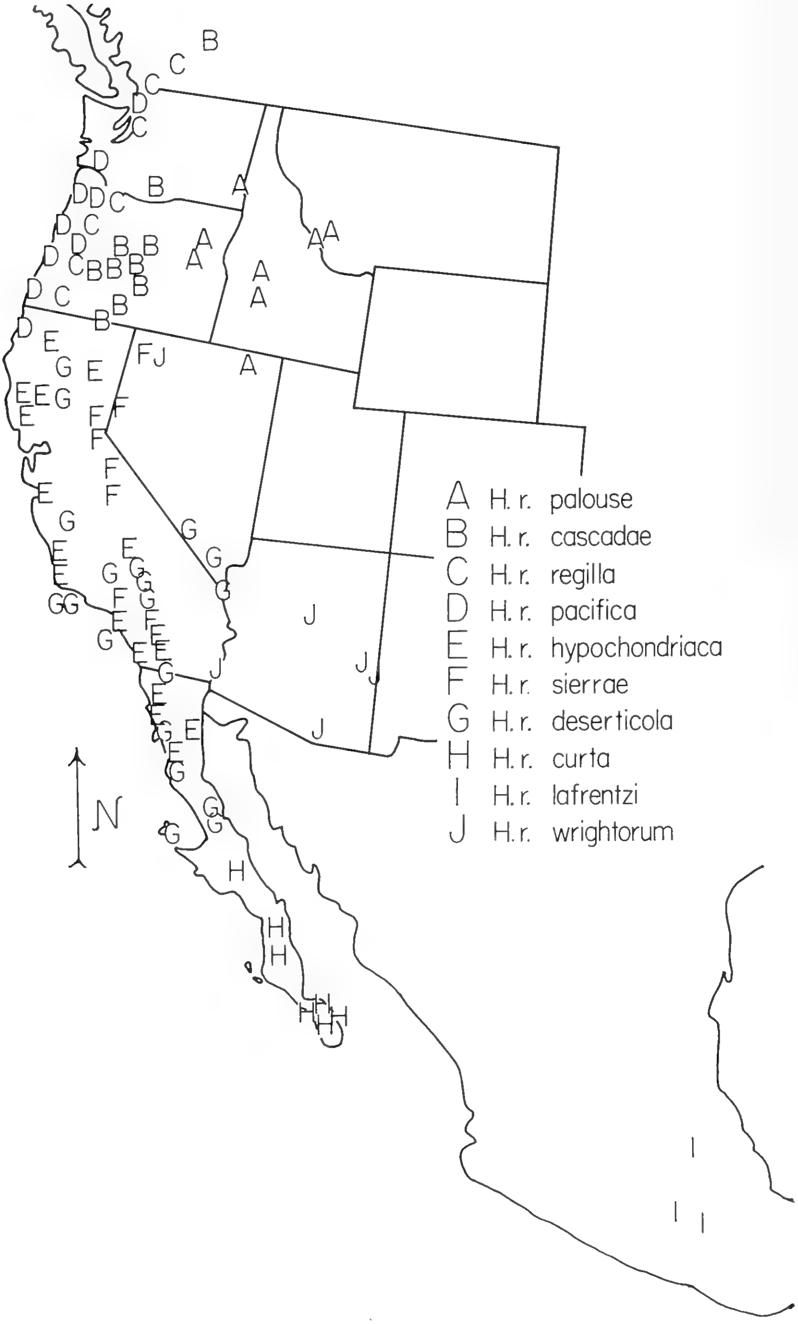

FIGURE 13. Map of the distribution of the samples used in the statistical analysis. Maps of the detailed distribution of all of the samples studied are not presented.

distribution of related forms which may or may not fit our concepts. *Dicamptodon ensatus, Plethodon vandykei,* and *Ascaphus truei* are species with populations isolated in the northern Rockies. In the Cascade Mountains we find *Rana cascadae* as an isolate and the relation between *Rana cascadae* and *Rana aurora* here is suggestive of the relation between *H. r. regilla* and *H. r. cascadae.* The Sierras have a number of endemic forms (*Hydromantes* and *Bufo canorus* are examples) and also have species which are wide-ranging, yet have well-differentiated populations (*Rana aurora draytoni, Ensatina eschscholtzi platensis*). The distribution of the two salamanders, *Plethodon dunii* and *Batrachoceps wrighti,* are suggestive of parts of the distribution of *H. r. regilla.* The relation of *H. r. lafrentzi* to the other forms is supported by the relation between *Rana boylii* and *Rana tarahumarae.* The number of forms isolated in the Cape region of Baja California is legend; we mention only *Scaphiopus couchi* to suggest the relation between the total distribution and the isolated forms. The distribution of fishes in the desert is extensively discussed by Hubbs (1948) and co-workers; these fish and *Bufo punctatus* have distributions comparable to that of *H. r. deserticola.* The large number of forms with distributions similar to *H. r. hypochondriaca* was a pleasant surprise to us since we had so much trouble understanding this form; the ranges of *Triturus torosus, Ambystoma tigrinum, Batrachoceps attenuatus, Aneides lugubris, Bufo m. californicus, Hyla californiae,* and *R. aurora* offer support to our conclusions.

One of the most interesting areas to us is that north and west of the Sierras and south and east of the Cascade Mountains. Here we find animals which are intergrades between *H. r. sierrae, H. r. cascadae, H. r. regilla, H. r. deserticola, H. r. pacifica,* and *H. r. wrightorum.* Into this area today one finds extensions of the ranges of *Dicamptodon ensatus, Ambystoma macrodactylum,* and *Aneides flavipunctatus* which suggest that secondary intergradation must be imposed on the original variation produced by isolation and relationships. Our active fieldwork in this area has not been adequate, but the same may be said of almost any area occupied by these animals. This is not meant as a complete biogeographic analysis of the amphibians of the West; the support for our position is obvious, yet tentative.

We conclude that the present distribution, abundance, and morphological variation of these animals is best explained by the adaptation to the varied habitats of the pluvial maximum followed by the restriction of ranges during the thermal maximum. We further conclude that the occurrence of similar mutations acted upon by similar selective adaptive requirements has resulted in parallel evolution of populations into recognizable subspecific entities even in the presence of genetic isolation.

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ERRATA

Page 99. Line 13 from bottom, for *Cephalopholus,* read *Cephalopholis.*
Page 140. Line 16 from top, for *wollbaeki*, read *wollebaeki.*
Page 208. Line 17 from top, for *Strangylaspis,* read *Strongylaspis;* line 18 from top, for vol. 72, read vol. 172; line 3 from bottom, for vol 72, read vol. 172.
Page 224. Line 10 from top, for *Monochamus*, read *Monochammus.*
Page 233. Line 1 from bottom, for *Monochamus,* read *Monochammus;* Line 4 from bottom, for *Monochamus,* read *Monochammus.*
Page 264. Line 2 from top, for *vermis,* read *vermes.*
Page 273 Line 5 from bottom, for *Liolopisma*, read *Leiolopisma.*
Page 569. First line of text, for *r. sierra,* read *r. sierrae.*
Page 579. Line 19 from bottom, for *H. r. sierra,* read *H. r. sierrae.*
Page 605. Line 3 from top, for heading *Hyla regilla* ***sierra***, new subspecies, read *Hyla regilla* ***sierrae***, Jameson, Mackey, and Richmond, new subspecies.