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A NEW GENUS OF NORTH AMERICAN SCORPIONS WITH A KEY TO THE NORTH AMERICAN GENERA OF VAEJOVIDAE (SCORPIONIDA: VAEJOVIDAE)

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Abstract: A new genus of North American vaejovid scorpions is described and named *Nullibrotheas*. *Nullibrotheas* is a monotypic genus, the only species being *Nullibrotheas allenii* (Wood). The systematic relationships of *N. allenii* are analyzed and it is concluded that the closest known relatives are in the vaejovid genera *Uroctonus* and *Vaejovis*. A key to the North American genera of Vaejovidae is included.

Introduction

In 1863, Horatio Wood described a new species of North American scorpion which he named "*Scorpius allenii*" (Wood, 1863a). This new taxon was based on specimens collected by L. J. Xantus de Vesey from Cabo San Lucas, in Baja California, Mexico, presumably between 1859 and 1861. This new species had the distinction of being one of the first species of North American scorpions to be described and named, and it has remained one of the most misunderstood taxa in North America. The actual identity and phylogenetic relationships of this species remained unknown until just recently.

The main purposes of this study are to more clearly define the species '*allenii*,' to determine its geographical distribution, to study its systematic affinities, and to erect a new genus to permit appropriate taxonomic placement of '*allenii*.' Most of the specimens cited as new records are deposited in the collections of the California Academy of Sciences.

Acknowledgments

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Nullibrotheas Williams, new genus

Type-species: *Scorpius allenii* Wood, 1863.

Description. Pedipalp palms greatly swollen, fingers shorter than palm or carapace; brachium with posterior border of inferior surface with six long trichobothria; fingers with supernumerary denticles flanking single principal row of denticles medially. Pectines with fulcra sub-triangular in shape; middle lamellae with elongate basal piece and one row of subcircular to ovate sclerites; males with longer comb, longer teeth, and greater number of teeth than females. Males with large distinct genital papillae on inner margins of genital operculum. Sternum pentagonal, with almost parallel sides; length approximates width or is slightly longer. Stigma of book lungs minute, circular in shape. Last tarsomere of walking legs with one row of short spines on ventral surface; two pedal spurs. Two median eyes on low ocular tubercule; median eyes entirely on anterior half of carapace; lateral eyes three per group, third eye reduced to degenerate, often giving appearance of two-eyed condition.

Nullibrotheas allenii (Wood).

(Figures 1–4; table 1.)

Scorpius allenii Wood, 1863a, p. 360 (original description); 1863b, p. 107.
Broteas allenii, Marx, 1887, p. 91.
Uroctonus privus Karsch, 1879, p. 103 (original description); Hjelle, 1972, p. 28–29.

Table 1. Measurements (in millimeters) of *Nullibrotheas allenii* Wood, SCW #116 (1), topotypes from Cabo San Lucas, Baja California Sur, Mexico.

	Male	Female
Total length	42	30
Carapace, length	5.0	4.5
width (at median eyes)	4.1	3.7
Metasoma, length		
segment I (length/width)	2.2/3.1	1.5/2.4
segment II (length/width)	2.6/2.7	1.9/2.2
segment III (length/width)	2.9/2.6	2.0/2.0
segment IV (length/width)	3.5/2.4	2.6/1.8
segment V (length/width)	5.7/2.3	4.3/1.8
Telson length	6.0	4.2
Vesicle (length/width)	4.4/2.4	2.8/1.8
depth	2.0	1.4
Aculeus, length	1.6	1.4
Pedipalp		
Humerus (length/width)	3.4/1.7	3.0/1.4
Brachium (length/width)	3.9/1.6	3.5/1.4
Chela (length/width)	7.7/2.7	6.7/2.5
depth	4.8	3.6
movable finger, length	4.3	3.5
fixed finger, length	2.4	2.2
Pectines, teeth (left/right)	11/11	8/9
Sternum (length/width)	1.1/1.1	1.1/1.2
Stigma (circular), diameter	0.2	0.2
Number middle lamellae	6	5
Genital operculum (length/width)	0.8/1.6	0.6/1.7

Uroctonus mordax (part), Kraepelin, 1894, p. 194 (synonymy of *U. privus*).
Broteas formosus Marx, 1889, p. 211.
Broteas alleni, Ewing, 1928, pp. 3, 6 (part); Hoffmann, 1931, pp. 332–333; Kraepelin, 1899, p. 176 (lists as doubtful species of chactid); Gertsch, 1958, pp. 2–5; Gertsch and Soleglad, 1966, p. 1; Diaz Najera, 1970, pp. 113–114.
Broteochactas allenii (part), Banks, 1910, p. 188.

Type data. *Scorpius allenii* Wood, two cotypes (one male, one female); collected at Cabo San Lucas, Baja California Sur, Mexico; male cotype deposited in U. S. National Museum (Type number S-5, jar 2), the location of the female cotype is unknown. The male cotype is intact, badly yellowed, and not well preserved. This specimen was designated as a lectotype by Gertsch (1958). It appears to be a subadult.

The type of *Uroctonus privus* Karsch is a holotype female with the following

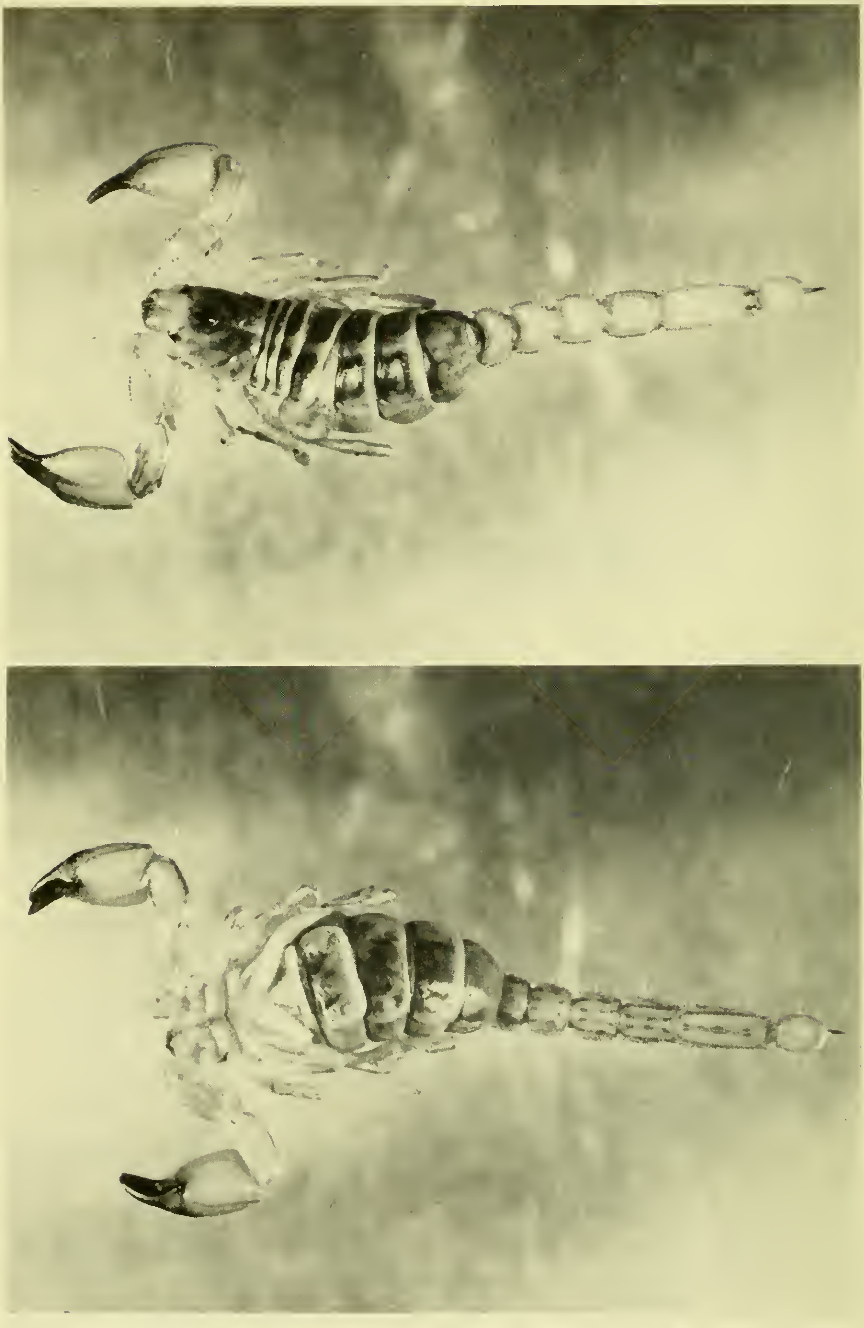

Figure 1. *Nullibrotheas allenii* (Wood), dorsal and ventral views of male topotype from Cabo San Lucas, Baja California Sur, Mexico.

data attached "Californien; leg. graber." It is deposited in the Zoological Museum of Berlin, DDR; catalog number 3036. The holotype is a small juvenile that does not differ significantly from the juveniles of *N. allenii* collected recently in the Cape region of Baja California, Mexico. The holotype is somewhat faded with age but the color pattern is still apparent; the metasoma is severed between segments 2 and 3.

Redescription based on topotypes from Cabo San Lucas. Variable species throughout range in coloration, cuticular granulation, hirsuteness, and body size; apparently forming many more or less isolated regional races. Typically with base color of cuticle golden yellow with underlying dusky to dark markings on carapace and mesosomal dorsum; pedipalps with dark reddish brown fingers; metasoma with inferior keels with more or less distinct dusky stripes; other parts of cuticle may or may not show underlying dusky markings.

Carapace. Anterior margin usually with deep median emargination and rounded lateral ends; lateral eyes generally three per group (sometimes apparently two per group); median eyes two in number, located on elevated ocular tubercule; median diad completely on anterior half of carapace. Sternum large, pentagonal; lateral sides almost parallel; length approximates width or is slightly longer; with deep median longitudinal furrow along posterior half.

Mesosoma. Terga 1 to 6 usually lustrous; seventh tergum with one pair short, obsolescent lateral keels, these granular; terga 1 to 6 lacking distinctly developed dorsal keels; sterna smooth and lustrous; stigma small, circular in shape; all sterna lack keels.

Metasoma. Dorsal and dorsolateral keels present and granular on segments I to IV; inferior lateral keels smooth to crenulate on I, irregularly crenulate on II and III, serrate on IV and V. Inferior median keels smooth to obsolescent on I, crenulate to obsolescent on II, crenular on III, serrate on IV and V.

Telson. Aculeus short, less than one-half length of vesicle; larger individuals normally with laterally swollen vesicle.

Pectines. Male with middle lamellae consisting of elongate basal piece and about five or six subcircular to ovate sclerites in single row; fulcra subtriangular; pectinal teeth six to nine in females, 10 to 14 in males; female comb much smaller than male, proximal one-fourth of female comb lacking teeth.

Genital operculum. In males completely divided longitudinally; in females divided only in posterior region of furrow; males with very large, conspicuous genital papillae, these lacking in females.

Chelicerae. Fixed finger with one simple tooth and one greatly elevated bicuspid tooth; movable finger with superior border armed with three or four simple teeth in addition to terminus; inferior border with three or four small denticles, these not conspicuous.

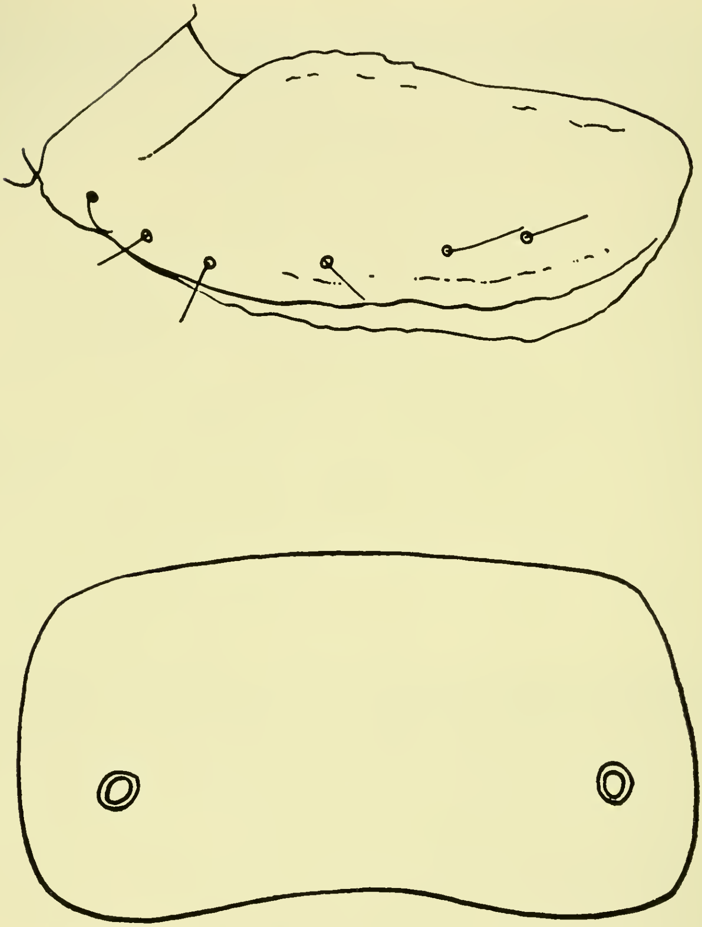

Figure 2. *Nullibrotheas allenii* (Wood) figured from topotype male from Cabo San Lucas, Baja California Sur, Mexico. Top. Ventral view of pedipalp brachium. Bottom. Mesosomal sternum showing openings to book lungs.

Pedipalps. Fingers very short, palm very deep and swollen; keels obsolete to smooth except for pronounced inferior keel; palm surface lustrous, smooth to finely granular. Movable finger distinctly shorter than carapace; fixed finger shorter than metasomal segment III. Each finger armed with one longitudinal row of small denticles; no distinct gap between fingers when chela closed. Fingers very hirsute. Brachium with six trichobothria on posterior border of inferior surface.

Walking legs. Two pedal spurs; one row of minute, longitudinally arranged hairs on ventral surface of last tarsomere.

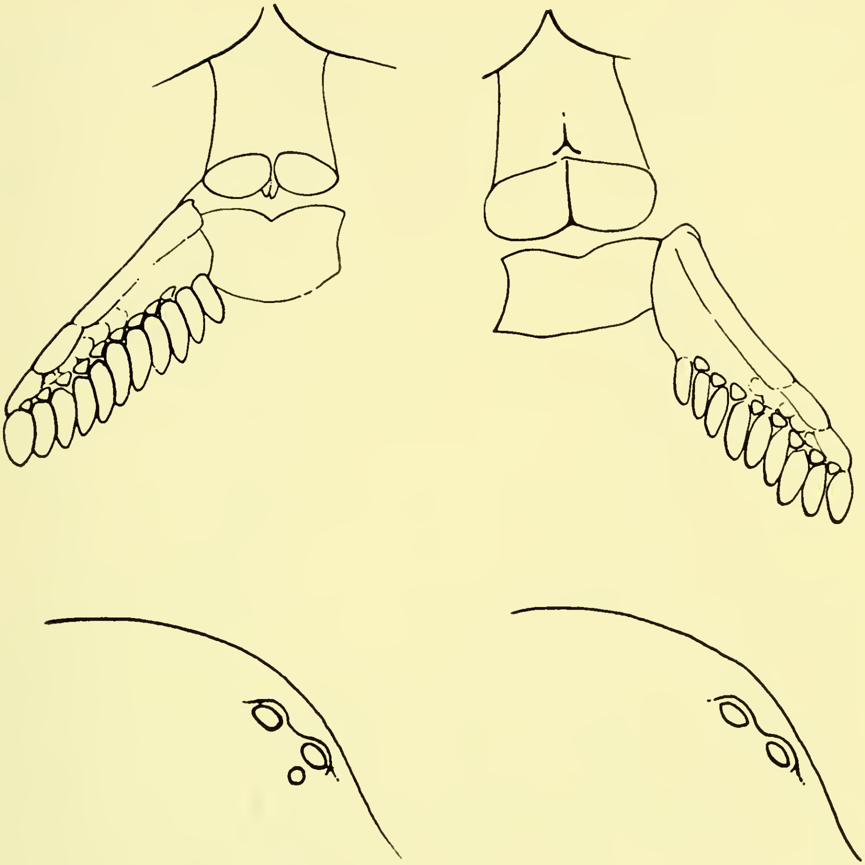

Figure 3. *Nullibrotheas allenii* (Wood), figured from topotypes from Cabo San Lucas, Baja California Sur, Mexico. Top left. Ventral view of male showing prosomal sternum, genital opercula, and pectines. Top right. Ventral view of female showing prosomal sternum, genital opercula, and pectines. Bottom left. Right anterolateral aspect of carapace showing three lateral eyes. Bottom right. Right anterolateral aspect of carapace showing two lateral eyes.

Geographical distribution. Known only from the southern region of the Baja California peninsula and associated islands. Specimens have been collected from Cabo San Lucas north to El Coyote on Bahia Concepcion. Reports of this species in the United States appear to be due to errors in locality records and to mistaken identification of this species.

New records. Known from the following localities in Baja California Sur, Mexico: 1 mi. SW. Rancho Canipole, elevation 800 ft., 16 May 1969, (S. C. Williams), 2 juveniles; 4 mi. SW. San Miguel de Comondu, elevation 900 ft., 15 May 1969, (S. C. Williams), 2 juveniles; 5 mi. SW. San Miguel de Comondu,

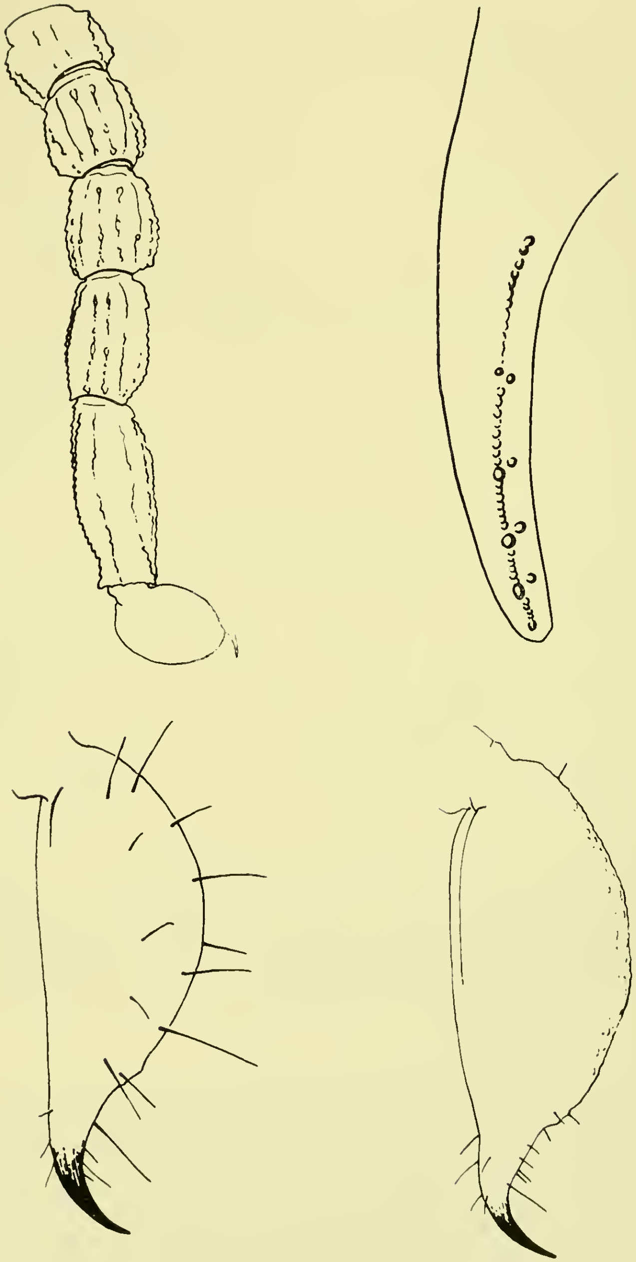

Figure 4. *Nullibrotheas allenii* (Wood), figured from topotypes from Cabo San Lucas, Baja California Sur, Mexico. Top left. Ventral view of male metasoma. Top right. Movable pedipalp finger of male. Bottom left. Female telson. Bottom right. Male telson.

elevation 1000 ft., 2 July 1968, (S. C. Williams, M. A. Cazier), 1 male, 1 female, 1 juvenile; 5 to 10 mi. SW. San Miguel de Comondu, elevation 1000 ft., 3 July 1968, (S. C. Williams, M. A. Cazier), 1 female, 3 juveniles; San Jose de Comondu, 15 February 1966, (V. Roth), 1 male, 1 female; 4 mi. W. La Purisima, elevation 375 ft., 1 July 1968, (S. C. Williams, M. A. Cazier), 1 female; Rancho Las Parras, 26 May 1970, (S. C. Williams, V. F. Lee), 1 juvenile; 9.9 mi. N. Loreto, 27 May 1970, (S. C. Williams, V. F. Lee), 1 juvenile; Loreto city dump, just N. Loreto, 20 June 1964, (Chris Parrish), 1 female; 8 mi. S. Loreto, base of La Gigantia, 27 January 1965, (V. Roth), 1 male juvenile; Puerto Escondido, 17 mi. S. Loreto, 27 May 1970, (S. C. Williams, V. F. Lee), 1 juvenile; 22 mi. NE. Santo Domingo, 15 February 1966, (V. Roth), 1 female, 1 juvenile; 51 mi. N. El Crucero, elevation 400 ft., 14 May 1969, (S. C. Williams), 1 male, 3 females, 7 juveniles; 10 mi. N. El Crucero, 15 February 1966, (V. Roth), 1 male juvenile, 1 female juvenile; Bahia Concepcion near El Coyote, 26.40 N., 111.50 W., 17 February 1966, (V. Roth), 3 males; 10.3 mi. SE. Santa Rita, 27 July 1968, (S. C. Williams, M. A. Cazier), 1 male, 1 female, 1 juvenile; 49.3 mi. SE. Santa Rita, 27 July 1968, (S. C. Williams, M. A. Cazier), 1 juvenile; 49.3 mi. SE. Santa Rita, 27 July 1968, (S. C. Williams, M. A. Cazier), 1 male, 4 juveniles; 31.0 mi. W. Los Aripes, elevation 800 ft., 25 July 1968, (S. C. Williams, M. A. Cazier), 3 juveniles; 1 mi. E. Los Aripes, 8 July 1968, (S. C. Williams, M. A. Cazier), 1 male; 1.4 mi. W. El Coyote, 30 December 1958, (H. B. Leech), 1 male, 3 juveniles; La Paz, 1 to 3 February 1965, (V. Roth), 1 female, 3 juveniles; 2 mi. E. La Paz, elevation 50 ft., 5 July 1968, (S. C. Williams, M. A. Cazier), 1 male; 12.4 mi. E. La Paz on road to Las Cruces, Arroyo Agua de los Pozos, 4 January 1959 (A. Leviton), 1 juvenile; 2 mi. NW. Los Pozos, 23 July 1968, (S. C. Williams, M. Bentzien, W. Fox), 8 juveniles; 14.5 mi. E. La Paz on road to Las Cruces, 4 January 1959, (H. B. Leech), 1 juvenile; .25 mi. N. La Paz airport, 12 July 1968, (S. C. Williams, M. A. Cazier), 1 juvenile; 6 mi. N. La Paz on road to Pichilingue, 6 January 1959, (H. B. Leech), 1 juvenile; 12.5 mi. N. La Paz on road to Pichilingue, 29 December 1958, (H. B. Leech), 1 female; Puerto Balandra, approximately 13 mi. N. La Paz, 3 September 1963, (P. R. & D. L. Craig), 1 juvenile female; 14 mi. NE. La Paz along A. Balandra road, 14 July 1968, (S. C. Williams, M. A. Cazier), 2 males, 1 female, 1 juvenile; 14 mi. NE. La Paz along A. Balandra road, 9 July 1968, (S. C. Williams, M. A. Cazier), 1 juvenile; 75 mi. NW. La Paz, elevation 200 ft., 4 July 1968, (S. C. Williams, M. A. Cazier), 1 female; 5 mi. SW. La Paz, 2 August 1968, (S. C. Williams, M. A. Cazier), 1 juvenile; Las Cruces, 5.0 mi. SW. Las Cruces, 30 July 1968, (S. C. Williams, M. A. Cazier), 2 females, 5 males, 4 juveniles; 5 to 6 mi. SW. La Paz, elevation 25 ft., 5 July 1968, (S. C. Williams, M. A. Cazier), 1 juvenile; 14.8 mi. N. Todos Santos, elevation 500 ft., 24 July 1968,

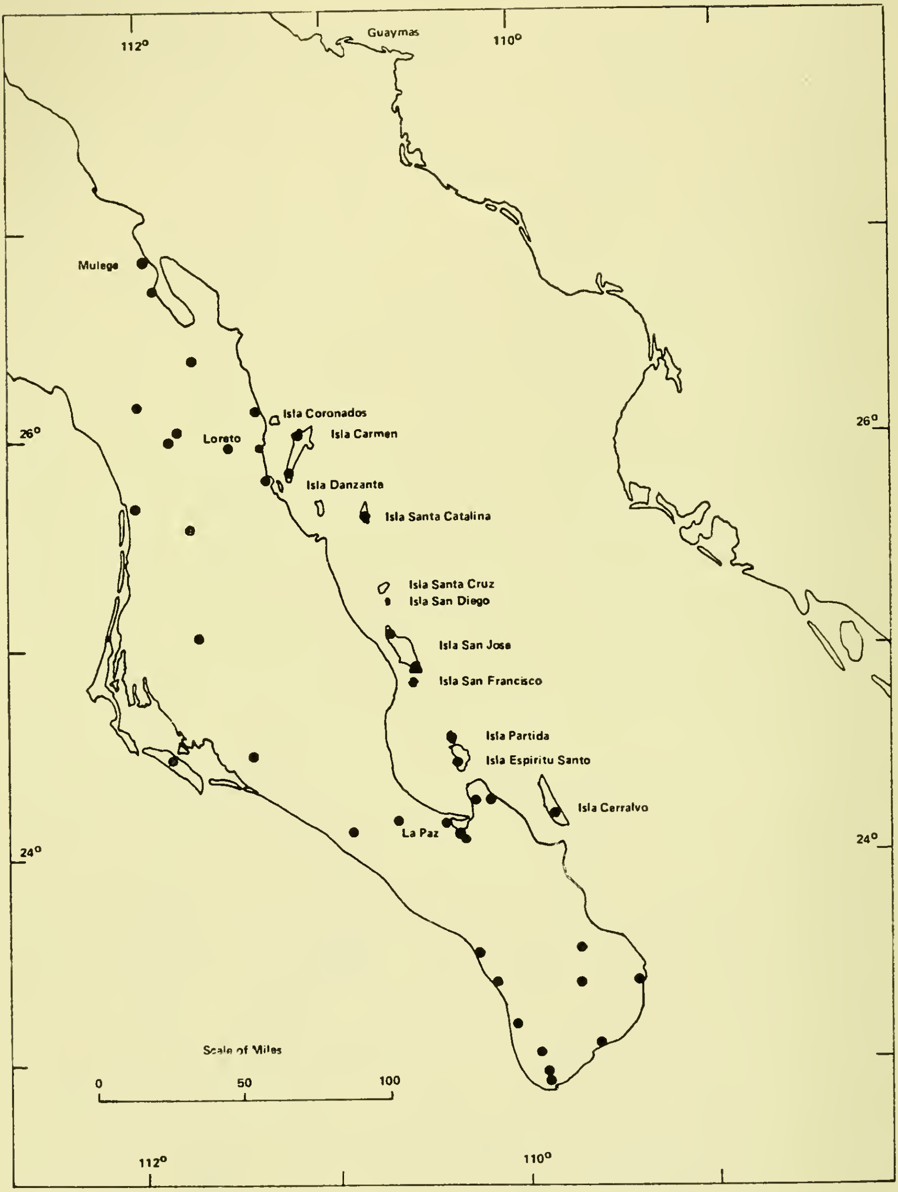

FIGURE 5. Distribution of *Nullibrotheas allenii* (Wood) in Baja California Sur, Mexico.

(S. C. Williams, M. A. Cazier), 1 female, 6 juveniles; 5.5 mi. NW. Todos Santos, road to La Pastora, 13 January 1959, (H. B. Leech), 1 juvenile; 5.9 mi. N. Todos Santos, elevation 500 ft., 24 July 1968, (S. C. Williams, M. A. Cazier), 14 males, 18 females; 9 mi. N. Todos Santos, elevation 200 ft., 4 May 1969, (S. C. Williams), 1 female; 3.5 mi. S. El Pescadero, elevation 20 ft., 23 July 1968, (S. C. Williams, M. A. Cazier), 1 male, 1 female, 4 juveniles; 4 mi. N. Tinaja, 23 July 1968, (S. C. Williams, M. Bentzien, W. Fox), 1 female, 1 juvenile; Santiago, 19 August 1964, (H. W. Campbell), 1 male, 1 female; Boca de la Sierra, near Miraflores, 10 February 1966, (V. Roth), 1 female; Bahia de los Frailes, 9 March 1947, (I. La Rivers), 1 male; 1.5 mi. NE. Punta Palmilla, elevation 50 ft., 16 July 1968, (S. C. Williams, M. A. Cazier), 4 males, 13 females; 1.5 mi. NE. Punta Palmilla, elevation 50 ft., 17 July 1968, (S. C. Williams, M. A. Cazier), 1 juvenile; 2.2 mi. SW. Punta Palmilla, 17 July 1968, (S. C. Williams, M. A. Cazier), 3 juveniles; 3.5 mi. SW. Punta Palmilla, 17 July 1968, (S. C. Williams, M. A. Cazier), 1 juvenile; 3.9 mi. SW. Punta Palmilla, 17 July 1968, (S. C. Williams, M. A. Cazier), 4 males, 6 females; 16.5 mi. NW. Cabo San Lucas, 23 July 1968, (S. C. Williams, M. Bentzien, W. Fox), 5 juveniles; 5 mi. N. Cabo San Lucas, 21 July 1968, (S. C. Williams, M. A. Cazier), 1 juvenile; 4 mi. N. Cabo San Lucas, 21 July 1968, (S. C. Williams, M. A. Cazier), 2 females, 1 juvenile; 2 mi. N. Cabo San Lucas, 19 July 1968, (S. C. Williams, M. A. Cazier), 1 male, 1 female, 1 juvenile; 3 mi. E. Cabo San Lucas, 18 July 1968, (S. C. Williams, M. A. Cazier), 2 females; Cabo San Lucas, 20 July 1968, (S. C. Williams, M. A. Cazier), 3 males, 9 females, topotypes; Isla Carmen, Puerto Ballandra, 24 May 1970, (S. C. Williams, V. F. Lee), 2 juveniles; Isla Carmen, Puerto Ballandra, 23 March 1971, (V. F. Lee), 1 female, 1 juvenile; Isla Carmen, Marquer Bar, 22 June 1964, (R. C. Banks), 1 juvenile; Isla Santa Catalina, 27 April 1964, (C. H. Croulet), 3 females, 6 juveniles; Isla Santa Catalina, NE. side, 10 April 1962, (Members Belvedere Expedition), 1 female, 1 juvenile; Isla Santa Catalina, NW. end, Punta Arena, 24 June 1964, (C. Parrish), 1 male; Isla Santa Catalina, cave on S. end, 25 June 1964, (R. C. Banks), 1 juvenile; Isla Santa Catalina, SW. end, 26 April 1964, (A. J. Sloan), 1 male, 1 female, 4 juveniles; Isla Santa Catalina, W. side, 9 April 1962, (Members Belvedere Expedition), 5 juveniles; Isla Coyote, 19 April 1962, (George Lindsay), 1 female, 2 juveniles; Isla San Diego, WNW. side, 18 April 1962, (C. Parrish, M. Soule), 1 female; Isla San Diego, 19 April 1962, (George Lindsay), 1 juvenile; Isla San Jose, N. side, 26 March 1971, (V. F. Lee), 3 juveniles; Isla San Jose, NE. side of Arroyo de Aguada, 11 April 1962, (Members Belvedere Expedition), 1 female, 3 juveniles; Isla San Jose, S. end near lagoon mouth, 27 June 1964, (C. Parrish), 1 juvenile; Isla San Jose, SW. end, near cattle ranch, 24 April 1964, (A. J. Sloan), 2 females; Isla San Jose, Los Ostiones, 12 April 1962, (Members Belvedere Expedition), 2 females, 1 juvenile; Isla Cayo, 28 June 1964, (C. Parrish, G. Lindsay,

I. Wiggins), 1 male, 2 females, 2 juveniles; Isla San Francisco, SW. side, 25 May 1969, (S. C. Williams), 1 juvenile; Isla San Francisco, S. end, 17 April 1962, (R. C. Banks), 1 male; Isleta Rock, N. Partida Island, 20 April 1962, (M. Soule), 1 male, 1 juvenile; Isla Partida, central valley, elevation 25 ft., 9 July 1968, (S. C. Williams, M. Bentzien, W. Fox), 1 male, 2 juveniles; Isla Partida, dry lake, 29 June 1964, (I. Wiggins), 1 female; Isla Ballena, 21 April 1962, (C. Parrish), 3 juveniles; Isla Espiritu Santo, SW. shore, 7 July 1968, (S. C. Williams, M. A. Cazier), 1 male, 2 females, 10 juveniles, 1 female with 23 in litter; Isla Espiritu Santo, Bahia San Gabriel, 24 May 1969, (S. C. Williams), 5 juveniles; Isla Espiritu Santo, Bahia Canon, 29 June 1964, (I. Wiggins), 2 juveniles; Isla Espiritu Santo, Bahia Candelaro, 30 June 1964, (I. Wiggins), 1 juvenile; Isla Cerralvo, Piedras Gordas, 17 May 1970, (S. C. Williams, V. F. Lee), 5 juveniles; Isla Cerralvo, sand dune area on SW. side, 16 April 1962, (C. Parrish), 1 juvenile; Isla Cerralvo, Arroyo Aguaje, 15 April 1962, (G. Lindsay), 2 juveniles; Isla Cerralvo, Rancho Ruffo, 16 April 1962, (I. Wiggins, G. Lindsay), 1 juvenile; Isla Magdalena, Puerto Magdalena, 17 March 1957, (R. Zweifel), 1 male; Santa Margarita Island, June 1970, (USNM), 1 specimen.

Remarks. *Nullibrotheas allenii* is an extremely variable species in coloration, cuticular granulation, hirsuteness of metasoma and telson, and body size. Throughout its distribution it appears to form series of local races with some evidence of genetic continuity between many of the races. For this reason it appears best to treat this as one variable species rather than as a complex of many poorly defineable, separate ones.

In regard to size, adults in most populations range from 30 to 45 millimeters in length. A few local populations have been found in which adults have attained much larger sizes, in the range of 50 to 60 millimeters. Such giant races have been found in the area of La Paz and on some of the islands of the gulf, notably on Isla Catalina.

In regard to color, most populations have a golden yellow base color with underlying dark coloration on the carapace and mesosomal dorsum. Some populations have the dark markings reduced to faint dusky markings, notably on the Magdalena Plain, while others may have these markings very dense and dark, notably in the volcanic habitats, such as around Comondu. South of Todos Santos the dark coloration of the mesosomal dorsum is divided longitudinally by a thin unpigmented stripe thus creating the appearance of one pair of dark longitudinal stripes. North of the Todos Santos area the metasomal dorsum is usually completely pigmented giving no indication of stripes. Around the Todos Santos and Las Cruces areas individuals are variable and show all forms of intermediate conditions.

The granulation of the cuticle, especially on the carapace, vesicle, and pedipalp palms is highly variable and difficult to interpret. It appears that the amount of granulation is determined by age, sex, length of time since last moult, and individual genetics. Most individuals with more distinctive granulation are larger than average.

The hirsuteness of the vesicle and metasoma is another variable character. In the Cabo San Lucas area the metasoma and telson are usually only moderately hirsute. The northern and island populations generally had both vesicle and metasomal segments IV and V considerably more hirsute than the southern populations. Samples taken from intermediate areas indicate the variation in hirsuteness is to some extent individual, and developmental, and over the range is somewhat clinal.

The collection records of this species indicate that individuals probably spend most of their life cycle in burrows in the ground. They do, however, appear to leave the burrow and seek shelter under suitable surface rocks during part of the year.

Of the hundreds of specimens collected during this study only two females were observed with litters on their backs. Both of these were discovered under the protection of moderate-size flat rocks during July. The females appear normally not to leave their protective shelters at time of birth or while carrying young on their backs. Both females had only small to moderate numbers of young in their litters. The first litter was found 4 miles N. of Tinaja on 23 July 1968 and consisted of the mother and 8 young. The second litter was found on Isla Espiritu Santo on 7 July 1968 and consisted of the mother and 23 young.

During the summer of 1970 the male cotype in the U. S. National Museum was examined and compared with topotypes recently collected at Cabo San Lucas. The type was almost identical to a sub-adult male topotype except for being more yellowish, less hirsute, and lacking the characteristic color pattern (three characteristics commonly altered in this way by poor preservation and age). It was interesting that the cotype was labeled "*Broteas alleni* Wood" by an old hand-written label included in the specimen jar. This was apparently a later addition or alteration of the original data since this species was originally named *Scorpius allenii*. It is notable that when Gertsch (1958) studied and redescribed the types two cotypes were present. In 1970 only one of the cotypes could be located, this presumably is the lectotype designated by Gertsch in 1958.

Taxonomic relationships of *Nullibrotheas*. *Nullibrotheas allenii* was first placed within the genus *Scorpius* by Wood in 1863 where it remained until 1887 at which time George Marx placed it within the chactid genus *Broteas*. Since this species has been relatively unstudied it has essentially remained placed in the genus *Broteas* and family Chactidae until now. However, Banks (1910) apparently realized that '*allenii*' was not properly placed within the genus *Broteas* because he assigned this species to the genus *Broteochactas* thus retaining it within the family Chactidae. Banks' generic assignment was, however, not followed by others working with North American scorpions.

It is interesting that European workers did not agree with the systematic placement of '*allenii*' by American workers. In 1879, Karsch studied a juvenile specimen of *N. allenii* and named it *Uroctonus privus*, thus placing it within the family Vaejovidae. Later Kraepelin (1899), considered *U. privus* (a junior synonym of *N. allenii*) to be a junior synonym of *Uroctonus mordax*, thus also retaining *N. allenii* within the family Vaejovidae. Kraepelin (1899) did not see the relationship between "*Broteas allenii*" and *Uroctonus privus*, but he did indicate that he believed "*B. allenii*" to be a good species, and doubted that it should be placed in the Chactidae.

The family placement of the genus *Nullibrotheas* is made somewhat difficult by the obscure relationship between the families Chactidae and Vaejovidae. The primary characteristic that has been used to differentiate these two families is the presence of two lateral ocelli at each anterolateral corner of the carapace in the Chactidae. The family Vaejovidae is contrasted by having three or more lateral ocelli at each anterolateral corner of the carapace. Numbers of lateral ocelli are not satisfactory criteria alone for placement of scorpions within a family. Several species which clearly belong to families other than the Chactidae have secondarily lost lateral ocelli. For example, in the Diplocentridae several species belonging to the *Didymocentrus* group show only two lateral ocelli at each anterolateral corner of the carapace. These were even considered by Stahnke (1968) to represent a new diplocentrid genus which he called *Bioculus*. Gertsch (1972) has found several species of *Vaejovis* and *Uroctonus* which either have external signs of the third lateral ocellus completely absent or in an obsolescent state. Actually, most species of *Vaejovis* and *Uroctonus* have the third lateral ocellus showing signs of becoming reduced in size or approaching obsolescence.

Nullibrotheas allenii clearly does not belong in the genus *Broteas* because it has the openings to the book lungs completely circular rather than linear, and the last tarsomere of the walking legs has one row of ventral hairs (not two parallel rows of spine-like hairs). *Nullibrotheas allenii* also clearly does not belong in the genus *Broteochactas* because it has six trichobothria in a posterior row on the ventral surface of the pedipalp brachium (not seven such trichobothria), and also because the walking legs have the last tarsomere with one row of ventral hairs (not with abundant irregular hairs).

Study of the lateral ocelli of *Nullibrotheas allenii* reveals two distinct eyes at each anterolateral corner of the carapace in some specimens. However, individuals usually show evidence of a third reduced or degenerate ocellus. This line of evidence indicates that this genus should be placed within the family Vaejovidae. Furthermore, in other characteristics it appears somewhat related to the genera *Uroctonus* and *Vaejovis* (both members of the family Vaejovidae).

Nullibrotheas can be clearly distinguished from *Vaejovis* and *Uroctonus* in that it has the ventral surface of the pedipalp tibia (brachium) with six trichobothria in a posterior row (not with two or three such trichobothria) and has minute, round openings to the book lungs (not slit-like or oval).

Considering all the morphological evidence available it appears that *Nullibrotheas* has no known close living relatives, but that it is more closely related to the vaejovid genera *Uroctonus* and *Vaejovis* than to any other living ones known. *Nullibrotheas* is therefore here considered to be a member of the family Vaejovidae.

Key to the North American genera of the family Vaejovidae

1. Book lung openings round .... *Nullibrotheas*, new genus
   Book lung openings not round, but oval or elongate 2
2. Metasoma with single, unpaired, inferior median keel on segments I to IV .... genus *Syntropis*
   Metasoma with inferior median keels of segments I to IV paired or obsolescent 3
3. Lateral ocelli four per group; pectines with middle lamellae angular and not circular .... genus *Anuroctonus*
   Lateral eyes three or fewer per group; pectines with middle lamellae subcircular 4
4. Inferior margin of movable cheliceral finger with one long, dark, conspicuous tooth; pedipalps with ventral surface of brachium with over 20 trichobothria .... genus *Hadrurus*
   Inferior margin of movable cheliceral finger with small teeth, minor denticles, denticle-like crenulation, or completely lacking denticles; pedipalps with ventral surface of brachium with two or three trichobothria along posterior border 5
5. Pectines with middle lamellae usually composed of 9 or fewer circular sclerites; openings to book lungs usually oval or long oval in shape and generally with length less than three times width; pedipalp with ratio of palm width to palm depth generally greater than 1.05; pedipalps with ventral surface of brachium with three trichobothria .... genus *Uroctonus*
   Pectines with middle lamellae usually composed of 10 or more circular sclerites; openings to book lungs usually elongate or slit-like and generally with length greater than three times width; pedipalp with ratio of palm width to palm depth generally less than 1.05; pedipalps with ventral surface of brachium always with 2 trichobothria (never with three) 6
6. Chelicerae with inferior margin of movable finger with one or several small denticles or crenulations .... genus *Paruroctonus*
   Chelicerae with inferior margin of movable finger smooth and completely lacking crenulations .... genus *Vaejovis*

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THE GENUS *CERCIDIUM* (LEGUMINOSAE: CAESALPINIOIDEAE) IN THE SONORAN DESERT OF MEXICO AND THE UNITED STATES

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Cercidium comprises nine taxa, five of which occur in the Sonoran Desert of Mexico and southwestern United States (figs. 1, 2). Of these five, only one, *C. praecox* (Ruiz and Pavón) Harms, has a widespread distribution, occurring from western and southern Mexico south to Peru. Of the remaining taxa, two occur in Texas and northern Mexico and two in Argentina. Thus, it can be seen that the greatest concentration of species occurs in the Sonoran Desert (Shreve, 1951, 1964).

Cercidiums, with their green branches which at a distance appear leafless much of the year, and are laden from March into June with a profusion of yellow, caesalpinoid flowers, are among the most conspicuous and characteristic trees of the Sonoran Desert. The newcomer to this region tends to refer to all these green-barked trees as *palo verde*, but if he goes into the field with a *paisano*, he soon learns that there is not only *palo verde*, but there are also *dipua* (*dipuga*), *palo brea*, and *palo estribo* (fig. 3). One other green-branched tree, closely related to *Cercidium*, also occurs in the Sonoran Desert. It is *Parkinsonia aculeata* Linnaeus, known locally in Baja California as *junco*. Continued experience with *palos verdes* in the field, especially in the Sierra de la Giganta of Baja California Sur, made it evident that they merited special attention in order to understand the relationships within the group.

As with so many Sonoran Desert plants, most species of *Cercidium* present an entirely different aspect in the dry season than they do following the rains. Speaking generally, in the southern part of the Sonoran Desert, the heaviest rains fall in brief, hard-hitting storms during the hot months of July through September, sometimes extending into October (Hastings and Humphrey, 1969). With this moisture most plants come into full leaf, but with the end of the rains, many are soon leafless again. In 'good' years, gentle winter rains also come to the southern part of the Sonoran Desert and many species repeat the leaf cycle. Farther north, in south-central Arizona, where the total rainfall is about equally divided between summer and winter, *Cercidium* usually has two leafy seasons. All of the cercidiums flower at the height of the dry season, March through June, when for the most part, the trees are leafless or nearly so. Sometimes there is minor 'off-season' fall flowering. Keys to the taxa are included herein for both the vegetative and the flowering and fruiting stages.

Although no attempt is made here to resolve the long-standing controversy as to whether *Cercidium* should be regarded as distinct from *Parkinsonia,* some points brought out in this paper may add fuel to the fire. Watson (1876) argued for union of these two genera; Sargent (1889), principally on the basis of the legume, maintained them as distinct; Johnston (1924a), on other grounds and after some realignment of the taxa within the two genera, also argued for their maintenance as distinct genera; Britton and Rose in 1930 erected the genus *Cercidiopsis* for *Cercidium microphyllum*; Brenan (1963), on consideration of additional African taxa which he placed in *Parkinsonia*, felt that it is not possible to maintain *Cercidium* as distinct from *Parkinsonia*, but he refrained from making any nomenclatural changes in the American material. In accordance with Johnston's delimitation, *Cercidium* in America is easily distinguished from *Parkinsonia* and is kept separate in recent floras. The question of generic relationships cannot be resolved without first making extensive comparative studies of these trees (their biology, morphology, cytology, genetics, etc.) from seedling stage to maturity. Lack of evidence for resolution of problems at the generic level, however, does not preclude our attaining a better understanding of relationships at the subgeneric level. For the purposes of this paper, I am following Johnston's generic delimitation.

The following key summarizes the differences between the species of *Cercidium* and *Parkinsonia aculeata* Linnaeus.

Armature comprised of the *first* leaf developing at a node having a long-persistent, indurate petiole and rachis which terminates in a sharp, stout spine; leaves with pinnae[1] 8 to 30 (-60) cm. long, the rachis 1 to 3.6 mm. wide, flattened, phyllodial, persistent; leaflets falling with drought, alternate and/or opposite, 10 to 40 on one

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[1] As used herein, the term "pinnae" refers to the secondary rachises plus leaflets of a bipinnate leaf. In many representatives of Caesalpinioideae the pinnae are reduced to a single pair.

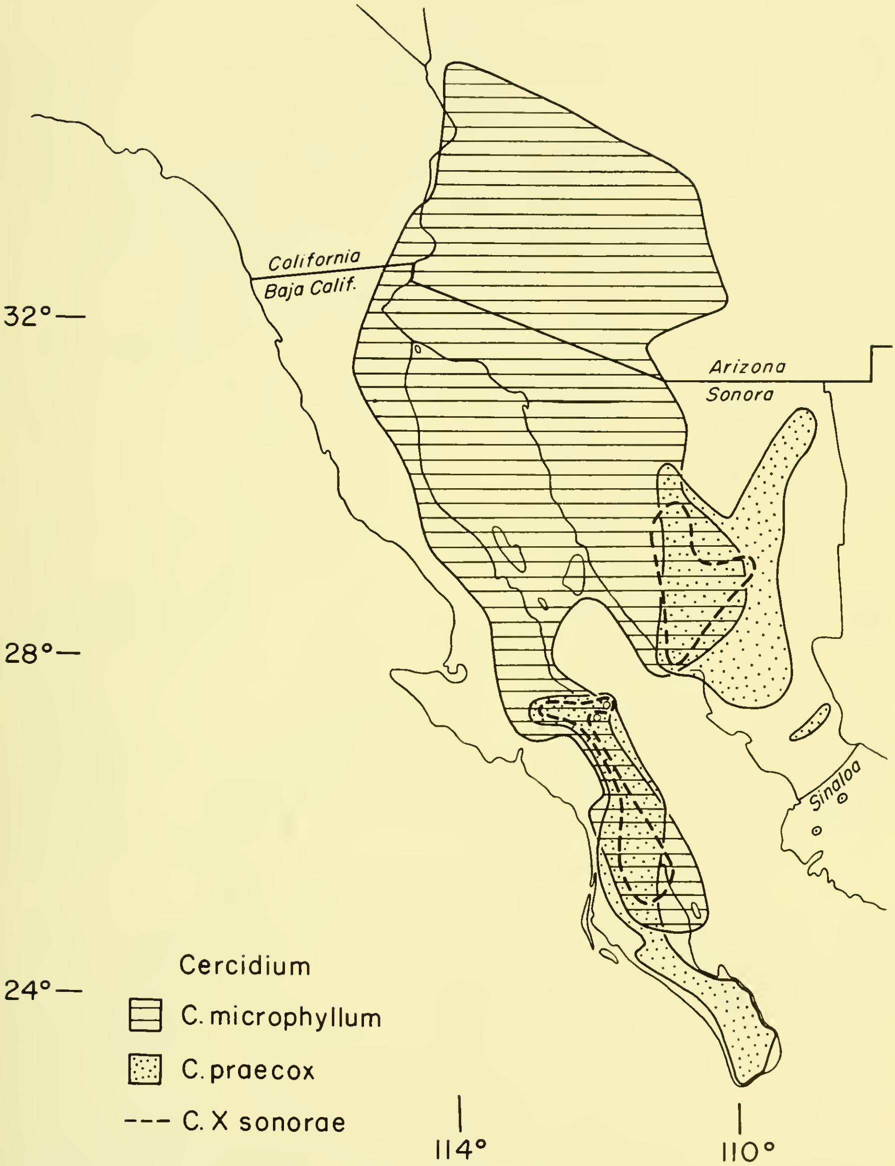

Figure 1. Distribution of *Cercidium microphyllum*, *C. praecox* and *C.* × *sonorae* in the Sonoran Desert of northwestern Mexico and southwestern United States.

side of a given rachis; axillary leaf-bearing shoots usually 2 to 12 (-23) mm. long; inflorescences developing with the leaves, the racemes much shorter than the pinnae; pedicels 10 to 21 mm. long (mean 14.4 mm.) .... *Parkinsonia aculeata*

Armature of one or two *axillary* thorns, or lacking; leaves with pinnae 0.3 to 6.5 cm.

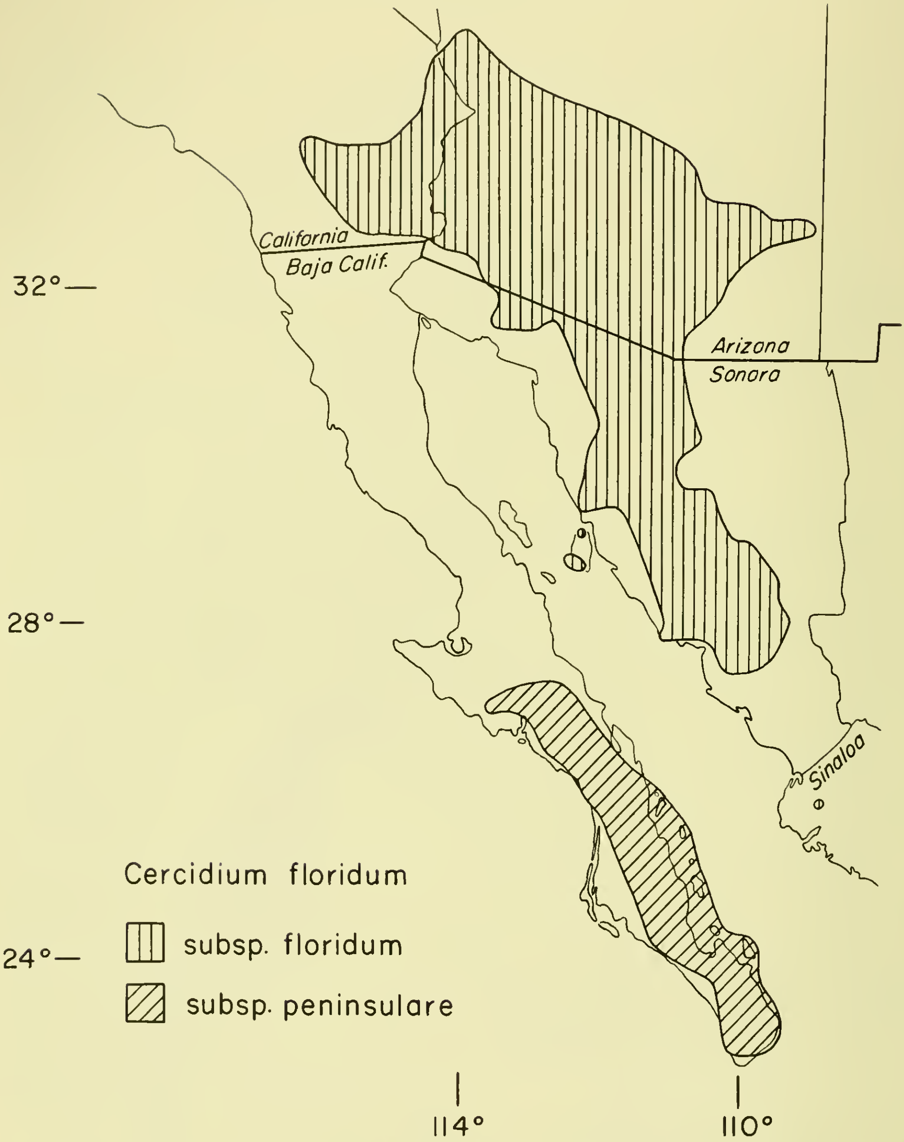

Figure 2. Distribution of *Cercidium floridum* subsp. *floridum* and *C. floridum* subsp. *peninsulare* in the Sonoran Desert of northwestern Mexico and southwestern United States.

long, the rachis less than 1 mm. wide, terete or sub-terete, not phyllodial, often falling with drought; leaflets opposite, 2 to 9 (-17) pairs; axillary leaf-bearing shoots so reduced that the leaves appear to arise in the primary leaf axil; inflorescences developing before the leaves or if with them, the racemes subequal to or exceeding the pinnae; pedicels 2.5 to 14 mm. long (mean 7.5 mm.) .... species of *Cercidium*

Herbarium material of *Cercidium* belonging to the following institutions has been studied: British Museum (Natural History), London (BM); California Academy of Sciences, San Francisco, California (CAS); Dudley Herbarium, Stanford University, California (DS); Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, México, D. F. (ENCB); Field Museum of Natural History, Chicago, Illinois (F); Gray Herbarium of Harvard University, Cambridge, Massachusetts (GH); Herbario Nacional del Instituto de Biología, Universidad Nacional Autónoma de México, México, D. F. (MEXU); Instituto de Botánica, "Antonio José Cavanilles," Madrid (MA); Missouri Botanical Garden, St. Louis (MO); New York Botanical Garden (NY); Rancho Santa Ana Botanic Garden, Claremont, California (RSA); The Herbarium and Library, Royal Botanic Gardens, Kew (K); San Diego Museum of Natural History, California (SD); United States National Museum, Washington, D.C. (US); University of Arizona, Tucson (ARIZ); University of California, Berkeley (UC). Abbreviations for these institutions are those given by Lanjouw and Stafleu (1964). Collections made by the author will be widely distributed. Specimens cited include, in addition to those indicating limits of distribution, representative flowering and fruiting specimens as well as all specimens cited in illustrative material. I wish to express my appreciation to the directors and curators of the herbaria at these institutions for enabling me to study their collections.

In citing collections from the peninsula of Baja California, political subdivisions are indicated as follows: *Baja California Sur* for the area from 28°N. southward to the tip of the peninsula, a territory of Mexico; *Baja California* [*Norte*] for the area from 28°N. northward to the Mexico-United States border, a state of Mexico.

Cercidium Tulasne

Cercidium Tulasne, 1844, Arch. Mus. Paris, vol. 4, p. 133.

Trees or large shrubs with smooth greenish bark, the branches usually armed with axillary thorns, or having short, spine-tipped branches. Stipules slender, foliaceous, caducous. Clusters of dry axillary bud scales usually present. Leaves usually not long persistent, sessile or petiolate, bipinnate with one to three pairs of pinnae, the leaflets small, opposite; leaf rachis terete or sub-terete, 1 mm. or less in diameter and terminating in a slender foliaceous or semi-indurate bract. Flowers borne in condensed to open axillary racemes. Pedicels jointed, the joint being in the distal half. Calyx tube green, broadly campanulate, 1.5–2 mm. long, 3–4 mm. wide, the lobes 5, narrowly ovate, valvate or subvalvate, 4–7 mm. long, 2 mm. wide, yellow or greenish yellow. Petals 5, yellow or creamy white, pubescent at base, the upper (posterior) with a conspicuous claw which usually elevates the limb of this petal above the others, the base of the limb auriculate, the auricles often curved over the apex of the claw to form a channel; other four

FIGURE 3. Comparison of leaves, legumes, and seeds of *Cercidium*: A, *C. microphyllum*, the upper figure is a single pinna of a bipinnate, sessile leaf; B, *C.* × *sonorae*, the leaves show variation in petiole length from subsessile to short-petiolate (one pinna has fallen from a leaf in *4945*); C, *C. praecox*; D, *C. floridum* subsp. *peninsulare*. Numbers refer to Carter, and/or Carter *et al.* collections; data for these are given under "Representative collections cited" for the respective taxa.

petals with shorter claws. Stamens 10, distinct; filaments pilose near the base; anthers versatile. Pods oblong to linear-oblong, or linear and torulose, coriaceous or papery. Seeds 1 to 4, flattened or subglobose.

Based on *Cercidium spinosum* Tulasne, 1844, p. 136: "Regionem Amazonum (Bonplandi herb. propr. *nunc* in herb. Mus. Paris), Colombiam prope Maracaibo (Plée, herb. No. 73), nec non prov. *Oaxaca* Novae Hispaniae propter Tehuacán (in Cordillera alt. 1700 metr. — Galeotti herb. No. 3212) habitat."

KEY TO *CERCIDIUM* IN THE SONORAN DESERT
(Based on vegetative characters)

Branches spinescent at tip; bark yellow-green, horizontally striate on older branches; axillary thorns lacking; leaves sessile, the pinnae of the primary[2] leaves borne on a scale-like, semi-indurate rachis which is tardily deciduous, the leaflets minute, 0.5–5 mm. long .... 1. *C. microphyllum*

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[2] The term "primary" leaf refers herein to the first leaf developing at a node in contrast to those developing subsequently from a succession of buds produced on a reduced shoot in the axil of the primary leaf or primary leaf scar.

Branches not spinescent at tip; axillary thorns usually present; leaves petiolate (sometimes subsessile in *C.* × *sonorae*), the leaflets larger, usually 3–12 mm. long.

  Pinnae usually bearing 4–12 (–17) pairs of leaflets.

    Nodes bearing one or two stout axillary thorns 2–18 (–25) mm. long and having conspicuous clusters of dry, dark bud scales in the axils; bark waxy-coated on older branches and having a fine, quadrate-pustulate pattern; petioles 4–11 mm. long. .... 2. *C. praecox*

    Nodes bearing a single slender axillary thorn 2–11 (–20 mm.) long (or sometimes none); dry bud scales present at nodes but usually not conspicuous; bark on older branches smooth or inconspicuously horizontally-striate, the waxy coat inconspicuous or lacking; petioles 0–3 (–12) mm. long .... 3. *C.* × *sonorae*

  Pinnae usually bearing 2–4 pairs of leaflets; nodes without conspicuous clusters of dark axillary bud scales; bark of older branches horizontally striate .... 4. *C. floridum*

    Branchlets of mature trees glabrous to glabrate; leaflets 4–8 mm. long, mostly 3 pairs per pinna (Sonoran Desert except Baja California). .... 4a. *C. floridum* subsp. *floridum*

    Branchlets villous or pilose, leaflets 6–15 mm. long, mostly 2 pairs per pinna; clusters of reddish brown glandular hairs in axil of primary leaves (confined to southern Baja California). .... 4b. *C. floridum* subsp. *peninsulare*

KEY TO *CERCIDIUM* IN THE SONORAN DESERT
(Based on flowering and fruiting characters)

Ovary glabrous at anthesis; legumes not strongly long-tapered at ends.

  Inflorescences borne in clusters along older branches; petals deep yellow, the upper often orange-dotted near base of limb; mature legumes papery, flat, conspicuously net-veined; seeds flattened, gray-brown with brown mottling. .... 2. *C. praecox*

  Inflorescences on terminal or subterminal branches; legumes when immature bearing conspicuous white dots (stomata) but these obscure in mature legumes, coriaceous, the veins inconspicuous; seeds oblong to ovate, flattened, brown with marginal area lighter and sometimes faintly mottled. .... 4. *C. floridum*

    Inflorescences open, the racemes with rachis 1.0–4.5 (–7.0) cm. long, pedicels 6–12 (–20) mm. long; petals bright yellow, the upper sometimes orange-dotted (Sonoran Desert except Baja California). .... 4a. *C. floridum* subsp. *floridum*

    Inflorescences somewhat congested, the racemes with rachis mostly 0.3–1.0 (–2.0) cm. long; pedicels 4–9 (–12) mm. long; petals deep or bright yellow, the upper not orange-dotted (confined to southern Baja California). .... 4b. *C. floridum* subsp. *peninsulare*

Ovary lightly pubescent to strigose at anthesis; legumes strongly tapered at both ends.

  Legumes torulose, lightly striate-veined; petals light yellow[3] except for the upper one which is white or creamy-yellow but never orange-dotted; seeds sub-globose, brown. .... 1. *C. microphyllum*

  Legumes sinuate, conspicuously striate-veined; petals light yellow[3] except for the upper one which is variable (whitish or pale yellow and sometimes orange-dotted); seeds oblong to ovate, flattened, dark mottled brown. .... 3. *C.* × *sonorae*

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[3] Petal color is useful only with fresh material; use vegetative key to distinguish these two species if only dry material is available.

1. **Cercidium microphyllum** (Torrey) Rose and Johnston.

Cercidium microphyllum (Torrey) Rose and Johnston in I. M. Johnston, 1924, Contr. Gray Herb., vol. 70, p. 66.

Parkinsonia microphylla Torrey, 1857, Pac. R. R. Rep., vol. 4, p. 82; 1859, Bot. Mex. Bound, p. 59.

Cercidiopsis microphylla Britton and Rose, 1930, N. Amer. Fl., vol. 23, p. 306.

Shrub or tree 3–4 m. tall and nearly as broad, occasionally up to 8 m., the branches usually ascending and often presenting a broom-like appearance; bark yellow-green with fine horizontal striations; branches pubescent (strongly strigose in Baja California), puberulent or pilose to glabrate, the branchlets rigidly divaricate, spinose-tipped; axillary thorns lacking, the nodes bearing few to many bud scales; leaves 1–2 per node, sessile [i.e. no petiole evident on the common rachis except in seedlings (fig. 7b)], the single pair of pinnae (3–65 mm. long) of the primary leaves borne on a scale-like, indurate rachis which is sometimes tardily deciduous after the pinnae fall; leaflets 1–7 (–13) pairs, broadly elliptical, obtuse to emarginate at apex, 0.5–5 mm. long, 0.75–1.5 (–2) mm. broad, puberulent when young; rachis of the raceme 0.2–4.5 cm. long, puberulent, bearing 1–6 (–10) flowers on pedicels 4–8 (–15) mm. long; calyx pubescent to glabrate; petals yellow except for the upper (posterior) whose limb is usually white but occasionally creamy or pale yellow; upper petal 7–10 mm. long, the limb 4–5 mm. long, 3.5–6.0 mm. wide, rhomboidal or broadly ovate, the claw 3–4 mm. long, subequal to the limb in length, the other four petals slightly shorter than the upper, the limb rhomboidal or lanceolate, the margins not overlapping one another at anthesis, the claw short, 1–2 mm. long; ovary at anthesis strigose to puberulent; legumes 3.5–11.0 cm. long, 7–9 mm. wide, strongly tapered basally and apically, torulose, circular in cross-section where the seeds are borne, longitudinally striate, not coriaceous, dehiscence irregular, the valves often breaking as well as the sutures opening; seeds 1–4, brown, sub-globose, 8 (–10) mm. long, 5–7 mm. wide.

Type. Mexican Boundary Survey: Diluvial banks of the Colorado, Ft. Yuma, 13 January 1854. *A. F. Schott* (NY, holotype; F!, date of 1855 is in error) [flowering specimen]; Williams' River [Arizona], 12–22 February [1854], *J. M. Bigelow* (N.Y.) [in fruit].

Representative specimens. MEXICO. Gulf of California Islands, Baja California Sur: S. end of Amortajada Bay, San José Island, 11 April 1952, *R. Moran 3772* (DS, UC); Puerto Balandra, Isla Carmen, 23 March 1971, *J. R. Hastings 71-131* (ARIZ, SD); Danzante Island, 7 April 1962, *Moran 9228* (CAS, SD); Arroyo de los Chivos, NE. side of San Marcos Island, 29 March 1962, *Moran 8981* (CAS, RSA, SD). Baja California [Norte]: main arroyo, San Esteban Island, 26 April 1966, *Moran 13054* (DS); ca. ½ mi. S. of Refugio

Bay, Isla Angel de la Guarda, 26 March 1963, *Moran 10427* (DS, UC). Sonora: Tiburón Island, 5 May 1952, *Moran 4064* (DS, SD, UC, US), 23 April 1966, *Moran 12992* (ARIZ, CAS, RSA, SD).

Peninsula, Baja California Sur: Rancho El Salto, Arroyo Coyote (ca. 24°47′N., 110°50′W.), altitude 525 m., 5 November 1971, *Moran 19020* (14 mi. [22.4 km.] (by road) W. of San Luis Gonzaga, 21 October 1964, *Turner & Hastings 64-380* (ARIZ); Agua Verde, 1 April 1911, *J. N. Rose 16578* (US); Portus Escondido, 2 February 1842, *Wosnessensky* (GH); 55 km. E. of Villa Insurgentes on highway to Loreto, 3 May 1972, *Carter 5670*; 1 km. W. of Las Parras summit, road from Loreto to San Javier, 6 May 1972, *Carter 5672*; Rancho La Venta, ca. 16 km. westerly from Loreto on road to San Javier, 21 April 1962, *Carter 4415*; Rancho Aguajito, Arroyo Gua between Loreto and Rancho Sauce, 24 April 1955, *Carter & Ferris 3446*; Arroyo Gua, N. of Loreto, 7 November 1960, *Carter 4110*; Rancho Naucajoa (26°16′N., 111°36.5′W.), W. of Llanos de San Juan, *Carter & Reese 4531*; Coyote Bay [Cove], Concepción Bay, 18 June 1921, *Johnston 4172* (CAS, F, K, MO, UC, US); wash 25 mi. [40 km.] S. of San Ignacio, 19 April 1931, *Wiggins 5434* (CAS, DS, GH, RSA); eastern bajada of Sierra Calvario, Systema de Sierra Viscaíno, 10–15 March 1947, *H. S. Gentry 7501* (DS). Baja California [Norte]: ca. 5 mi. [8 km.] N. of Misión de San Borja along road to Bahía de Los Angeles, 17 May 1959, *I. L. & D. B. Wiggins 14857* (CAS, DS); Cajón de Santa María, 12 May 1889, *T. S. Brandegee s.n.* (DS, UC); San Luis Gonzales [Gonzaga] Bay, 29 April 1921, *Johnston 3348* (CAS, US); San Felipe Desert between El Cajón and Algodones, along eastern foot of Sierra San Pedro Mártir, altitude 2500 ft., [800 m.], 10 May 1941, *Wiggins 9845* (DS, UC, US). Sonora: island in harbor, Guaymas, 14 April 1921, *Johnston 3084* (CAS, US); hills NW. of shrimp cannery, Guaymas, 6 April 1962, *Carter 4363*; 26 km. S. of Hermosillo on Guaymas road, 21 March 1934, *Ferris 8759A* (DS); between Hermosillo and Kino Bay, 21 December 1968, *V. Rudd 3038*, with *P. Bauer & A. C. Fox* (ARIZ, SD, US); Sonora Alta, 1830, *Coulter 490* (K, 2 sheets, one lacking collection number); N. of bay, within 5 mi. [8 km.] of coast, vicinity of Libertad, 2 May 1928, *E. H. Graham 3822* (DS); 7 mi. [11 km.] S. of Altar, 4 May 1928, *Graham 3906* (DS); Pasa de San Luis [Poso de Luis on US sheet], 4 June 1894, *E. A. Mearns 2697* [Int. Bound. Commission] (DS, US).

UNITED STATES. Arizona: Tumamoc Hill, Tucson Mts., Pima Co., 8 June 1938, *H. S. Gentry 3777* (CAS); 5 mi. [8 km.] S. of Florence, Pinal Co., 26 July 1927, *H. W. Graham s.n.* (DS); Tempe Butte, altitude ca. 1300 ft. [415 m.], Maricopa Co., 4 May 1952, *E. P. Killip 42150* (US); Government Springs, 3.5 mi. [5.6 km.] N. of Bumblebee, State Highway 69, Yavapai Co., 3 July 1940, *Ferris 9902* (CAS, DS, GH, RSA, UC); 14 mi. [22 km.] NE. of Topock, Mohave Co., 10 June 1967, *Carter 5243.* CALIFORNIA: 1 mi. [1.6 km.] S. of Copper Basin Lake, Whipple Mts., San Bernardino Co., 22 April 1940, *A. M. Alexander & L. Kellogg 1200* (DS, GH, RSA, US); base of Whipple Mts. adjacent to Colorado River 11 mi. [18 km.] above Earp on road to Parker Dam, San Bernardino Co., 15 March 1940, *Wolf 9721* (RSA).

Coarse soil of plains and hillslopes, mostly below 600 m., but also between 700 and 800 m. in north central Sonora and southeastern Arizona. The trees leaf out following the rainy seasons, but the leaves are ephemeral. Flowering is mostly from March through May, the height of the Sonoran Desert dry season. Leaves, if present during flowering, are confined to non-floriferous branches. This is the most widespread of the taxa in Baja California where it is known as *dipua* and extends from a little south of Latitude 25°N. northward to the United States border. It is also abundant in west central Sonora and southwestern Arizona where it extends to Latitude 35°N.

Even when leafless, the branches are an important source of food for stock. Trees with their upper branches lopped off by machetes indicate that a traveller rested nearby and provided food for his mule, burro, or horse. In times of drought, the branches are also cut to feed cattle. The seeds are edible.

As an historical aside, it is interesting to note that Thomas Coulter collected both *Cercidium microphyllum* and *C. floridum* in "Sonora Alta" [vicinity of Hermosillo, Sonora] in 1830. According to the correspondence between Harvey and Bentham [Kew archives], some years after the packages of Coulter's collections were received at Trinity College, Dublin, Harvey separated the legumes and sent them to Bentham at Kew for identification. Specimens of both taxa are annotated in Bentham's hand as new species. At about that time, Asa Gray visited Kew, presumably saw all of the Coulter material, and subsequently published *Cercidium floridum* Benth. ex Gray. Five years later, John Torrey, in describing material collected on the Mexican Boundary Survey, named *Parkinsonia microphylla*, chose a Schott specimen as type, and made no mention of the much earlier Coulter collection to which Bentham had applied the same specific epithet.

The following collections are putative hybrids between *Cercidium microphyllum* and *C. floridum* subsp. *floridum*: *P. Kamb 2014.* Bottom of NE. caldera of Molina Crater, altitude ca. 950 ft. [310 m.], crater region NW. of Sierra Pinacate, Sonora, Mexico, 29 April 1951 (DS, UC). The leaves are petiolate. The leaflets are larger than typical for *C. microphyllum* and there are too many leaflets for it to be *C. floridum.* It has the stem pubescence and the strigose ovary of *C. microphyllum* and thorns similar to those of *C. floridum.* On both of the above cited sheets of this collection, the flowering branch is the putative hybrid and the separate fruiting branch—presumably from a different tree—is typical *C. floridum* subsp. *floridum.* Both of the putative parents are known to occur in this area (Hastings, Turner and Warren, 1972). A sheet at University of Arizona bears only a fruiting branch and this is typical *C. floridum* subsp. *floridum*.

C. B. Wolf 9722. Base of Whipple Mts., adjacent to Colorado River, 11 mi. [18 km.] above Earp on road to Parker Dam, altitude ca. 400 ft. [130 m.], San Bernardino Co., California, 15 July 1940 (DS, RSA). Collector's note: "This lone tree looks like a typical *C. microphyllum* in olive-green color and shape, but the pods are rich brown, somewhat flattened, and not constricted between the seeds, which are larger and flattened. Leaflets somewhat larger than typical *C. microphyllum* and *C. floridum*. Both species grow here in abundance." The valves of the pods are coriaceous, striate, and white-dotted. The stems are sparsely appressed-pubescent and bear short spines.

Papers treating these and other putative hybrids in *Cercidium* are published elsewhere (Carter, 1974; Carter and Rem, 1974).

2. **Cercidium praecox** (Ruiz and Pavón) Harms.

(Figure 4.)

Cercidium praecox (Ruiz and Pavón) Harms, 1908, Bot. Jahrb., vol. 42, p. 91.

Caesalpinia [*Sappania*] *praecox* Ruiz and Pavón, 1802, Fl. Peruv., vol. 4, pl. 376, plate only [Entire volume published by Consejo Superior de Investigaciones Científicas, Madrid, 1957].

Caesalpinia praecox Ruiz and Pavón, 1833, *in* Hooker and Arnott, Bot. Misc., vol. 3, p. 208.

Cercidium spinosum Tulasne, 1844, Arch. Mus. Paris, vol. 4, p. 134.

Rhetinophloem viride Karsten, 1862, Fl. Columb., vol. 2, p. 25, pl. 113.

Cercidium viride Karsten, 1887, Bot. Jahrb., vol. 8, p. 346.

Cercidium plurifoliolatum M. Micheli, 1903, Mém. Soc. Phys. et Hist. Nat. Genève, vol. 34, p. 269, pl. 18.

Cercidium unijuga Rose, 1905, Contrib. U. S. Nat. Herb., vol. 8, p. 301, 1905.

Cercidium Goldmanii Rose, 1905, Contrib. U.S. Nat. Herb., vol. 8, p. 301. [*Goldman 735*, type (US!): leaves glabrous; waxy coating of stems only slightly visible.]

Shrub or tree usually 2–4 m. tall, but up to 9 m. in forested areas of northeastern Sonora, the crown usually rounded, or flat-topped and spreading in exposed habitats, erect and less branched in sheltered habitats; branches and trunk bright green to the base, the bark with a minute quadrate-pustulate pattern and bearing a heavy coating of wax, the branchlets glabrate to pubescent, the hairs usually appressed; axillary bud scales prominent; thorns axillary, stout, usually one but sometimes two per node, 2–18 (–25) mm. long (mean 8.6 mm.), often dark brown; leaves 1–3 (–6) per node, pubescent, the petiole (1–) 4–11 (–21) mm. long, bearing 1 (occasionally 2–3) pair of pinnae 0.4–4.5 cm. (–5.0, *Wiggins 6473*) cm. long; leaflets (3–) 5–9 (–17, *Wiggins 6473*) pairs, oblong, rounded at apex, 3–10 mm. long, 1.4–3.8 mm. wide; inflorescences borne in

FIGURE 4. *Cercidium praecox*, *palo brea*, showing typical growth form in open habitat (*Carter, Hastings* & *Turner 5577*, northeastern Sonora between Moctezuma and La Noria).

clusters along mature branches, usually compact, 1–3 (4) per node, the rachis (1.5–) 2–11 (–15) mm. long, sparingly pilose, bearing 1–6 (–9) flowers on pedicels 7–10 mm. long; petals deep yellow, the upper often orange-dotted near base of limb; upper petal 9–11 mm. long, the limb 6–7 mm. long, 6–8 mm. wide, broadly ovate, the claw 3–5 mm. long, shorter than the limb, the other four petals slightly shorter than the upper, the limb broadly ovate and sometimes auriculate at base, the claw 1–2 mm. long; ovary glabrous at anthesis; legumes 3–6 (–8) cm. long, 0.6–1.0 cm. wide, flat and papery, not narrowed between the seeds, the veins conspicuous, forming an elongate-reticulate pattern; seeds 1–2 per pod, oblong, flattened, gray-brown with dark brown mottling, up to 1 cm. long, 3–4 mm. wide.

TYPE. Middle western Peru. Ruiz and Pavón plate. [cf. Johnston, 1924, p. 67.] (Ruiz and Pavón collections, MA!).

REPRESENTATIVE SPECIMENS. MEXICO. GULF OF CALIFORNIA ISLANDS, BAJA CALIFORNIA SUR: summit, Ildefonso Island (26°37′N., 111°27′W.), 17 May 1921, *Johnston 3753* (CAS), 2 April 1962, *Moran 9066* (RSA, SD, US); Tortuga Island (27°26′N., 111°54′W.), 24 April 1952, *Moran 4007* (DS), 30 March 1962, *Moran 9016* (SD), 11 May 1921, *Johnston 3592* (CAS, GH, K, UC, US). PENINSULA, BAJA CALIFORNIA SUR: San José del Cabo, 26 March 1911, *J. N. Rose 14466* (US); La Paz, 10 August 1944, *Maximino Martínez s.n.*

(US); along dry washes between Médano and Venancio, 29 April 1931, *Wiggins 5532* (DS, RSA, UC, US); between Rancho Segundo Paso and San Javier, altitude 300 m., 21 April 1962, *Carter 4412*; between Cañón de Las Calaveras and La Tinaja, western side of Mesa de San Alejo, altitude 690 m. (ca. 25°51′N., 111°36′W.), 11 November 1961, *Carter 4306*; along old mission trail SE. of Comondú, altitude 420 m., 20 April 1955, *Carter & Ferris 3424* (ARIZ, DS, GH, SD, UC, US); Cuesta de Los Encinos, SE. of Cerro Giganta, altitude 500 m., 29 March 1960, *Carter & Ferris 4046* (UC), same tree, 9 November 1960, *Carter 4146* (UC); 4 mi. [6 km.] (by road) E. of San Lina (suburb of San Ignacio), 29 October 1963, *Turner & Hastings 63-294* (ARIZ, DS, SD). Sinaloa: La Constancia, Munic. El Fuerte, December 1924 [sic! on original label at DS; US copied label is 1926], *Jesus Gonzales Ortega 6200* (DS, GH, MEXU, US). Sonora: Alamos study area, 7.5 mi. [12 km.] W. of Alamos, 28 April 1967, *R. D. Krizman 16* (ARIZ); Agua Caliente N. of Alamos, 2 November 1939, *Gentry 4839* (ARIZ, MO, distributed as *C. torreyanum* and so cited by Gentry, 1942, p. 131); San Bernardo, Río Mayo, 1 March 1935, *Gentry 1377* (ARIZ, GH, MEXU, UC, distributed as *C. torreyanum* and so cited by Gentry, 1942, p. 131); Cerro de Bayajori, 12 mi. [19 km.] W. of Navajoa, 11 April 1948, *Gentry 7947* (UC, US, distributed as *C. floridum*); island in Bay, Guaymas, 14 April 1921, *Johnston 3078* (CAS, US); low hills and flats near tannery E. of Guaymas, 28 February 1933, *Wiggins 6348* (DS, RSA, US); small valley 20 mi. [32 km.] N. of Guaymas, 8 March 1933, *Wiggins 6473* [spines up to 30 mm. long, pinnae 45–50 mm. long, leaflets up to 15 pairs] (DS); 20 km. S. of Carbó junction, 3 May 1971, *Carter, Hastings & Turner 5597*; Horcasitas, 17 April 1932, *Abrams 13360* (DS); 2 mi. [3 km.] S. of Los Hoyos, altitude 810 m., 23 April 1971, *Carter, Hastings & Turner 5576*; 4.2 km. S. of Los Hoyos, 4 July 1971, *Hastings 71-199* (SD); Colonia Oaxaca, 24 July 1938, *Stephen S. White 663* (ARIZ, GH).

Ranging from coastal plains up to bajadas, mesas, hills, and mountains at elevations up to 825 m. in Baja California and 1115 m. in the mountains of northeastern Sonora. Flowering is from March through May with the peak in April, before the leaves develop.

In Baja California, *C. praecox* extends from near the tip of the peninsula (23°N.) northward to the vicinity of San Ignacio (27° 25′ N.). On the mainland, it occurs in southern Mexico and is abundant in Sonora from a little south of Guaymas (27° 56′ N.) almost to the United States border (30° 54′ N.). Occasional collections have been made as far south as 26°N. in Sinaloa. This is the only one of our Sonoran Desert species of *Cercidium* having a disjunct distribution. According to Johnston (1924a), in South America it occurs from extreme middle-western Peru to northern Venezuela.

During the months when the trees are leafless, *C. praecox* may be recognized readily by the bright green bark extending down to ground level, and the conspicuous accumulation of dark bud scales at the nodes. Development of new branch growth appears to be limited, and most seasonal growth (production of leaves and flowers) is axillary year after year on the old branches. In addition, the stout, often dark brown spines, which may reach a length of 2.6 cm., set it apart from the other taxa. It is the only one of our *Cercidium* species with bark having a quadrate-pustulate pattern. When in flower, the species may be recognized easily by the usually deep yellow flowers borne in close clusters along the length of the old branches.

The common name, *palo brea,* is derived from the fact that the waxy substance coating the bark, after being scraped from the branches and melted by heat, is used as a 'gum' for gluing together leather objects and furniture; thus it is used just like *la verdadera brea.*

The following Mexican collections are putative hybrids between *Cercidium praecox* and *Parkinsonia aculeata*: edge of town, Coyuca, Mina, Guerrero, 11 May 1934, *G. B. Hinton 6040* (BM, NY), 25 March 1937, *Hinton 9968*; (ARIZ, BM, K, MEXU, NY, RSA, TEX); near Los Hoyos, northeastern Sonora, 23 April 1971, *Carter, Hastings* & *Turner 5575* (to be distributed). This material is discussed in a separate paper (Carter and Rem, 1974).

3. **Cercidium × sonorae** Rose and Johnston.

(Figure 5.)

Cercidium × sonorae ROSE AND JOHNSTON, 1924 (pro sp.) stat. nov., *in* I. M. Johnston, Contr. Gray Herb., vol. 70, p. 66. (April). [*C. microphyllum* (Torrey) Rose and Johnston × *C. praecox* (Ruiz and Pavón) Harms].

Cercidium molle I. M. JOHNSTON, 1924, Proc. Calif. Acad. Sci., IV, vol. 12, p. 1038. (May).

Spreading tree 4–8 m. tall, usually with lax branches (but sometimes the branches short and stiff), the bark smooth or sometimes faintly horizontally striate, green to yellow-green, sometimes with an inconspicuous, thin, waxy coating, branches short-villous, pilose, or sometimes glabrate; axillary thorns present or lacking, slender (2–) 5–11 (–20) mm. long (mean 6.5 mm.), variable as to presence on a given tree; bud scale clusters prominent to inconspicuous; foliage bright yellow-green, the leaves 1 to 3 per node, the petioles usually 1–3 mm. long, but varying from 0 to 12 mm.; pinnae 1 to 2 pairs, 0.7–5.0 cm. long, the leaflets (3–) 6–8 (–12) pairs elliptical-oblong, (1.5–) 2–3 (–6.0) mm. long, (1.0–) 1.5 (–3.0) mm. wide; inflorescence usually open, the rachis of the racemes 0.5–4.0 cm. long, bearing 1 to 10 flowers on pedicels 6–10 (–14) mm. long; petals light yellow, except for the upper whose limb may be whitish, creamy, or creamy and yellow and often orange-dotted near the base of the limb; upper petal 10–12 mm. long, the limb 5–7 mm. long, 5–8 mm. wide, broadly ovate but with

Figure 5. *Cercidium* × *sonorae*, *palo estribo*, showing typical habit of a mature tree (*Carter* & *Reese 4554*, Baja California, Sierra de la Giganta west of Loreto).

pointed apex, the claw 4–5 mm. long, shorter than the limb; the other four petals slightly shorter than the upper, the limb ovate, the claw short, 1.5–3 mm. long; ovary strigose at anthesis; legumes 3–8 cm. long, 7–10 mm. wide, slightly flattened and somewhat coriaceous, sinuate if more than one-seeded, long-tapering to each end, the surface with conspicuous longitudinal striations, dehiscing along the sutures or irregularly; seeds 1 to 2 (4), oblong to oblong-ovate or ovoid, dark mottled brown, flattened or thick, 9–10 (–12) mm. long, 4–5 mm. wide.

Type. Dry hills in the vicinity of Guaymas, Sonora, Mexico, 1910, *Rose*, *Standley* & *Russell 12586* (US!).

Representative specimens. MEXICO. Baja California Sur: Arroyo San Ramón just W. of Rancho San Ramón (25°14.5′N., 111°17′W.), 21 October 1964, *Carter 4818*; Rancho Tasajera, ca. 3.5 km. NE. of San José de Agua Verde, 3 June 1965, *Carter* & *Sharsmith 4936*; Agua Verde Bay, 26 May 1921, *Johnston 3877* (CAS!, type of *C. molle,* DS, GH, K, MO, UC, US); Puerto Agua Verde [Bahía Agua Verde], 5 June 1965, *Carter* & *Sharsmith 4945*, 23 August 1971, *Carter 5610*; Misión San Javier, 36 km. SW. of Loreto, 6 May 1972, *Carter 5679*; Arroyo Ranchito, ca. 9 km. SE. of Llanos de San Julio on road from San Javier to Comondú (26°02′N., 111°39′W.), 5 June 1963, *Carter* & *Reese 4554*; Cuesta de Los Encinos, SE. of Cerro Giganta, altitude ca. 500 m., 29 March 1960, *Carter* & *Ferris 4045,* and from same tree 9 November 1960, *Carter 4145*; La Higuera, NE. base of Cerro Giganta, 18 October 1966, *Carter* & *Sousa 5212*;Arroyo Hondo, N. side of Cerro Giganta, altitude 540 m., 17 October 1966, *Carter* & *Sousa 5199*; Tortuga Island, 11 May 1921, *Johnston 4409* (CAS, K, UC, US), 16 mi. [26 km.] from San Ignacio on road to Santa Rosalía, 10 March 1934, *Ferris 8626* (US); 10.5 [17 km.] mi. ENE. of San Ignacio, 27.4°N., 112.8°W., altitude 170 m., 17 October 1971, *Turner* & *Hastings 71-134* (ARIZ). SONORA: N. of Guaymas (0.6 mi. [.96 km.] N. of junction with Bahía San Carlos road), 2 May 1971, *Carter*, *Hastings* & *Turner 5595*; 25 mi. [40 km.] N. of Guaymas, 2 April 1935, *Shreve 7310* (MO; sheets at ARIZ and F bear both *C.* × *sonorae* and *C. praecox*); 31 mi. [50 km.] N. of Guaymas, 2 April 1935, *Shreve 7313* (ARIZ, F, MO); El Pozo, 26 km. S. of Hermosillo on road to Guaymas, 21 March 1934, *Ferris 8761* (DS, US); Torres, 10 February 1903, *F. V. Coville 1664* (US); Sierra Lopez Rancho [37 mi., 59 km. NW. of Hermosillo], 13 April 1932, *Abrams 13327* (DS,F).

Plains and hillslopes below 600 m. Flowering March to June with the peak in April; leaves usually present when trees in flower.

In Baja California, where it is known as *palo estribo*, *Cercidium* × *sonorae* occurs principally in the Sierra de la Giganta from about 25°15′N. (opposite the northern end of Isla San José) northward to the northern slopes of Cerro Giganta (26°10′N.). One outlying collection (*Turner* & *Hastings* 71-134) is from east of San Ignacio (27.4°N.). In Sonora, *C.* × *sonorae* is most abundant from near Guaymas northward to the vicinity of Carbó (i.e., from about 28° to 30° N.). On neither side of the Gulf of California is *C.* × *sonorae* as abundant as *C. microphyllum* and *C. praecox*, one or the other or both of which appear always to occur in the vicinity of trees of *C.* × *sonorae*. Throughout its range, but especially noticeable in Baja California, is the fact that *C.* × *sonorae* occurs only within the limits of the distributional overlap of *C. microphyllum* and *C. praecox*. In characters of bark surface, spininess, pubescence, flower color, and seed shape, *C.* × *sonorae* appears to be more variable than any of the other taxa in the group. In several morphological characters, *C.* × *sonorae* falls between *C. praecox* and *C. microphyllum*; furthermore, pollen of *C.* × *sonorae* stained with ‘cotton blue’ (aniline-blue-lactophenol) shows a much lower percentage of presumably viable grains than does the pollen of either of its putative parents. These facts lead to the hypothesis that *C.* × *sonorae* is of hybrid origin, the putative parents being *C. microphyllum* and *C. praecox*. Discussion of the hybrid origin of *C.* × *sonorae* and of other hybrids involving species of *Cercidium* is published elsewhere (Carter, 1974; Carter & Rem, 1974).

In 1965 while on a field trip to Agua Verde Bay in search of Johnston’s *Cercidium molle*, I was told that a large *palo estribo* tree comparing favorably to that described by Johnston (1924b) had been cut down some twenty years before. On a subsequent trip I explored the "huge amphitheater-like canyon" (Johnston, 1924b, p. 1056) south of the *puerto* of Agua Verde Bay and found only a few trees of *palo estribo*. Collections from one of these (*Carter 5610*) closely approach the type specimen of *C. molle* in its lack of spines, its pubescence, flower size, and leaflet size, but differ in the pinnae being shorter, and the leaflets more closely spaced than in the type. Considering the amount of variation occurring in *C.* × *sonorae*, however, *C. molle* falls well within the limits of that taxon. Had Johnston been able to explore further in the Sierra de la Giganta (instead of being limited to short sallies from aboard ship), he undoubtedly would have encountered trees of *palo estribo* similar to that which he described from across the Gulf near Guaymas as *C. sonorae* and would have realized the close affinity of the trees as they occur on both sides of the Gulf.

In his excellent discussion of *Cercidium* species in the "Vegetation of the Sonoran Desert" Shreve (1951, p. 145; 1964, p. 153) unfortunately confused *C. sonorae* with the much more abundant *C. praecox*. The description and distribution given under the heading "Cercidium sonorae" and the common name *brea* apply to *C. praecox*.

The strong, tough wood of *Cercidium* × *sonorae* is used to make stirrups, hence the name, *palo estribo*.

4. **Cercidium floridum** Bentham ex Gray.

[Synonymy and references given under subspecies.]

Trees or shrubs 2.5–8.0 (–12) m. tall, bark of main branches above main trunk green, horizontally striate; leaves 1 or 2 per node, petiolate; pinnae 1 (occasionally 2) pair, bearing 2–4 pairs of leaflets; flowers yellow, the petals clawed, the claw of the upper petal longer than those of the other four petals; ovary glabrous at anthesis (occasionally a very few hairs present); legumes linear-oblong, flat, cuneate at base and apex, coriaceous, white-dotted (stomata) when immature, obscurely so when mature, inconspicuously reticulately-veined; seeds oblong to ovate, somewhat flattened, brown, the lighter margin sometimes slightly mottled.

4a. **Cercidium floridum** Bentham ex Gray subsp. **floridum**.

Cercidium floridum Bentham ex Gray, 1852, Plantae Wrightianae, vol. 1, p. 58, subsp. *floridum*.

Parkinsonia florida Watson, 1876, Proc. Amer. Acad., vol. 2, p. 135.

Parkinsonia torreyana Watson, 1876, Proc. Amer. Acad., vol. 2, p. 135.

Cercidium torreyanum Sargent, 1889, Garden & Forest, vol. 2, p. 388.

Tree 4–8 (–12) m. tall, the crown spreading, branchlets of mature trees usually slender, flexuous or drooping, the trunk gray-green; bark with fine horizontal striations, often dark in the indentations; branches glabrous or sparingly pubescent; thorns absent or 1.8–5.4 mm. long (mean 3.6 mm.), slender, solitary; bud scales not accumulating at the nodes to form conspicuous dark clusters; foliage blue-green; leaves with petiole (1–) 2–5 (–11) mm. long bearing one pair of pinnae (occasionally more) 0.3–1.0 (–1.6) cm. long; leaflets mostly 3 pairs per pinnae, but often 2 and occasionally 4 pairs, oblong or obovate, sometimes emarginate, 4–8 mm. long, 2–5 mm. wide, slightly pubescent or glabrate; inflorescence open, glabrous or nearly so, borne on the younger branches; rachis of the racemes 1.0–4.5 (–7.0) cm. long, bearing 1–7 (–10) flowers on pedicels 6–12 (–20) mm. long; petals bright yellow, the upper sometimes orange-dotted near base of limb, the upper petal 9–15 mm. long, the limb 5–9 mm. long, 6–13 mm. wide, broadly ovate, cordate at base, the claw 3–5 mm. long, shorter than the limb, the other four petals slightly shorter than the upper, the limb broadly ovate, the claw short, 1.5–2.0 mm. long; legumes linear to elliptic, not or only slightly narrowed between the seeds, 3–11 cm. long, 1.0–1.5 cm. wide; seeds usually 3 per legume, 9–12 mm. long, 5–7 mm. wide.

Type. "Sonora Alta," Mexico in 1830, *Thomas Coulter* (Trinity College, Dublin, Ireland; also 2 duplicate specimens bearing name in Bentham's hand, K!)

The nomenclatural problem concerning *Cercidium floridum* and *C. torreyanum* is ably discussed by Johnston (1924a) and Benson (1940).

Representative specimens. MEXICO. Sinaloa: La Constancia, Munic. El Fuerte, December 1924 [sic! on original label at DS; US copied label is 1926], *Jesus Gonzalez Ortega 6199* (DS, GH, MEXU, US); vicinity of San Blas, 22 March 1910, *Rose, Standley* & *Russell 13203* (GH, US), 28 January 1927, *M. E. Jones 23086* (RSA); Sonora: vicinity of Guaymas, 23 April 1910, *Rose, Standley* & *Russell 15038* (US); plain N. of Empalme, 6 April 1962, *Carter 4359*; 20 mi. [32 km.] from Guaymas on Hermosillo road, 20 March 1934, *Ferris 8752* (DS, US); 3.5 mi. [5.6 km.] (by road) N. of Desemboque, 29 April 1964, *Turner* & *Hastings 64-49* (ARIZ, DS, SD); El Alamo, near Magdalena, 25 May 1925, *P. B. Kennedy 7010a* (UC, US); W. side of Isla Tiburón just N. of Punta Willard, 19 March 1962, *Wiggins 17150* (DS); Isla Tiburón, 19 March 1962, *Moran 8723* (RSA, SD), desértico espinosa, altitude 60 m., 3 May 1971, *C. L. Diaz Luna 2266* (ENCB); Molina Crater, crater region NW. of Pinacate Crater, 29 April 1951, *Kamb 2014* (ARIZ). [The sheets of this collection number at UC and DS are mixed collections, the branch bearing only flowers being a putative hybrid between *Cercidium microphyllum* and *C. floridum*.] Papago Tanks, Pinacate region, 15 March 1959, *R. M. Turner 59-30* & *C. H. Lowe 2979* (ARIZ, CAS); Pozo de Luis, 4 January 1894, *Mearns 2696* [Int. Bound. Commission] (US). UNITED STATES. Arizona: Sabino Canyon, Santa Catalina Mountains, Pima Co., 25 May 1917, *Shreve 5202* (ARIZ); vicinity of Coolidge Dam, 13 May 1935, *Bassett Maguire 11321* (UC); Black Cañón Road, 23 mi. [37 km.] N. of Phoenix, Maricopa Co., 21 October 1931, *John W. Gillespie 8657* [2 sheets, one fl., one fr.] (DS, GH, UC, US); washes W. of Castle Dome Mts., Yuma Co., 22 April 1949, *J. H. Thomas 396* (DS); Topock, Mohave Co., 24 May 1919, *A. Eastwood 8886, 8887* (CAS, GH), 29 May 1950, *J. T. Howell 26618* (ARIZ, CAS). California: Whipple's Expl. R. R. route, 35th parallel, 1853–54, *Bigelow* (K); 20 mi. [32 km.] NE. of Ogilby, Imperial Co., 6 April 1932, *Munz & Hitchcock 12166* (F, GH, MO, RSA, UC); Box Canyon at Shafer's Well, Chocolate Mts., Riverside Co., 14 June 1918, *Ferris 977* (CAS, DS); 10 mi. [16 km.] W. of Coachella, Riverside Co., April 1905, *H. M. Hall 5784* (ARIZ, UC, US); Palm Springs (Agua Caliente), desert base of San Jacinto Mt., Riverside Co., 4–13 April 1896, *S. B. Parish 4115* (BM, GH, K, MO, US); 4 mi. [6 km.] NW. of Desert Center on Aqueduct Road, Riverside Co., 10 April 1947, *P. A. Munz 11722* (ARIZ, RSA, SD); ca. 5 mi. [8 km.] E. of Clark Lake in Borrego unit of Anza State Park, San Diego Co., 21 April 1955, *Guy Fleming 45817* (DS, SD); near Needles, San Bernardino Co., 3 June 1929, *H. L. Mason 5362* (DS, UC); base of Whipple Mts. adjacent to Colorado R., 2 mi. [3.2 km.] above Earp on road to Parker Dam, 15 July 1940, *Wolf 9723* (RSA).

Flowering from March to June with the peak in April and with occasional off-season blooming from August to November.

The blue *palo verde*, as it is called in Arizona, occurs principally in fine soil along washes and on flood plains, for the most part at altitudes below 1100 m. Its water requirements appear to be greater than those of *C. microphyllum*. It occurs in the Colorado Desert area of southeastern California, in southern Arizona from 35°N. near the Colorado River, southeast to ca. 33°N. on the eastern border of Arizona and southward through the coastal and middle portion of Sonora to 27°30′N. Outlying collections have been made in coastal Sinaloa as far southward as 26°N. *Cercidium floridum* and *C. microphyllum* are the most widely distributed members of the genus within the Sonoran Desert, but *C. floridum* subsp. *floridum* is the only one restricted to the mainland. Although current floras indicate *C. floridum* subsp. *floridum* as occurring in Baja California, and Goldman (1916, p. 335) cites it as being there, no specimens have been seen which support such a distribution.

In most areas, the peak of the blooming season of *Cercidium floridum* is about two weeks in advance of that of *C. microphyllum*.

4b. **Cercidium floridum** Bentham ex Gray subsp. **peninsulare** (Rose) stat. nov. and comb. nov.

Cercidium peninsulare Rose, 1905, Contrib. U.S. Nat. Herb., vol. 8, p. 301.

Shrub or tree 2.5–8 m. tall, openly branched, but with a dense, symmetrically-rounded crown; bark gray and scaly-fissured at base, bright green above, inconspicuously horizontally striate; branchlets not flexuous, having pilose or sparse, appressed-villous hairs when young, glabrate to glabrous in age; a single axillary thorn usually present at a node, 2–3 (–7) mm. long (mean 3.87 mm.), slender to stout; axillary bud scales, when present, not dark and conspicuous; leaves with petiole 1–4 (–10) mm. long bearing 1 (rarely 2) pair of pinnae 0.3–1.7 (–2.1) cm. long, the leaflets mostly 2 pairs per pinna but many (25 percent) with 3 pairs, obovate and sometimes emarginate, 6–11 (–18) mm. long, 3–7 mm. broad, sparingly pilose to glabrate; inflorescences borne on old wood as well as on younger branchlets, more or less compact, the racemes with rachis sometimes almost absent, but usually 3–10 (–20) mm. long, pubescent, bearing 3–5 flowers on pubescent pedicels 4–9 (–12) mm. long; calyx sparingly pubescent to glabrous; petals deep or bright yellow, the upper 7.5–9.0 mm. long, the limb 5–7 mm. long, 5.0–6.5 mm. wide, ovate or rhombic ovate, the claw 2 mm. long, the other four petals slightly shorter to subequal to the upper, limb ovate, the claw short, 1.5–2.0 mm. long; legumes 1.5–5.5 cm. long, 8–15 mm. wide, flat, the margins slightly constricted between the seeds, seeds 1–2 (3) per legume, 9–10 mm. long, 6–7 mm. wide.

Type. La Paz, Lower California, Mexico, in 1890, *Palmer 112* (US!).

Representative specimens. MEXICO. Islands, Baja California Sur: arroyo leading eastward from old Ruffo Ranch, Isla Ceralvo, 16 April 1962, *Wiggins 17758* (DS, ENCB); Arroyo de Agueda, NE. side of San José Is., 11 April 1962, *Moran 9402* (CAS, RSA, SD); arroyo above Ensenada Ballena, Espíritu Santo Is., 21 April 1962, *Moran 9634* (SD, US); S. end of Santa Cruz Is., 18 April 1962, *Moran 9577* (SD, UC); arroyo above spring, Santa Catalina Is., 14 April 1952, *Moran 3866* (DS), 10 April 1962, *Moran 9369* (SD); Puerto Ballandra [Balandra], Carmen Is., 21 May 1921, *Johnston 3802* (CAS, DS, GH, K, UC, US); 4 June 1963, *Carter & Reese 4546*. Peninsula, Baja California Sur: San José del Cabo, March–June 1897, *A. W. Anthony 363* (F, GH, K, UC, US); Arroyo San Lázaro, ca. 10 mi. [16 km.] NW. of San José del Cabo, 2 May 1959, *Thomas 7775* (ARIZ, CAS, DS, SD, UC, US); Arroyo del Salto, E. of La Paz, 30 March 1949, *Carter 2595* (DS, UC); La Paz, 16 April 1899, *E. A. Goldman 388* (GH, US! Type); Arroyo San Ramón W. of Rancho San Ramón (25°14.5'N., 111°17'W.), 25 October 1964, *Carter 4866*; vicinity of Puerto Agua Verde, 4 June 1965, *Carter & Sharsmith 4943*; arroyo S. of Bahía Agua Verde, 5 June 1965, *Carter & Sharsmith 4946*; Arroyo Peloteado, W. of Rancho Peloteado (25°45'N., 111°30'W.), 21 April 1962, *Carter 4410*; San Javier, 21 April 1962, *Carter 4414*; Rancho Viejo, ca. 28 km. from Loreto on road to San Javier, 6 May 1972, *Carter 5680*; Rancho Quiñí, on old mission trail SE. of Comondú, 20 April 1955, *Carter & Ferris 3423* (DS, MEXU, SD, UC, US); alluvial arroyo margin, Las Cuevitas below Comondú, 12 April 1939, *Gentry 4458* (ARIZ, GH, K, MO, UC, US); Valle de Los Encinos, S. side of Cerro Giganta, altitude 750 m., 8 November 1960, *Carter 4134*, 8 June 1963, *Carter &*

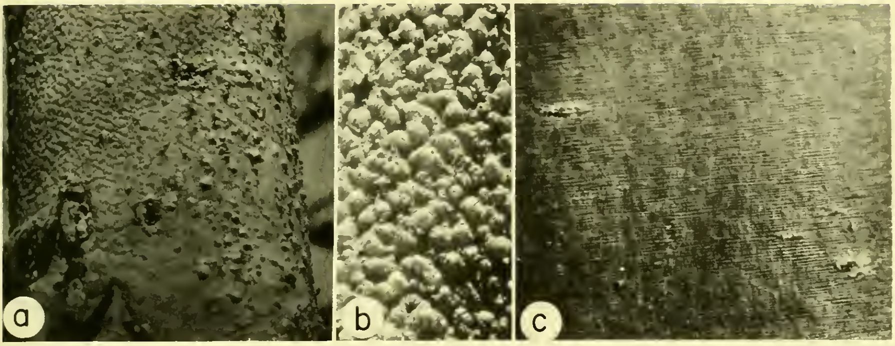

Figure 6. Bark patterns in *Cercidium*: a, b, *C. praecox* showing the quadrate-pustulate surface typical of this species, a, ca. × 1½, b, ca. × 10; c, *C. floridum* subsp. *floridum* showing the horizontally striate pattern characteristic of this species and of *C. microphyllum*.

Reese 4573; coastal strand, San Bruno (26°12.5′N., 111°23′W.), 1 June 1963, *Carter* & *Reese 4537*; Arroyo Mulegé, ca. 10 mi. [16 km.] W. of town on road to El Potrero, 11 April 1963, *Wiggins 18231* (CAS, DS, K, MEXU, US); Picachos de Santa Clara, Desierto Viscaíno, 5–10 November 1947, *Gentry 7754* (DS); wash 16 mi. [26 km.] from San Ignacio on Calmallí road, 10 March 1934, *Ferris 9037* (DS, US).

Flowering is from March to June with the peak in April, the branches usually bearing leaves at the same time. The flowering period precedes that of its congeners in the same area.

It grows on coastal plains and along washes and canyons into mountain valleys from sea level up to 750 m. This tree, known locally as *palo verde* is the only taxon in *Cercidium* restricted to Baja California, where it is moderately common from near the tip of the peninsula northward to San Ignacio (27°25′N., 112°52′W.). As noted by Gentry on one of his collections (*4458*), this tree has a denser, leafier, more symmetrical crown than any other members of the genus. Also, it retains its leaves for a greater portion of the year than any of the others. The upper petal of *C. floridum* subsp. *peninsulare* is not as conspicuously elevated above the other four petals as it is in the other taxa.

Discussion

In an attempt to understand the relationships between the Sonoran Desert taxa of *Cercidium* as set forth above, the following characters were of use and merit some discussion.

Bark. Inasmuch as most cercidiums retain only a few leaves during much of the year, or have minute leaves, photosynthesis also occurs in the green bark which is relatively smooth except for the lower trunks of large trees. In *C.*

praecox, the bark is bright green clear to the ground, whereas in the others the main trunk becomes grayish and often fissured. The bark of *C. praecox* differs also in having a minute quadrate-pustulate surface pattern (fig. 6a,b), easily visible with a hand lens or even to the naked eye, and in being conspicuously coated with a waxy substance. Shreve (1951, p. 145; 1964, p. 153) mentioned these characteristics, but he attributed them to *C.* × *sonorae* which he at that time mistook for *C. praecox.* The bark of *C. microphyllum* and *C. floridum,* on the other hand, is finely horizontally striate (fig. 6c) and, especially in *C. floridum* subsp. *floridum,* often dark in the indentations, thus giving a 'dirty-neck' appearance. These striations are less conspicuous in *C. floridum* subsp. *peninsulare.* The bark of *C.* × *sonorae* is usually smooth, but sometimes horizontal striations are visible with a hand lens. On some specimens of *C.* × *sonorae* there is a thin, inconspicuous layer of waxy material which suggests *C. praecox.*

PUBESCENCE. Young branchlets of *Cercidium* show varying degrees of pubescence; older branchlets are glabrous to glabrate. In *C. floridum* subsp. *floridum,* branchlets are essentially glabrous, but sometimes with a few hairs, especially southward in its range. In *C. floridum* subsp. *peninsulare,* on the other hand, the young branchlets are conspicuously pubescent with pilose or sparsely appressed villous hairs. In *C. microphyllum* there is some correlation between geographic distribution and type of pubescence on the stems: all of the Baja California material is strongly strigose; the Sonoran collections studied are puberulent or pilose (especially in the interior); in Arizona and California some collections have glabrate branchlets. Branchlets of *C. praecox* vary from glabrate to pubescent. In *C.* × *sonorae* the branchlets may be strigose, short villous, or pilose, or occasionally the branchlets are glabrous.

The pubescence of the ovary at anthesis is of diagnostic value. In both subspecies of C. *floridum* and in *C. praecox* the ovary is glabrous; in *C. microphyllum* and *C.* × *sonorae* it is lightly pubescent to strigose at anthesis.

ARMATURE AND BRANCHING PATTERN. Most treatments of *Cercidium* refer to the thorns as "nodal" or "stipular," but Kearney and Peebles (1960, p. 407) describe them as "rudimentary branches transformed into spines." This concept (except for the use of the term "spine" instead of "thorn") is in accordance with Blaser's (1956) definition, which is followed herein, of a thorn being a reduced determinate shoot. Leaves of seedling plants and of young seasonal growth of *Cercidium* bear a pair of inconspicuous, slender, foliaceous stipules; these do not form spines, but are fugaceous. Thorns, when present, are the first shoots to develop in a primary (first to develop at a node) leaf axil. Their shoot nature is clearly shown in the early stages by the presence of a cluster of rudimentary leaves at the distal end of the developing thorn (fig. 7c). These soon disappear as the thorn increases in size and hardens (fig. 7d). Subsequent growth at a node results in either inflorescence, leaf, or shoot development from buds on an

Figure 7. Developmental stages in leaves and thorns of *Cercidium*. a, three week's old seedling of *C. praecox* showing simply pinnate basal leaves and bipinnate upper leaves (*Turner*); b, five week's old seedling of *C. microphyllum* with petiolate primary leaves (*Carter* & *Reese 4531*), × 2; c, young branch of *C. praecox* showing immature axillary thorns bearing rudimentary leaves at apex (*Carter, Hastings*, & *Turner 5597*); d, more mature thorn of *C. praecox* after rudimentary leaves have fallen (*Carter, Hastings*, & *Turner 5597*).

extremely shortened stem in the axil of the primary leaf. However, the positional relationship of the thorn primordia to the shoot, leaf, and flower primordia cannot be determined without more extensive morphological investigation.

In *Cercidium microphyllum*, none of the buds in a primary leaf axil develop

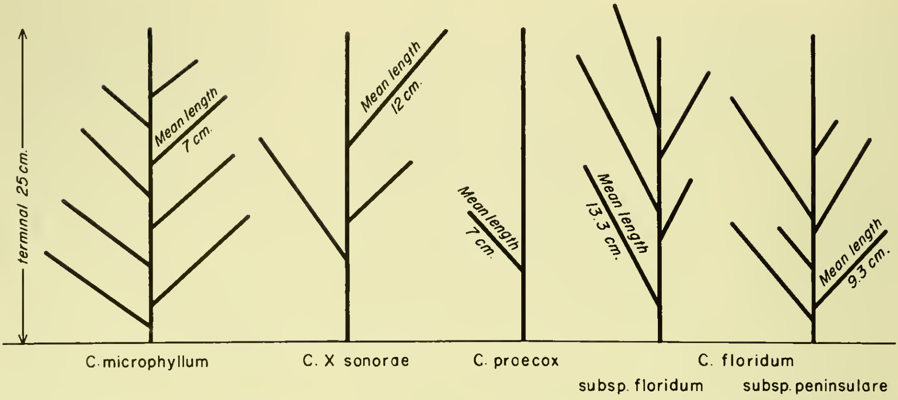

FIGURE 8. Branching patterns in *Cercidium*, based on number and length of branchlets in the terminal 25 cm. of a stem.

into a short leafless thorn; rather, at the majority of nodes one bud develops into the stout, determinate, leafy branch, spinescent at the tip, which is so characteristic of this species. *Cercidium praecox* is consistently the thorniest of the Sonoran Desert members of the genus inasmuch as at each node one, and occasionally two, axillary buds develop into thorns. When two thorns occur at a node, one is always larger. In *C. floridum* subsp. *floridum*, comparatively few axillary buds develop,—the resulting mature tree having long, slender branchlets, a less divaricately branched appearance, and fewer thorns (especially in the northern part of its range) than do most other species. However, Shreve (1951, p. 142; 1964, p. 150) states that young trees of *C. floridum* less than 2 m. in height have very thorny twigs. *Cercidium floridum* subsp. *peninsulare* and *C.* × *sonorae* are variable in the number of axillary buds which develop into thorns. In many instances, *C.* × *sonorae* is thornless.

Cercidium microphyllum, which, as noted above, has no axillary thorns but bears only spine-tipped, determinate branchlets, has the greatest number of branchlets (mean, 8) in the terminal 25 cm. of a branch, whereas *C. praecox*, the thorniest of the species, has the fewest branchlets (fig. 8). In *C. microphyllum*, there is usually a gradual reduction in length of the branchlets toward the distal end of the branch in contrast to the other taxa where reduction in branchlet length often shows no correlation with position on a stem segment. *Cercidium* × *sonorae* has an intermediate number of branchlets in comparison with its putative parents and the branchlets are longer and more flexuous than those of either parent. The average number of branchlets developing in the terminal 25 cm. of the branches of the two subspecies of *C. floridum* is rather close: 5.4 branchlets in *C. floridum* subsp. *floridum* and 6.1 branchlets in *C. floridum* subsp. *peninsulare,* but the mean length of the branchlets diverges significantly. The flexuous branchlets of *C. floridum* subsp. *floridum* have a mean length of 13.3 cm. and the stouter and stiffer branches of *C. floridum* subsp. *peninsulare* have a mean length of 9.3 cm. (fig. 8). These means for number and length of branchlets help to indicate their relationship within the group, but in all cases, the range of these measurements within each species and the overlap with other species, is too great for use of the characters in keys.

Leaves. The seedlings of all Sonoran Desert taxa of *Cercidium* have conspicuous cotyledons, 23 to 25 mm. long in *C. floridum* and 6 to 18 mm. long in the others. In the seedlings, each of the first few nodes (usually up to five) bears a pinnate leaf with several pairs of large leaflets; following these, the bipinnate leaves more typical of each of the various taxa develop (figs. 3, 7a). The inconspicuous, foliaceous stipules are caducous. The pinnae (i.e., the secondary rachises with their leaflets) are short (0.3 to 6.5 cm. long) and the leaflets are opposite. A small, foliaceous or semi-indurate bract is borne at the apex of the leaf rachis and at the apex of each of the pinnae. Because of the need to discuss them separately, the first leaf developing at a node is herein designated as a 'primary' leaf and those developing subsequently in the axil as 'axillary' leaves. Buds produced in the axil of the primary leaf may develop into a thorn (a short determinate shoot), or into foliaceous or floral shoots. The foliaceous shoots are usually so reduced that the leaves borne on them appear to arise directly in the axil of the primary leaf or leaf scar; one to eight such leaves may be present at a time. Leaves are deciduous in most taxa, usually falling before the blooming period or with periods of drought.

Leaves of *Cercidium microphyllum* differ from those of the other taxa in being non-petiolate, except in the seedling stages wherein the primary leaf may have a slightly winged petiole from 1 to 4 mm. long which merges inconspicuously with the broadened rachis area where the pair of pinnae arises. In later stages, the primary leaf pinnae are borne on an indurate, scale-like structure, the basal portion of which usually is not distinguishable from the rachis as a petiole. The indurate terminal bract is also indistinguishable from the rachis. The two pinnae fall separately from this scale-like rachis and it remains on the branch for some time before falling and exposing the primary leaf scar. (Sometimes in *C. microphyllum*, the leaflets fall before the pinnae do.) In the other species of *Cercidium* the entire leaf abscisses at the base of the petiole. (Occasionally in *C. floridum* subsp. *floridum* the pinnae fall from the apex of the petiole, or from the rachis if the leaf bears two pairs of pinnae, and the petiole, or petiole and rachis remain on the stem for a short time.) In specimens of *C.* × *sonorae* with subsessile leaves, the shortened petiole and the rachis become somewhat indurate,

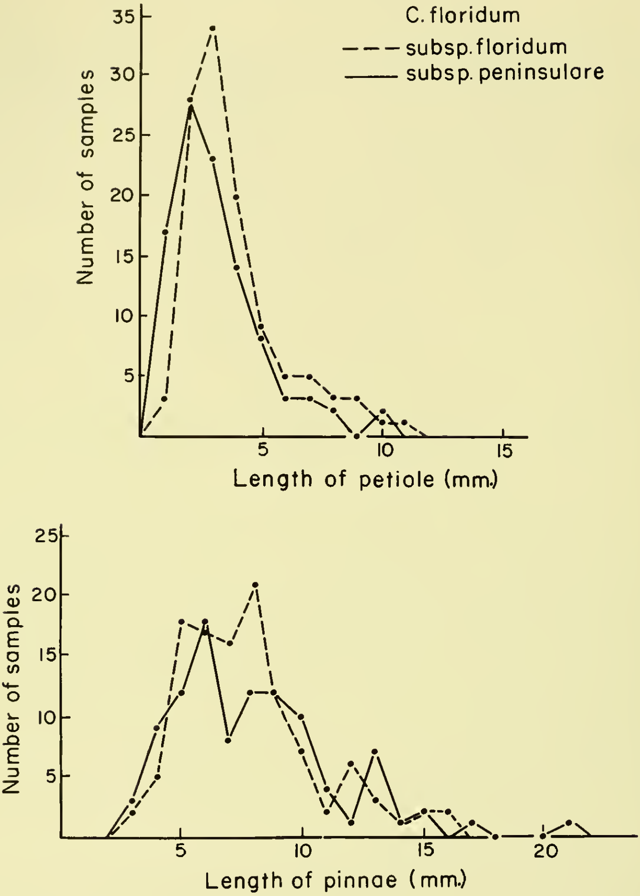

Figure 9. Comparison of length of petioles and pinnae in *Cercidium floridum* subsp. *floridum* and *C. floridum* subsp. *peninsulare.*

but they fall with the rest of the leaf instead of being tardily dehiscent as in *C. microphyllum.* In *C. praecox* and *C.* × *sonorae,* the scar of the primary leaf is conspicuous on younger branches; in *C. floridum* subsp. *floridum* it is inconspicuous. In *C. floridum* subsp. *peninsulare,* the scar of the primary leaf is often obscured by a cluster of reddish-brown glandular hairs in the axil.

In *Cercidium praecox* and *C. floridum* the bract at the apex of the rachis tends to be linear and foliaceous rather than indurate. In specimens of *C.* × *sonorae* with petiolate leaves, the elongate apex of the rachis is usually slightly indurate, while in those having subsessile leaves the rachis is an indurate, long-tipped scale similar to that of *C. microphyllum.*

Cercidium floridum leaves have pinnae usually less than 1 cm. long and mostly bearing 2 to 4 pairs of leaflets, whereas the other three taxa (*C. microphyllum*, *C. praecox*, and *C.* × *sonorae*) have pinnae up to 6.5 cm. long bearing 4 to 9 pairs of leaflets. At a significance level of 1 percent the means for both characters differ between members of the two groups.

As indicated by the graphs (figs. 9, 10), the two subspecies of *C. floridum* are similar in characters of petiole length, pinna length, and leaflet number. Each subspecies exhibits its greatest variability in length of pinnae. Mean length, however, is about the same for the two (7.8 mm. for *C. floridum* subsp. *floridum*, 7.9 mm. for *C. floridum* subsp. *peninsulare*) and the difference between the means is not statistically significant. At a 1 percent significance level the only leaf difference is the mean number of leaflet pairs. In the primary as well as axillary leaves, *C. floridum* subsp. *floridum* usually has 3 pairs (mode 3, mean 2.7) and *C. floridum* subsp. *peninsulare*, usually either 2 or 3 pairs (mode 2, mean 2.5). In all of these structures, the measurements show too much overlap to make them principal key characters. That these characters differ in degree rather than in kind supports the subspecific disposition of *C. floridum peninsulare.*

Among the other three taxa, petiole length is useful in recognizing entities: the leaves of *C. microphyllum* are non-petiolate, i.e., the pinnae are sessile (except in seedling stages); the leaves of *C. praecox* always have conspicuous petioles; those of *C.* × *sonorae* vary from no petioles up to petioles 12 mm. long (fig. 11). The mean petiole length for each taxon differs significantly ($P = 0.99$) from that of the other two. As with *C. floridum* the pinnae in each species exhibit great variability in length, but the means, although clustered, are not so close (table 1). At a 1 percent significance level the only difference occurs between those for *C.* × *sonorae* and *C. praecox.* As to the leaflet number, the members of this group overlap considerably and show no significant difference in mean number of pairs. Both in this character and in petiole length the mean for *C.* × *sonorae* is intermediate between that for *C. microphyllum* and *C. praecox.* In pinna length, however, the mean for *C.* × *sonorae* exceeds that of the other two taxa; but its value is close to the mean for *C. microphyllum*, and the two values do not differ significantly.

As suggested by the common name for *Cercidium floridum*, blue *palo verde*, leaf color has been utilized in identification, but because interpretations of color differ so markedly, no attempt has been made to include precise shades of green in the detailed descriptions. The following field observations, however, point up the foliage color differences in the taxa of *Cercidium* as they occur in Sonora (correspondence: Hastings to Carter, August 10, 1971).

> "I made a trip to Sonora again week before last and the summer rains have wrought their usual alchemy there. The parched country we saw in April is green and incredibly lush. Also incredibly muggy, buggy and muddy.

TABLE 1. *Comparison of selected characters in Sonoran Desert taxa of* Cercidium

Character	*C. microphyllum*	*C. praecox*	*C.* × *sonorae*	*C. floridum*	
				subsp. *floridum*	subsp. *peninsulare*
Petiole (length, mm.)	0	(1–) 4–11 (–21)	0–3 (–12)	(1–) 2–5 (–11)	1–4 (–10)
Mean	0	7.6	2.0	3.8	3.13
Pinnae (length, mm.)	3–65	4–45	7–50	3–16	3–17 (–21)
Mean	19.7	16.7	20.3	7.8	7.9
Leaflets, number of pairs	1–7 (–13)	(3–) 5–9 (–17)	(3–) 6–8 (–12)	2–4	2–4
Mean	6.4	6.5	6.4	2.75	2.5
Leaflets (length, mm.)	0.5–5.0	3–10	(1.5–) 2–3 (–6.0)	3–8	(3–) 6–11 (–18)
Mean	2.0	5.9	3.5	4.9	7.1
Inflorescence (pedicels)					
Total pedicel length (mm.)	4–8 (–15)	7–10	6–10 (–14)	6–12 (–20)	4–9 (–12)
Mean	6.0	8.1	8.0	10	5.9
Length from calyx to pedicel joint (mean)	1.5	2.3	2.0	2.9	1.9
Ratio—total pedicel length: length from pedicel joint to calyx	4.3:1	3.8:1	4.2:1	3.6:1	3.5:1
Thorns (length, mm.)	0	2–18 (–25)	(2–) 5–11 (–20)	1.8–5.4	2–3 (–7)
Mean	0	8.6	6.5	3.6	3.9

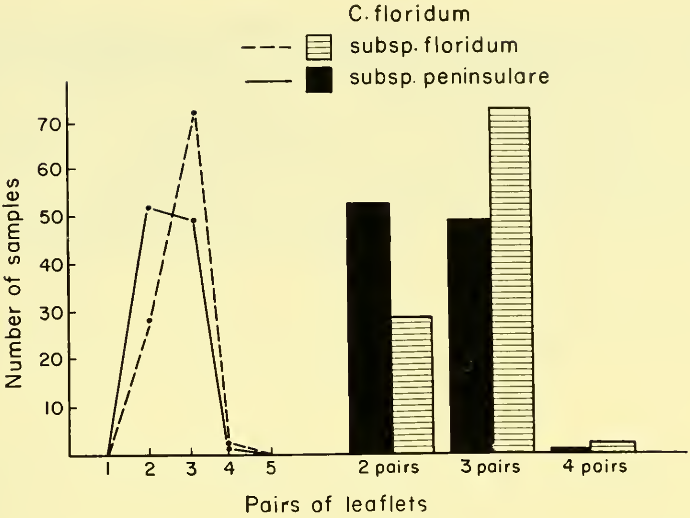

FIGURE 10. Comparison of number of pairs of leaflets in *Cercidium floridum* subsp. *floridum* and *C. floridum* subsp. *peninsulare*.

> "All four palo verdes were in full leaf and seeing them that way did a good bit to restore my ego. Not only is it possible easily to tell *Cercidium floridum* from *C. microphyllum*, [but also] *C. praecox* and *C.* × *sonorae* can be distinguished at a glance. *Cercidium praecox* shows up as blue—even bluer than *C. floridum*. *C.* × *sonorae*, on the other hand, is relatively yellow—not the nearly chlorotic yellow of *C. microphyllum*, but about the color of the stems on both *C.* × *sonorae* and *C. praecox*."

INFLORESCENCE. In all of the Sonoran Desert taxa of *Cercidium*, except *C. floridum* subsp. *peninsulare*, when both flowers and leaves are present concurrently, the inflorescences exceed the leaves in length. In *C. microphyllum*, *C. praecox*, and *C.* × *sonorae*, the inflorescences normally develop before the leaves; if leaves are present, they are usually on separate branches. In *C. floridum* subsp. *floridum*, flowering precedes leafing on about 30 percent of the collections studied. In *C. floridum* subsp. *peninsulare*, where both flowers and leaves are usually present on a given branch, the inflorescences are equal or subequal to the leaves; occasionally, flowering precedes leafing.

The flowers are borne in compact or open racemes, which may be either single or fascicled at the nodes. For the most part, the inflorescences are borne in profusion on the terminal branchlets, but *C. praecox* departs strongly from this pattern in having its usually compact inflorescences strongly fascicled along the stems, none of which are as branched as in the other taxa. Shreve (1951, p. 145; 1964, p. 153) pointed out this striking characteristic of *C. praecox*, but here again, he mistakenly attributed it to *C.* × *sonorae*. In *C. floridum* subsp.

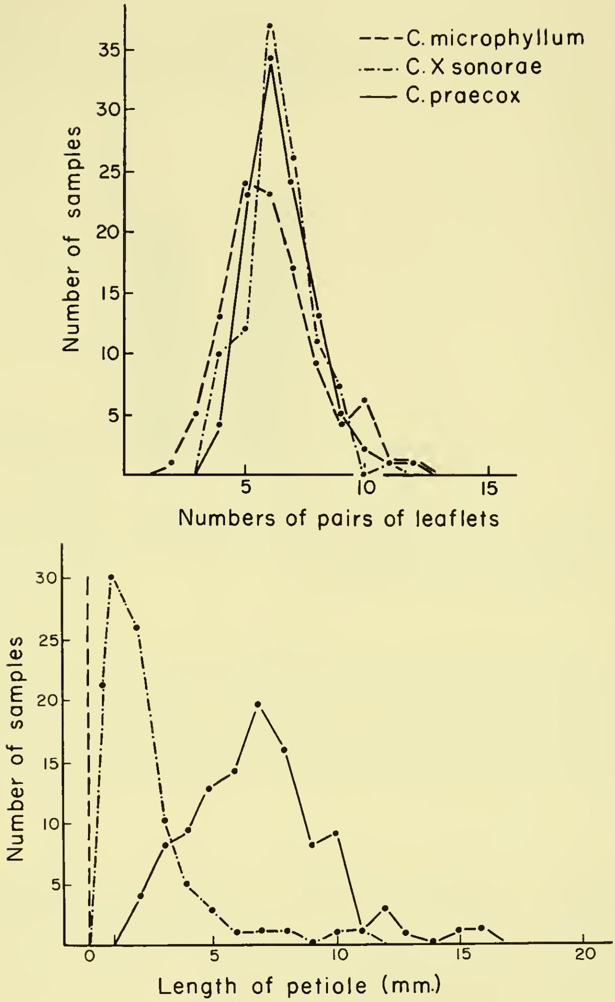

Figure 11. Comparison of number of pairs of leaflets and length of petiole in *Cercidium microphyllum*, *C.* × *sonorae* and *C. praecox.*

peninsulare, some racemes are borne on older branches; therefore the trees do not have the strong terminal flowering aspect of *C. floridum* subsp. *floridum.*

Inflorescence rachis length varies both within the taxa and between them. In *C. floridum* subsp. *floridum* the rachises vary from 1.0 to 4.5 cm., while in *C. floridum* subsp. *peninsulare* they are usually 0.3 to 1.0 cm., but occasionally up to 2 cm. In *C. microphyllum* they are 0.2 to 4.5 cm. long, while in *C. praecox* they are 0.2 to 1.0 cm. long. Those of *C.* × *sonorae* (0.5–4.0 cm.) fall between those of *C. microphyllum* and *C. praecox.*

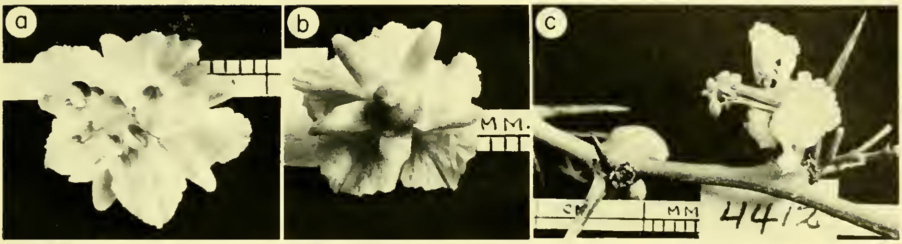

Figure 12. Flowers of *Cercidium*: a, front view showing larger, elevated upper (posterior) petal (*C.* × *sonorae*, *Carter 4411*); b, back view (*C. floridum* subsp. *peninsulare*, *Carter 4410*); c, side view showing elevated upper petal bearing cinnamon-colored spots (*C. praecox*, *Carter 4412*). Numbers refer to Carter and/or Carter *et al.* collections; data for these are given under "Representative collections cited" for the respective taxa.

The pedicel is jointed, with the joint in the distal half. The distance between joint and calyx varies less than that between joint and rachis. In total length of the pedicel, as in rachis length, *C. floridum* subsp. *floridum* and *C. floridum* subsp. *peninsulare* fall at opposite ends of the spectrum for the five taxa. Their respective means, 10.0 mm. and 5.9 mm., differ significantly at $P = 0.99$. So do

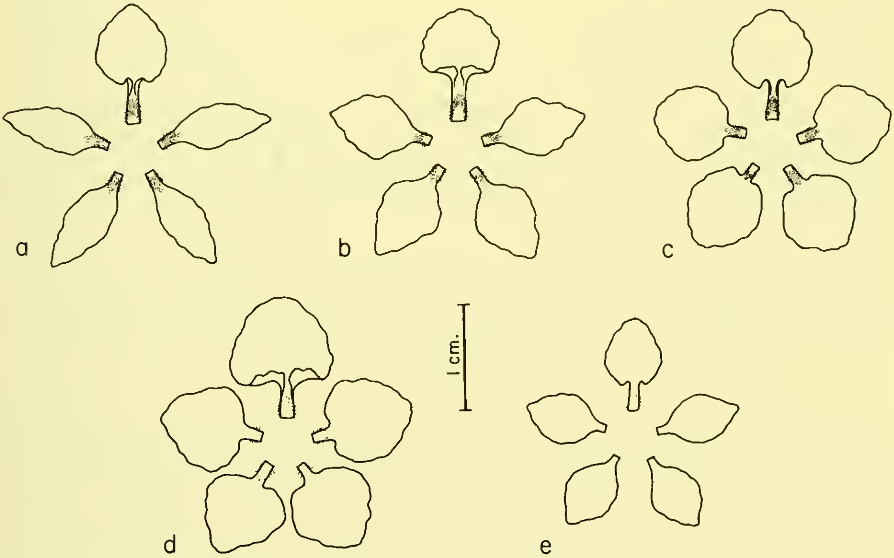

Figure 13. Comparison of petal shape and size in *Cercidium*: a, *C. microphyllum* (*Carter 5683*); b, *C.* × *sonorae* (*Carter 5679*); c, *C. praecox* (*Carter 5678*); d, *C. floridum* subsp. *floridum* (*Turner*, Arizona, pickled material); e, *C. floridum* subsp. *peninsulare* (*Carter 5680*). Numbers refer to Carter and/or Carter *et al.* collections; data for these are given under "Representative collections cited" for the respective taxa.

the means for *C. microphyllum* (6.0 mm.) and *C. praecox* (8.1 mm.). The average pedicel length for *C.* × *sonorae* (8.0 mm.) falls between those of its putative parents, but does not differ significantly from that of *C. praecox* (table 1).

As for the caesalpinoid flowers (figs. 12, 13), there is size variation within each taxon, but the flowers of *C. floridum* subsp. *floridum* are the largest in the group and those of *C. microphyllum* and *C. floridum* subsp. *peninsulare* are the smallest. Flowers of *C. microphyllum* differ also in having the limb of the long-clawed upper petal white, or occasionally cream or pale yellow and the other four petals rhomboidal or lanceolate rather than broadly ovate (figs. 12, 13). The upper, long-clawed petal of *C. praecox* nearly always bears a cluster of small orange dots near the base of the limb; these are also often present in *C. floridum* subsp. *floridum*, but they are lacking in *C. floridum* subsp. *peninsulare*. The upper petal of *C.* × *sonorae* is extremely variable. It may be white, creamy, or light yellow, and it may or may not bear orange dots.

The tricolpate pollen grains, which vary in diameter from 18 to 34 microns, are prolate spheroidal and supra-reticulate (Carter and Rem, 1974). The lumina are reduced in diameter and depth near the margin of the furrows.

Legumes and seeds. The venation of the valves of *Cercidium* legumes is of diagnostic value: the valves of *C. praecox* are somewhat papery with conspicuous reticulate venation; those of *C. microphyllum* and *C.* × *sonorae* are striate—especially noticeable in the latter; and those of *C. floridum* are smooth with veins scarcely visible to the naked eye. The surface of the valves of immature legumes of *C. floridum* bear conspicuous white-dotted areas. These are stomatal pores; apparently the young fruits as well as the bark carry on photosynthesis at a time when the trees are nearly leafless. Stomata are present also in the legumes of the other taxa, but they are somewhat obscured by the prominent venation.

Although Brenan (1963, p. 207, table) used the upper suture of the pod as a distinguishing character, this is more variable within our Sonoran Desert taxa than he indicated. The legumes are tardily dehiscent along the sutures or indehiscent; in *Cercidium microphyllum* and *C.* × *sonorae* the thin-walled valves also sometimes break irregularly. Differences in shape and size of legumes and seeds may be compared in figure 3. In characters of legume venation and shape, *C.* × *sonorae* approaches *C. microphyllum* more closely than it does *C. praecox*.

As to surface pattern, seeds of *C. praecox* and *C.* × *sonorae* are gray-brown with various degrees of brown mottling on the flat surfaces; seeds of *C. microphyllum* and *C. floridum* are brown with the marginal area somewhat lighter and sometimes faintly mottled. In all of the taxa the hilum and micropyle are subterminal; in some species they are in a slightly recessed or notched area

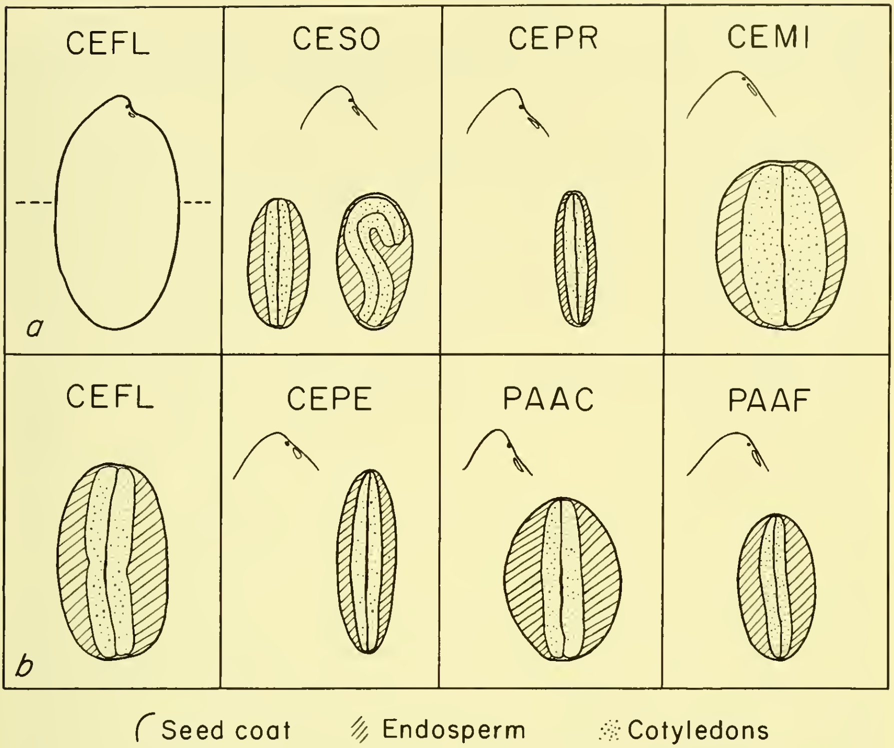

Figure 14. Comparison of seeds (cross section and position of hilum and micropyle) in *Cercidium* and *Parkinsonia*: CEFL, *C. floridum* subsp. *floridum*, a, side view to indicate position of cross section (b) to entire seed (*E. E. Schellenger 6*, Chucawalla [Chuckawalla] Bench, Colorado Desert, California, 25 July–14 August, 1903, UC); CESO, *C.* × *sonorae*, note variation in form of cotyledons (*Carter & Sousa 5212*); CEPR, *C. praecox* (*Carter 4146*); CEMI, *C. microphyllum*, note thick cotyledons (*Ferris 9902*); CEPE, *C. floridum* subsp. *peninsulare* (*Carter 4821*); PAAC, *Parkinsonia aculeata* (*Harbison & Higgins*, San Telmo, Baja California, 17 December 1953, UC); PAAF, *Parkinsonia africana* (*Rodin 2156*, Namib Desert near Swakop River, Southwest Africa, 31 October 1947, UC). Diagrams drawn after seeds had soaked in water overnight. Seeds, × 2½, side view of apex, × 1½.

(fig. 14). As seen in cross section, the thick, oblong or subglobose seeds of *C. microphyllum* are distinct in having large cotyledons in comparison to the amount of endosperm (fig. 14). The other taxa, with more flattened and oblong or oblong-ovate seeds, follow much the same pattern in cross-section (fig. 14) as that illustrated by Boelcke (1946) for *C. australe* Johnston, the Argentinian species closely related to *C. praecox*.

Chromosome numbers. Chromosome counts of 2n = 28 have been reported for *Cercidium floridum*, *C. microphyllum* and *C.* × *sonorae* (Turner and Fearing, 1960). Although contraindicated in the publication, no voucher was preserved for the *C.* × *sonorae* count (correspondence, B. L. Turner to Carter, 5 July 1972). It is probable, however, that the seeds provided for this count were those of *C. praecox* rather than of *C.* × *sonorae* (correspondence, R. M. Turner to Carter, 23 June and 18 August, 1972).

Hybridization. Few putative hybrids between *Cercidium microphyllum* and *C. floridum* subsp. *floridum* have been noted, whereas *C.* × *sonorae*, which occurs in the area of overlap of *C. microphyllum* and *C. praecox*, is relatively abundant. A six-year record kept by W. G. McGinnies for trees in the foothills north of Tucson, Arizona, shows that *C. floridum* subsp. *floridum* blooms about two weeks earlier than *C. microphyllum* and *C. praecox* (the latter being a cultivated tree in that area). So, although there is some overlapping of the blooming period of *C. floridum* subsp. *floridum* and *C. microphyllum* in the Tucson area at least, the peak is reached at different times (correspondence, Hastings to Carter, 24 January 1972); no putative hybrids have been reported from this area. On the other hand, in the lower Colorado River basin between Arizona and Colorado, these two species do reach peak of bloom at approximately the same time and a small percentage of putative hybrids has been noted (pers. comm., Jones to Carter, September 1973). Ultraviolet light studies show that the flowers of these two species appear different to pollinating insects: *C. microphyllum* petals absorb UV light and all are "bee purple," while in *C. floridum* subsp. *floridum* only the upper petal absorbs UV light and the other four reflect it. The pollinators appear to be highly selective in accordance with these ultraviolet patterns (pers. comm., C. E. Jones to Carter, September 1973). In the case of *C.* × *sonorae*, on the other hand, whose putative parents, *C. microphyllum* and *C. praecox*, bloom concurrently and have the same ultraviolet absorption patterns as the above mentioned taxa (Carter, 1974), it appears that their pollinators are not selective in their visits inasmuch as there is apparently ample cross-pollination. No putative hybrids have been noted between *C. floridum* subsp. *peninsulare* and the other three taxa occurring with it in southern Baja California. Normally this species blooms before its congeners; its ultraviolet absorption pattern is the same as that of *C. floridum* subsp. *floridum* and of *C. praecox*, i.e., the upper petal absorbs and the other four reflect ultraviolet light.

Relationship between *Cercidium* and *Parkinsonia*. As indicated in the key at the beginning of this treatment, a number of characters serve to distinguish members of the New World genus *Cercidium* from *Parkinsonia aculeata* Linnaeus, the only member of the latter genus considered to be native to the western hemisphere. Treatments of these two genera fail to clarify the structure of the *primary* leaf and its relationship to thorns or spines; many floras merely state "stems armed" or "stems unarmed." As detailed above, armature in *Cercidium*, when present, consists of thorns which develop in the axil of a primary leaf.

In *Parkinsonia aculeata,* on the other hand, there are no axillary thorns. The conspicuous armature consists of the short petiole and rachis of the primary leaf itself, which has become enlarged, thickened and indurate, plus the tip of the rachis which has developed into a long, stout, sharp spine. Hutchinson (1969, pp. 70–71, fig. 64E), misinterpreted this structure, calling it a stipule. Also, he failed to differentiate between primary and axillary leaves. The stipules are either early deciduous or develop into short, indurate lateral spines, which, however, may fall long before the indurate petiole and rachis. One to three pairs of long (10 to 60 cm.) pinnae are produced on the short leaf rachis. In both primary and axillary leaves the secondary rachises are conspicuously flattened (phyllodial). In her anatomical comparison of *Parkinsonia aculeata* and *Cercidium torreyanum* (*C. floridum*), Scott (1935) found that only in the rachises of the pinnae and in the pulvinae is there a marked difference between these two taxa. She did not include armature in her studies. The small, caducous leaflets borne along the margins of the pinna rachis may be either opposite or alternate on the same pinna. The long phyllodial pinnae usually remain until the onset of winter and lend the trees a graceful, drooping aspect. When pinnae of the primary leaves fall, the indurate, spinose-tipped petiole and rachis remain on the branch. On older branches, this structure (spine) also eventually falls, leaving a conspicuous scar at the node. Burkart (1952, fig. 36) illustrates the spinose nature of the leaf rachis. He does not point out, however, that these stout spines are restricted to the first leaf at a node of a main branch and are only slightly, if at all, developed on leaves of the usually short axillary branches which are from 2 to 12 (–23) mm. long in contrast to the completely reduced axillary shoots in *Cercidium.*

Until the recent work of J. P. M. Brenan (1963), only one other taxon has currently been considered as belonging to the genus *Parkinsonia*, the African species *P. africana* Sonder. The primary leaf of *P. africana* is similar in some respects to that of *Cercidium microphyllum.* In *Parkinsonia africana* a single pair (occasionally one of the pair aborts) of pinnae 4 to 17 cm. long arises from a small, bractlike, nearly sessile leaf rachis which has a short, slender, foliaceous tip; stipules are inconspicuous, caducous, bractlike structures; the pinnae are not flattened, but are elliptical in cross section and bear tiny opposite, caducous leaflets, as is the case in the axillary leaves. Troll (1939; p. 1611, fig. 1372; p. 1612, fig. 1373), considers these leaves to be a reduced form of the typical caesalpinoid leaf which is petiolate and bears several pairs of pinnae. Armature, when present, is a short, stout, determinate stem (thorn) in the axil of the primary leaf. Johnston (1924a, p. 63) erred by indicating in his key to *Cercidium* and *Parkinsonia* that both *P. aculeata* and *P. africana* have similar armature. Presence or absence of these axillary thorns is extremely variable in *P. africana,* as it is also in some taxa of *Cercidium.* In all of these characters except the somewhat longer pinnae with leaflets caducous, *Parkinsonia africana* resembles *Cercidium microphyllum* more than it does *Parkinsonia aculeata*. Torrey (1859, p. 60) reached a similar conclusion.

The inconspicuous, bractlike rachis of the primary leaf in both *Cercidium microphyllum* and *Parkinsonia africana* might well be considered a rudimentary expression of the highly developed spine of the primary leaf of *Parkinsonia aculeata*. So, in this character, *Cercidium microphyllum* tends to resemble *Parkinsonia* more closely than it does its congeners with petiolate leaves (both primary and axillary) which fall entire. However, in the short pinnae which are not flattened and in the opposite leaflets which usually are not caducous, it falls within *Cercidium*.

It has not been possible to make careful examination of the other African trees placed in *Parkinsonia* by Brenan: *P. anacantha* Brenan and *P. scioana* (Chiovenda) Brenan [*Peltophoropsis scioana* Chiovenda]; so comparisons cannot be made regarding the structure of the primary leaves (matters which are not adequately treated in the descriptions of these two taxa).

There is a significant difference in pedicel length ($P = .99$) between *Parkinsonia aculeata* and *P. africana*, on the one hand, and the species of *Cercidium* studied, on the other. The mean pedicel length for the taxa of *Cercidium* ranges from 5.9 to 10.0 mm., with the ratio of total pedicel length to length from pedicel joint to calyx ranging from 3.5:1 to 4.3:1. In *Parkinsonia aculeata* the mean length is 14.5 mm.; the ratio, 6.4:1. In *P. africana* the mean pedicel length is 13.0 mm., not significantly different from that of *P. aculeata*. But the ratio is only 2.4:1, i.e., the joint occurs almost at the midpoint of the pedicel, whereas in *P. aculeata* it is relatively close to the calyx. In *Cercidium*, the joint is in the distal half of the pedicel, but never proportionately so close to the calyx as in *Parkinsonia aculeata*. Material was not available to carry the comparison to the other African taxa placed in *Parkinsonia*.

Pollen studies in relation to hybridization in *Cercidium* and *Parkinsonia* have shown that putative hybrids between taxa in *Cercidium* have a much higher percent of presumably viable pollen (as indicated by staining with aniline-blue lactophenol) than do the few known hybrids between *Parkinsonia aculeata* and species of *Cercidium* (Carter and Rem, 1974). In addition, pollen grains of putative hybrids between species of *Cercidium* are not malformed whereas those of putative hybrids between *Parkinsonia aculeata* and species of *Cercidium* are irregular in shape (Carter and Rem, 1974, fig. 1). No putative hybrids between *C. microphyllum* and *Parkinsonia aculeata* have been noted even though these two taxa sometimes occur in the same area.

As seen under the scanning electron microscope, pollen grains of the several species of *Cercidium* studied and those of *Parkinsonia aculeata* have similar

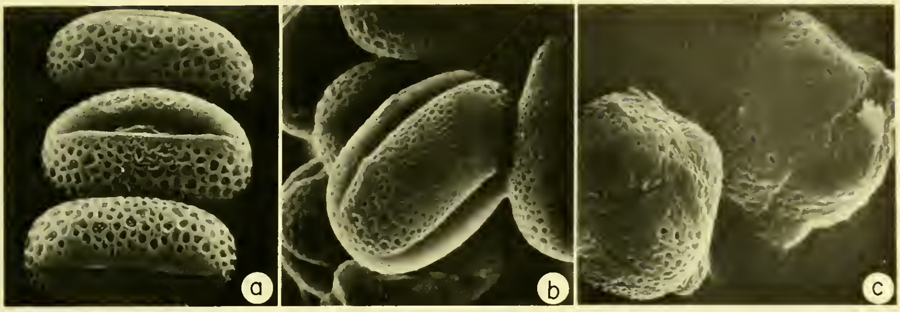

FIGURE 15. Pollen as seen under scanning electron microscope: a, *Cercidium floridum* subsp. *peninsulare* (*Carter 2595*); b, *Parkinsonia africana* (*Seydel 1230*, Namibrand: Karibib, Okomitundu, Southwest Africa, UC); c, *Parkinsonia* [*Peltophoropsis*] *scioana* (*Burger 2731*, Erer Rarea, 60 km. west of Dire Dawa, Ethiopia, 9°31′N., 41°25′E., 21 April 1963, K). All ca. × 1000. Photographs taken at Electronics Research Laboratory, University of California, Berkeley.

supra-reticulate sculpturing (Martin and Drew, 1969, 1970; Carter and Rem, 1974). Pollen of *Parkinsonia africana* (fig. 15), on the other hand, although being reticulately sculptured, has many shallow lumina as well as the deep lumina characteristic of *Cercidium* and *Parkinsonia aculeata*. Furthermore, in *P. africana* the lumina are much smaller and the muri thicker than in the above-mentioned taxa. Pollen of *Parkinsonia* [*Peltophoropsis*] *scioana* (fig. 15) is triporate with three large pores; its sculpturing differs markedly in that the reticulate surface appears rugose and the lumina are small and the muri wide. Unfortunately, the material of *P. anacantha* available contained insufficient pollen for a scanning electron microscope preparation or for satisfactory light microscope examination.

The legumes of *Cercidium microphyllum* resemble those of *Parkinsonia aculeata* more than they do those of other species of *Cercidium*. They are thin-walled and strongly torulose, i.e., much constricted on either side of the 1 to 4 seeds; dehiscence is irregular, as well as occurring along the sutures. Legumes of *C.* × *sonorae* resemble those of *C. microphyllum* in dehiscence. Those of other species of *Cercidium* appear to be indehiscent, or only slightly dehiscent. Legumes of *Parkinsonia aculeata* are sinuate or somewhat torulose and 1 to 5 seeded; otherwise they are similar to those of *Cercidium microphyllum*. Legumes in *Parkinsonia africana* material at hand are sinuate, flattened, and strongly dehiscent, while those of *P. scioana* and *P. anacantha* are flattened, but not constricted; those of *P. scioana*, at least, are indehiscent. Also, *P. scioana* is unique in the group in having long-funicled seeds. Although *Cercidium microphyllum* strongly resembles *Parkinsonia aculeata* in the character of its legumes, it stands apart from that species, and from other species of *Cercidium*, in a seed character: the cotyledons are thick in relation to the endosperm (fig. 14). Also, in dehiscence of the pinnae from the scale-like leaf rachis, *C. microphyllum* approaches *Parkinsonia aculeata*, but in the majority of characters it is more at home in *Cercidium* than in *Parkinsonia*.

As stated in the introduction, resolution of the generic relationship of *Cercidium* and *Parkinsonia* should be based upon extensive comparative biological, morphological, cytological, and genetic studies. On the basis of present information, however, one can say that *Cercidium* forms a discrete, easily recognizable unit confined to the Americas, with *C. microphyllum* most closely related to *Parkinsonia*. Study of Brenan's comparative chart (1963, pp. 206, 207) shows that among the taxa included, *Parkinsonia aculeata* is the most discordant element. Furthermore, the American species of *Cercidium* included agree in more gross morphological characters than do the African taxa placed in *Parkinsonia*. Pollen of two African taxa, as seen under the scanning electron microscope is of two distinct types whereas in *Cercidium* it is all similar. Pollen studies (Carter & Rem, 1974) indicate that species of *Cercidium* are more closely related to each other than they are to *Parkinsonia aculeata*, a species thought to be native to America, but which has been introduced widely throughout the warmer parts of the world. I would like to suggest that *Parkinsonia* be considered a monotypic genus comprised of *P. aculeata* Linnaeus, and that the relationships of the three African species (*P. africana*, *P. anacantha*, and *P. scioana*) be considered further before accepting them as congeneric with *Parkinsonia* and *Cercidium* as proposed by Brenan.

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THE COMPARATIVE MORPHOLOGY OF EXTRINSIC GASBLADDER MUSCULATURE IN THE SCORPIONFISH GENUS *SEBASTES* (PISCES: SCORPAENIDAE)

By

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Abstract: Phylogenetic relationships within the rockfish genus *Sebastes* (Scorpaenidae) are not well understood. Study of variation in the structure of extrinsic gasbladder musculature within this group may help clarify understanding of evolutionary relationships. Eighty-two species of rockfishes were dissected for examination of gasbladder muscles. Possible evolutionary implications are discussed. The function of the gasbladder muscles is sound production, but they may also be used for sound reception.

Introduction

The rockfish genus *Sebastes*, of the family Scorpaenidae, contains approximately 100 species, ranging in size from about 200 mm. to 1000 mm. standard length as adults (Phillips, 1957; Eschmeyer and Hureau, 1971). Unlike most species of scorpionfishes which are tropical in distribution, rockfishes inhabit cold temperate seas. They are found principally in the North Pacific from Japan to Mexico, although a few species can be found in the North Atlantic and in the temperate Southern Hemisphere (Eschmeyer and Hureau, 1971). Fifty species of rockfishes may occur at a single latitude with up to 10 species occurring at a single collecting station. This high degree of congeneric sympatry

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is of interest to community ecologists studying division of resources and isolating mechanisms.

Although rockfishes are important to commercial and sports fisheries, little is known about their biology. All rockfishes are believed to be generalized large-mouthed carnivores. They vary from benthic hole-dwelling solitary species to schooling species that live off the bottom in the kelp canopy or in open water. They are ovoviparous, giving birth to large numbers of yolk-sac larvae (Moser, 1967).

Field observations made in 1970 by the author indicated that several species can be stimulated to produce sounds under stress. Recent work by McInerney and Yearsley (in press) shows that rockfishes produce sounds during agonistic encounters. The sound producing mechanism consists of a pair of muscles, one on each side of the midline, originating on the occipital portion of the cranium and inserting on the gasbladder. Gasbladder muscles of this sort were first called "extrinsic" by Dufosse (1874) because they inserted on the gasbladder at one end and elsewhere at the other end. Muscles with both points of insertion on the gasbladder wall, such as those found in triglids (Tower, 1908), were labeled by Dufosse as "intrinsic." In this paper, muscles originating on the cranium and inserting on or near the gasbladder will be called extrinsic gasbladder muscles or, simply, gasbladder muscles.

The first major work which described these gasbladder muscles for a variety of scorpaenid fishes was that of Matsubara (1943). All the scorpaenids dissected by Matsubara have some type of muscle associated with the gasbladder, although a variety of morphological patterns exist. For Oriental rockfishes, he showed that intrageneric variations in the structure of these muscles do exist. Dissections made on 82 species of rockfishes in the present study also reveal great variations in the patterns of the gasbladder muscles within *Sebastes*.

The species in the genus *Sebastes* are well known from several regional works (Matsubara, 1943; Phillips, 1957; Barsukov, 1964), but a worldwide review has not yet been attempted. One character that may be useful in an attempt to clarify phylogenetic relationships within this genus is the variation in the structure of the extrinsic gasbladder musculature.

As a result of the attempt to clarify the possible origin and evolution of the various rockfish muscle patterns, dissections were made on representatives from 23 other genera in the family Scorpaenidae and on fishes from 9 other families in the order Scorpaeniformes. The classification of groups within this order is uncertain (Greenwood *et al.*, 1966), and it is possible that an eventual overall survey of gasbladder musculature will aid in the understanding of phylogenetic relationships in the so-called mail-cheeked fishes.

Another character not surveyed in this study that may also prove useful in clarifying phylogenetic relationships within *Sebastes* is variability in gasbladder structure itself. The morphology of rockfish gasbladders appears to be diverse. Variability in the thickness of gasbladder walls, in attachment of the bladder, and in division of the bladder into two chambers is apparent (see also Matsubara, 1943, p. 126–147).

Acknowledgments

Specimens used in this study were obtained from a variety of sources. Eastern Pacific material came principally from the California Academy of Sciences fish collection, although some material was obtained from the collection at California State University at San Diego and the Scripps Institution of Oceanography. Western Pacific material came from the California Academy of Sciences fish collection and from the Museum of Zoology of the University of Michigan.

Field collections were made during the course of this study to provide fresh material. I wish to thank the following people for their aid: Dr. George W. Barlow of the University of California at Berkeley who first advised the author of sound production by rockfishes; Dr. John S. Stevens of Occidental College and the crew of the research vessel *Van Tuna*, who provided specimens from Catalina Island off southern California; Dr. Lo-chai Chen of California State University at San Diego and the Scripps Institution of Oceanography for supplying a boat for collections made off La Jolla, California; Dr. Tomio Iwamoto of the California Academy of Sciences, who collected specimens off British Columbia from the research vessel *G. B. Reed*; Dr. William N. Eschmeyer of the California Academy of Sciences, who collected specimens off the Oregon coast from the Oregon State University vessel *Yaquina*; Dr. Eschmeyer, Dr. Chen, Christopher Tarp, Frederick Jones, and Ernest W. Iverson, who assisted in making collections from sportfishing boats; David W. Behrens, Kenneth R. McKaye, and divers from the University of California at Berkeley Diving Program, who aided the author in netting and spearing shallow water species; Daniel J. Miller and Robert N. Lea of the California Department of Fish and Game, who donated specimens; Dr. Reeve M. Bailey, Dr. Robert R. Miller, and staff of the Museum of Zoology of the University of Michigan, who provided the assistance to Dr. William N. Eschmeyer which resulted in the loan of Oriental specimens from their University collection; Dr. John E. McInerney and Dr. John H. Yearsley for allowing me to read their manuscript on sound production by rockfishes.

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METHODS

In this paper the term gasbladder has been applied to the structure more commonly referred to as the airbladder or swimbladder. This follows the terminology suggested by Lagler, Bardach, and Miller (1962). Since the gasbladder in rockfishes is physoclistous (no duct connects the gasbladder to the alimentary canal) and inflated by means of a gas gland, the term gasbladder seems more appropriate than either alternative expression. In accordance with this terminology, any specialized muscles associated with the gasbladder have been referred to by this author as gasbladder muscles rather than the more commonly used 'swimbladder muscles'.

Extrinsic gasbladder muscles were exposed for examination by dissection. These muscles appear to have arisen from the ventral fibers of the epaxialis (the dorsal half of the lateral body musclature). All species have a pair of muscles, one on each side of the midline. They extend posteriorly from their origin on the occipital region of the cranium to the gasbladder or vertebral parapophyses where they insert by means of tendens. Since their position relative to skeletal structures is constant throughout the genus, one standard dissection technique was sufficient for all rockfish species and could be done with a scalpal and forceps. In preliminary dissections, the muscles from both sides of specimens were examined with no structural differences being observed. All subsequent dissections were made on the right side of specimens, with only the muscle on the right side being examined. A large patch of skin was removed, its perimeter extending along the rear of the cranium and pectoral girdle, posteriorly along the base of the spinous dorsal fin to its end, downward to the ventral half of the fish's side and forward to the pectoral fin axil.

All exposed muscle tissue lying dorsal to the right dorsal ribs was removed. The right gasbladder muscle was exposed to view by gently breaking away the dorsal ribs. Care was taken while removing the first two dorsal ribs since the gasbladder muscle lies just ventral to them. In most species of rockfishes the muscle passes between the second and third ventral ribs so that it is found on the visceral cavity side of the third through eighth ventral ribs.

Once the gasbladder muscle was exposed, all skeletal muscle tissue surrounding it was plucked away cautiously to expose the muscle from its point of origin on the cranium to its points of insertion on the gasbladder or vertebral parapophyses. The insertion points were determined by clearing away all intercostal muscle between the ventral ribs. Once the first eight or nine ribs were exposed, the dense tendon tissue of the gasbladder muscle was seen extending laterally just under the ribs. These whitish tendons were followed to their points of insertion on the vertebral parapophyses. In species where these tendons inserted first upon the gasbladder, an incision into the body cavity was made to examine posterior insertion sites.

Another method was sometimes used in species where the insertion points on the vertebral parapophyses were not readily determined from a dissection of lateral body musculature. The body cavity was entered from the ventral side and the viscera and the gasbladder were removed. Once the gasbladder was removed, the whitish tendons of the gasbladder muscle could be seen inserting on the vertebral parapophyses.

Dissections of other members of the order Scorpaeniformes were conducted in much the same manner since their gasbladder muscles were located in the same general area of the lateral skeletal musculature. The notable exceptions were members of the suborder Cottoidei. In species of this group, muscles termed "cranioclavical muscles" by Barber and Mowbray (1956) extend from the posterior cranium to the pectoral girdle. To expose these cranioclavical muscles, only musculature situated directly behind the cranium was removed.

At the onset of the study, radiographs were taken of dissected specimens to clarify the topographic relationships of the origin and insertion points of the extrinsic gasbladder musculature. Once the anatomy of these fishes became familiar, radiography was no longer required for the majority of species.

Specimens used in the study are listed in the appendix.

Results

Dissection of 82 species of rockfishes reveals considerable variation among species in gross morphology of the extrinsic gasbladder musculature. In species where both sexes were examined no sexual dimorphism was observed. Several insertion points may be listed for one muscle because of the fact that in most cases, the striated muscle tissue of the gasbladder muscle ends in one to several tendons after the muscle passes under the third rib. In several species, only one or two tendons develop from the muscle, but later branch to insert on several different vertebral parapophyses. Table 1 summarises origin and insertion points for the gasbladder muscles of all rockfishes examined.

Table 1. *Muscle type and points of insertion of the gasbladder muscle for all species of* Sebastes *examined. Where more than one specimen of a species was examined, the information on each specimen examined is listed. Abbreviations for the points of insertion are as follows: gb represents the gasbladder, r-1 thru r-4 represent the first through the fourth ventral ribs, and v-7 through v-11 represent the seventh through the eleventh vertebrae. Muscle category includes major type (either Type I or Type II) and the subdivision within a type: a-z =* aleutianus-zacentrus, *a-v =* atrovirens-vexillaris, *i-v =* ijimae-vulpes, *p =* paucispinis, *s =* serriceps, *t =* taczanowskii, *m =* marinus.

Species	Muscle Category	Points of Insertion									
		gb	r-1	r-2	r-3	r-4	v-7	v-8	v-9	v-10	v-11
aleutianus	I a-z						×	×	×		
alutus	I a-z			×		×	×	×			
"	I a-z			×		×	×	×	×		
auriculatus	I a-z							×	×	×	
"	I a-z							×	×	×	
"	I a-z							×	×	×	
aurora	I a-z			×		×	×				
atrovirens	II a-v	×						×	×	×	
"	II a-v	×						×	×	×	
babcocki	I a-z		×	×		×					
baramenuke	I a-z						×	×	×	×	
borealis	I a-z						×	×	×		
brevispinis	I a-z			×		×	×				
capensis	I a-z							×	×		
carnatus	II a-v	×						×	×	×	
caurinus	II a-v	×							×	×	
"	II a-v	×						×	×	×	
chlorostictus	I a-z						×	×	×		
chrysomelas	II a-v	×							×	×	
ciliatus	I a-z				×			×	×	×	
constellatus	I a-z						×	×	×		
crameri	I a-z						×	×	×		
dallii	I a-z			×				×	×		
"	I a-z						×	×	×		
diploproa	I a-z					×		×	×		
elongatus	I a-z			×			×	×	×		
emphaeus	I a-z									×	
"	I a-z						×	×	×		
ensifer	I a-z							×	×		
entomelas	I a-z								×	×	
eos	I a-z							×	×		
exsul	I a-z						×	×	×	×	
flameus	I a-z			×		×	×				
flavidus	I a-z						×		×	×	
gilli	I a-z					×	×	×			
glaucus *	I a-z							×	×	×	
goodei	I a-z		×	×	×						

* Not examined. Information from Matsubara (1943).

Table 1. *Continued*

Species	Muscle Category	Points of Insertion									
		gb	r-1	r-2	r-3	r-4	v-7	v-8	v-9	v-10	v-11
helvomaculatus	I a-z					×		×	×		
"	I a-z						×	×	×		
hopkinsi	I a-z								×	×	
hubbsi	I a-z							×	×		
ijimae	II i-v								×	×	
inermis	II i-v							×	×	×	×
"	II i-v							×	×	×	×
iracundus *	I a-z				×	×	×				
itinus *	I a-z							×	×	×	
jordani	I a-z			×		×					
joyneri	I a-z						×	×	×		
kawaradae *	I a-z				×		×	×	×		
lentiginosus	I a-z						×	×	×		
levis	I a-z		×	×			×	×	×		
longispinis	I a-z							×	×	×	
macdonaldi	I a-z		×	×	×	×	×	×	×		
maliger	II a-v	×							×	×	
"	II a-v	×							×	×	
marinus	I m				×			×	×	×	
"	I m							×	×	×	×
"	I m								×	×	×
matsubarae	I a-z			×	×		×	×	×	×	
melanops	I a-z						×	×	×		
melanostictus *	I a-z				×		×	×	×		
melanostomus	I a-z		×	×			×	×	×		
"	I a-z						×	×	×		
miniatus	I a-z						×	×	×		
mystinus	I a-z					See Table 2					
nebulosus	II a-v	×						×	×		
nigrocinctus	I a-z			×	×		×				
nivosus	II i-v								×	×	
oblongus	II i-v							×	×		
ovalis	I a-z						×	×	×	×	
owstoni	I a-z			×	×			×			
pachycephalus	II i-v							×	×	×	
paucispinis	II p	×								×	
"	II p	×								×	
phillipsi	I a-z					×	×				
pinniger	I a-z						×	×	×	×	
proriger	I a-z					×		×	×	×	
rastrelliger	I a-z							×	×		
reedi	I a-z					×	×	×	×		
rosaceus	I a-z							×	×	×	
rosenblatti	I a-z					×	×	×			

* Not examined. Information from Matsubara (1943).

TABLE 1. *Continued*

Species	Muscle Category	gb	Points of Insertion								
			r-1	r-2	r-3	r-4	v-7	v-8	v-9	v-10	v-11
ruberrimus	I a-z						×	×	×	×	
rubrivinctus	I a-z			×	×	×	×				
rufus	I a-z						×	×	×	×	
saxicola	I a-z			×		×	×				
schlegelii	II i-v								×	×	×
"	II i-v								×	×	×
scythropus	I a-z				Points of insertion decayed						
serranoides	I a-z					×	×	×			
serriceps	I s			×			×				
simulator	I a-z							×	×		
sinensis	I a-z							×	×		
steindachneri	I a-z									×	×
taczanowskii	II t	×							×	×	×
thompsoni	II i-v						×	×	×		
trivittatus	II i-v								×	×	×
umbrosus	I a-z						×	×	×		
variegatus	I a-z						×	×	×	×	
vexillaris	II a-v	×							×	×	
vulpes	II i-v							×	×		
wakiyai *	I a-z						×			×	×
wilsoni	I a-z								×	×	
zacentrus	I a-z							×	×	×	
"	I a-z							×	×	×	

* Not examined. Information from Matsubara (1943).

For the purpose of determining the extent of variation within a species, dissections were done on 17 specimens of the blue rockfish, *Sebastes mystinus.* These dissections revealed only slight variations in the size and shape of the extrinsic gasbladder muscles, but they did indicate great intraspecific variation in posterior insertion points (table 2). No apparent sexual dimorphism was found. The size range of this series, consisting of eight males and nine females, was 70 mm. to 376 mm.

On the basis of morphological variations, two basic divisions in gasbladder muscle structure are recognized for the genus *Sebastes.* These divisions have arbitrarily been designated Type I and Type II. Type I consists of all muscle variations that attach firmly to the pectoral girdle as they pass posteriorly from their origin on the occipital cranium to their points of insertion on the vertebrae (fig. 1). Type II is comprised of muscle variations that *bypass* the pectoral girdle as they pass posteriorly from their origin on the occipital cranium to their points of insertion on the gasbladder or vertebrae (fig. 2). Each division is further subdivided into subtypes on the basis of additional structural variations.

Table 2. *Muscle type and points of insertion of the gasbladder muscle for 17 specimens of the blue rockfish,* Sebastes mystinus. *Sex and standard length (S.L.) are listed for each specimen. Abbreviations for the points of insertion are the same as in table 1.*

			Points of Insertion							Points of Insertion			
Sex	S.L.	Muscle	v-7	v-8	v-9	v-10	Sex	S.L.	Muscle	v-7	v-8	v-9	v-10
♂	222 mm.	I a-z			×	×	♀	112 mm.	I a-z			×	×
♂	231 mm.	I a-z		×	×	×	♀	157 mm.	I a-z			×	×
♂	251 mm.	I a-z		×	×	×	♀	191 mm.	I a-z			×	×
♂	258 mm.	I a-z			×	×	♀	264 mm.	I a-z	×	×	×	
♂	260 mm.	I a-z				×	♀	265 mm.	I a-z				×
♂	267 mm.	I a-z		×	×	×	♀	294 mm.	I a-z			×	×
♂	275 mm.	I a-z		×	×		♀	342 mm.	I a-z			×	×
♂	289 mm.	I a-z			×	×	♀	376 mm.	I a-z			×	
♀	70 mm.	I a-z		×	×	×							

Type I contains three subdivisions that are nominally denoted: aleutianus-zacentrus, serriceps, and marinus. Type II contains four subdivisions: paucispinis, ijimae-vulpes, atrovirens-vexillaris, and taczanowskii.

Subdivision nomenclature was determined by simply listing all species with a particular type of musculature in alphabetical order. The first and last species names on the list were taken to denote the subdivision name for that particular muscle type. Hence, the aleutianus-zacentrus subdivision is the pattern in all species in alphabetical order from *Sebastes aleutianus* through *Sebastes zacentrus* that possess dorsoventrally flattened muscles, originating on the cranium, attaching to the cleithrum, and inserting on the vertebral parapophyses. Four of the subdivisions are found in only one species each, so only one species name is listed for each of these four systems.

TYPE I

All species with musculature of this major category have extrinsic gasbladder muscles that attach firmly to the pectoral girdle as the muscles pass posteriorly from their origin on the occipital cranium to their insertion points on the vertebral parapophyses. Subdivisions of this major category have been formed on the basis of additional structural variations.

ALEUTIANUS-ZACENTRUS SUBDIVISION. This was the basic muscle structure found in the genus *Sebastes* with 62 of the 82 species dissected having this morphology. (See fig. 1A). Unlike some of the other muscle types which are found only in one geographic region, this type occurred in species taken throughout the geographic range of the genus.

The gasbladder muscles of this group are dorsoventrally flattened with the point of origin being the cranium. The specific site of attachment to the cranium is only slightly variable, and is usually around the exoccipital-opisthotic suture,

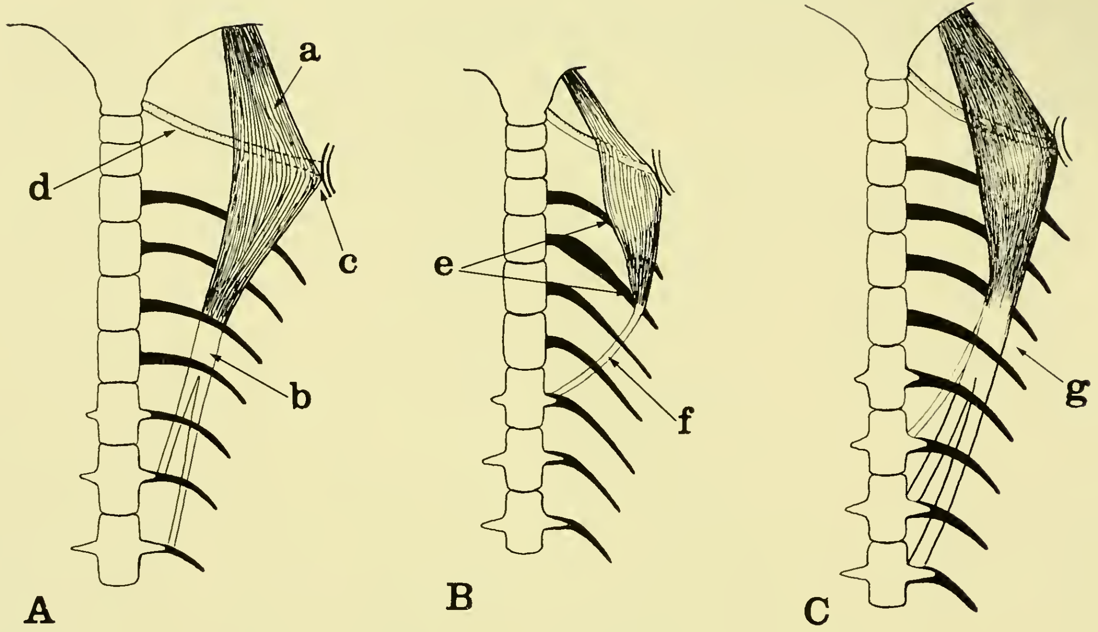

Figure 1. *Sebastes* Type I gasbladder muscles (right side only) showing characteristic attachment to the pectoral girdle as the muscles pass posteriorly from their origin on the occipital cranium to their insertion on the ribs or vertebrae. The tendons do not attach to the gasbladder in these subtypes. A: Dorsal view of aleutianus-zacentrus subtype vertebral column and gasbladder muscles showing (a) striated muscle portion, (b) tendon portion, (c) attachment to pectoral girdle, and (d) Baudelot's ligament. Drawing made from *Sebastes rastrelliger*, 198 mm. standard length. B: Dorsal view of serriceps subtype showing (e) attachment of striated muscle to the ribs, and (f) the single tendon inserting on the parapophysis of the seventh vertebrae. Drawing made from *Sebastes serriceps*, 251 mm. standard length. C: Dorsal view of marinus subtype showing (g) muscle passing between the third and fourth ribs as opposed to between the second and third ribs in all other 81 species of *Sebastes* dissected. Drawing made from *Sebastes marinus*, 205 mm. standard length.

although in some species the attachment site seems wholly on one or the other of these two bones, or on the opisthotic. As the muscle passes posteriorly, some of its fibers attach to the supracleithral bone near the distal attachment site of Baudelot's ligament. Insertion by tendons occurs on the ribs or vertebral parapophyses.

The points of insertion, which tend to vary interspecifically, are listed in table 1 for all 62 species included in this muscle category. Unless otherwise stated in table 1, only one specimen of each species was dissected. The species of *Sebastes* examined, listed alphabetically, are as follows: *aleutianus*, *alutus*, *auriculatus*, *aurora*, *babcocki*, *baramenuke*, *borealis*, *brevispinis*, *capensis*, *chlorostictus*, *ciliatus*, *constellatus*, *crameri*, *dallii*, *diploproa*, *elongatus*, *emphaeus*, *ensifer*, *entomelas*, *eos*, *exsul*, *flameus*, *flavidus*, *gilli*, *goodei*, *helvomaculatus*, *hopkinsi*, *hubbsi*, *jordani*, *joyneri*, *lentiginosus*, *levis*, *longispinis*, *macdonaldi*, *matsubarae*, *melanops*, *melanostomus*, *miniatus*, *mystinus*, *nigrocinctus*, *ovalis*, *owstoni*, *phillipsi*, *pinniger*, *proriger*, *rastrelliger*, *reedi*, *rosaceus*, *rosenblatti*, *ruberrimus*, *rubrivinctus*, *rufus*, *saxicola*, *scythropus*, *serranoides*, *simulator*, *sinensis*, *steindachneri*, *umbrosus*, *variegatus*, *wilsoni*, and *zacentrus*.

Species of *Sebastes* dissected by Matsubara (1943) possessing this type of musculature are as follows: *baramenuke*, *flameus*, *hubbsi*, *longispinis*, *matsubarae*, *owstoni*, *scythropus*, and *steindachneri*; plus those examined by Matsubara but not by the author (Matsubara's results are included in table 1): *glaucus*, *iracundus*, *itinis*, *kawaradae*, *melanostictus*, and *wakijai*.

SERRICEPS SUBDIVISION. This muscle arrangement is found only in the treefish, *Sebastes serriceps*, an eastern Pacific species. The gasbladder muscles of this species are very similar to those of the aleutianus-zacentrus subdivision, being dorsoventrally flattened muscles with the point of origin on the cranium. As the muscles in this species pass posteriorly, a portion of the muscle fibers attach to the supracleithral bone. The mode of insertion of the gasbladder muscles in *S. serriceps* is however quite different from that found in the species listed in the aleutianus-zacentrus group. In the treefish, the posterior margin of the gasbladder muscle inserts primarily on the second rib, without first becoming a tendon. Careful examination revealed one small tendon coming off the muscle that passed between the second and third ventral ribs and inserted to the parapophysis of the seventh vertebra (see fig. 1B).

MARINUS SUBDIVISION.[1] The extrinsic gasbladder muscles of *Sebastes marinus* are similar in overall structure to those found in the aleutianus-zacentrus group (fig. 1C). Each muscle originates on the occipital region of the cranium and attaches to the pectoral girdle as it passes posteriorly to insert by means of tendons to the vertebral parapophyses. The major difference between this species and all other rockfishes is that the muscle crosses between the third and fourth

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[1] See addendum.

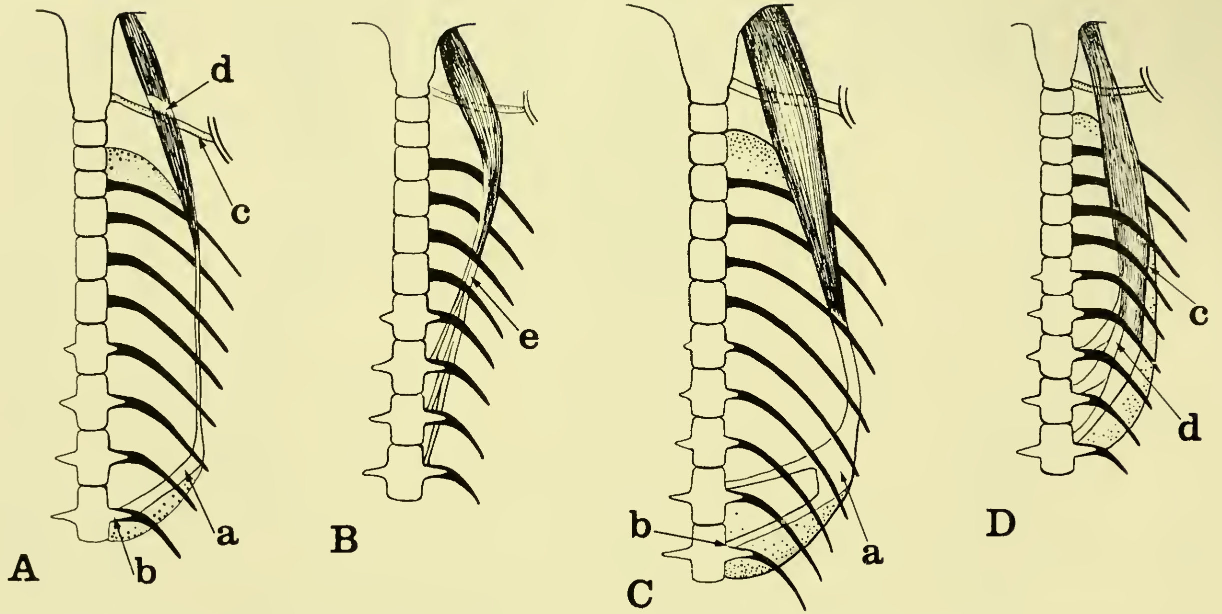

FIGURE 2. *Sebastes* Type II gasbladder muscles (right side only) showing the characteristic bypass of the pectoral girdle as the muscles pass posteriorly from their origin on the occipital cranium to their insertion on the vertebrae or gasbladder. A: Dorsal view of paucispinis subtype vertebral column and gasbladder muscle showing (a) the single tendon's attachment to the gasbladder, (b) the insertion of this tendon to the parapophysis of the tenth vertebra, (c) Baudelot's ligament, and (d) fascia that divides the striated muscle tissue into two parts. Drawing made from *Sebastes paucispinis*, 259 mm. standard length. B: Dorsal view of ijimae-vulpes subtype showing (e) the tendon portion that inserts on the vertebrae. No attachment to the gasbladder in these species. Drawing made from *Sebastes vulpes*, 161 mm. standard length. C: Dorsal view of atrovirens-vexillaris subtype showing (a) the attachment of the tendon portion to the gasbladder, and (b) insertion of the tendons to the vertebral parapophyses. Drawing made from *Sebastes caurinus*, 330 mm. standard length. D: Dorsal view of taczanowskii subtype showing (c) the attachment of the striated muscle tissue directly to the gasbladder, and (d) the three short tendons that insert to the parapophyses of the ninth, tenth, and eleventh vertebrae. Drawing made from *Sebastes taczanowskii*, 122 mm. standard length.

ventral ribs as it passes posteriorly towards the vertebrae, instead of passing between the second and third ventral ribs as in all other rockfish species examined. See table 1 for points of insertion in all *Sebastes marinus* dissected.

Type II

All species having muscular of this major category have extrinsic gasbladder muscles that *bypass* the pectoral girdle as the muscles pass posteriorly from their origin on the occipital cranium to their insertion points on the gasbladder or vertebral parapophyses. The muscles of this category tend to be more massive and cylindrical than those of the Type I category. Subdivisions of this Type II category are delineated by the author on the basis of additional structural variations.

PAUCISPINIS SUBDIVISION. This muscle arrangement is found only in the bocaccio, *Sebastes paucispinis*, an eastern Pacific species. In this species the gasbladder muscles have the point of origin on the cranium. As the muscles pass posteriorly, they do not make a connection with the pectoral girdle. This species, unlike any others in the genus, has the striated muscle tissue of the gasbladder muscles divided into two parts by a thin fascia (fig. 2A). The gasbladder muscles insert, each by means of a single tendon, on the posterior portion of the gasbladder. This tendon, while firmly fastened to the gasbladder wall, curves dorsally to anchor the gasbladder to the parapophysis of the tenth vertebra.

IJIMAE-VULPES SUBDIVISION. The gasbladder muscle pattern included in this group was found in nine species, all from the Orient. In these fishes, as in the rest of the genus, the extrinsic gasbladder muscles have the area of origin on the cranium, near the suture of the opisthotic and exoccipital. Like the muscles found in *Sebastes paucispinis*, these do not make a connection to the pectoral girdle as they pass posteriorly. The muscles have a striated portion that is slightly more massive than those described in previous groups. They are not quite as broad as the dorsoventrally flattened muscles of the aleutianus-zacentrus or serriceps subdivisions, but are of greater girth, being more cylindrical in shape. They appear to insert by tendons to the vertebral parapophyses without first attaching to the gasbladder (fig. 2B). Points of insertion for all species in this group are listed in table 1. The species of *Sebastes* falling into this group are as follows: *ijimae*, *inermis*, *nivosus*, *oblongus*, *pachycephalus*, *schlegeli*, *thompsoni*, *trivittatus*, and *vulpes*.

ATROVIRENS-VEXILLARIS SUBDIVISION. The muscles of this grouping and the next (taczanowskii subdivision) are the largest in the genus *Sebastes*. These gasbladder muscles originate on the cranium. As they pass posteriorly they do not make a connection to the pectoral girdle. They insert as tendons that attach firmly to the gasbladder before swinging up and attaching to the vertebral parapophyses (figs. 2C and 3). In several of the species, one of the two tendons

Figure 3. Right extrinsic gasbladder muscle of atrovirens-vexillaris subtype (*Sebastes* Type II) showing (a) the large cylindrical striated muscle band, and (b) the attachment of the muscle tendons to the side of the gasbladder. Photograph is of copper rockfish, *Sebastes caurinus*, 250 mm. standard length.

initially attaching to the gasbladder diverges so that three tendons are firmly attached to the gasbladder wall and anchor the gasbladder to three vertebral parapophyses. Points of insertion for all species in this group are listed in table 1. The species of *Sebastes* characterized by this muscle pattern are as follows: *atrovirens, carnatus, caurinus, chrysomelas, maliger, nebulosus,* and *vexillaris.*

TACZANOWSKII SUBDIVISION. This type is represented by one species, *Sebastes taczanowskii,* an Oriental form. It is much like that of the previous group (atrovirens-vexillaris) except that the muscle attaches to the gasbladder wall as muscle rather than as tendon. Originating on the cranium, the muscle passes posteriorly to attach to the outer wall of the gasbladder. No connection to the pectoral girdle occurs. While connected to the gasbladder, the muscle passes posteriorly along the gasbladder to a point approximately under the sixth rib where it then diverges to form three tendons. These three tendons, while firmly attached to the gasbladder wall, curve dorsally to anchor the gasbladder to the parapophyses of the ninth, tenth, and eleventh vertebrae (fig. 2D).

Other Scorpaeniform Dissections

Dissection of specimens from 23 other genera within the family Scorpaenidae and nine other families within the order shows many to have muscles similar to the extrinsic gasbladder muscles found in the genus *Sebastes.* As might be expected, the highest degree of similarity in structure of these muscles occurs within families, but general similarity in structure does occur even between some families in different suborders, as is the case of the first group listed below. Dissections of scorpaeniform representatives were made primarily for general comparison and were not as precise as those done on rockfish specimens.

Muscle types similar to *Sebastes* Type I. All fishes placed in this group have two lateral muscles similar in structure to those found in Type I muscles as defined for the genus *Sebastes.* This structural form is the most widespread and common in the order, being predominant in four of the five suborders examined. The notable exceptions were members of the suborder Cottoidei.

The species listed below possess muscles that are dorsoventrally flattened like those in the *Sebastes* Type I category. These muscles, like those in the rockfish group have the point of origin on the occipital cranium. As the muscles pass posteriorly, they make a connection with the pectoral girdle. The points of insertion in all cases appeared to be the vertebral parapophyses. Unless the precise points of insertion were determined, however, species in the group are simply listed. The species examined are as follows:

Scorpaenidae: *Ectreposebastes imus*; *Gymnapistes marmoratus*; *Helicolenus dactylopterus*; *Inimicus cuvieri*; *Iracundus signifer*; *Minous monodactylus*; *Minous pictus*; *Neomerinthe beanorum*; *Parascorpaena* species; *Plectrogenium nanum*;

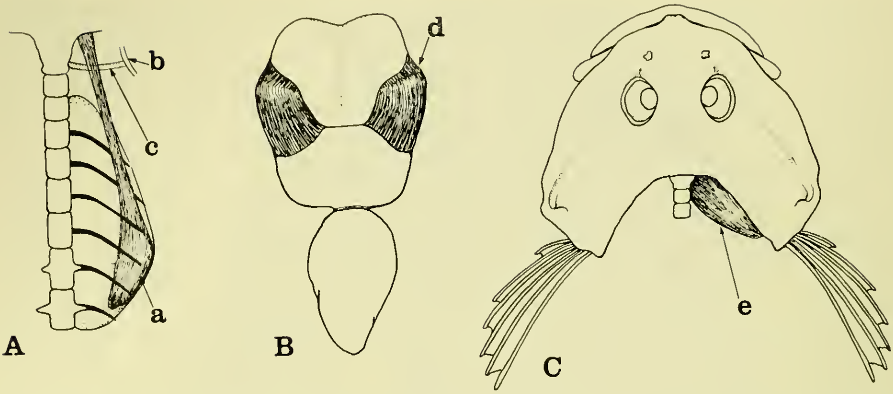

Figure 4. Other types of gasbladder musculature found in the order Scorpaeniformes. A: Dorsal view of the right extrinsic gasbladder muscle of *Sebastiscus marmoratus* showing (a) the broadened striated muscle tissue that inserts directly onto the gasbladder, (b) the pectoral girdle, and (c) Baudelot's ligament. This muscle system is similar in morphology to the *Sebastes* Type II muscles. Drawing from specimen 131 mm. standard length. B: Dorsal view of gasbladder from *Apistes* species showing (d) the fully intrinsic muscle tissue on the anterior lobe of the gasbladder. Drawing made from specimen 109 mm. standard length. C: Dorsal view of right cranioclavical muscle in *Cottus asper* showing (e) the short striated muscle band. Drawing from specimen 110 mm. standard length.

Pontinus longispinis; *Scorpaena agassizi*, *Scorpaena albobrunnea*, *Scorpaena brasiliensis*, *Scorpaena elongata*, *Scorpaena guttata*, *Scorpaena mystes*, *Scorpaena porcus*, and *Scorpaena russula*, all with four tendons, one attaching to each of the parapophyses of the sixth, seventh, eighth, and ninth vertebrae; *Scorpaenopsis* species; *Sebastosemus* species; *Setarches longimanus*; *Synanceia verrucosus.*
Hexagrammidae: *Hexagrammos decagrammus*
Platycephalidae: *Platycephalus* species
Hoplichthyidae: *Hoplichthys langsdorfi*

Muscle types similar to *Sebastes* Type II (taczanowskii subdivision). The species listed in this group have two large gasbladder muscles similar in overall structure to the muscle system listed for *Sebastes taczanowskii.* These muscles are in most cases rather large and cylindrical, originating on the occipital portion of the cranium and inserting usually on the bladder (fig. 4A). No connection to the pectoral girdle occurs. Species listed below are from the family Scorpaenidae. Once again, dissections were not as exact as for the genus *Sebastes*, and precise posterior attachment sites were not exactly determined. The species listed in this group are as follows:

Scorpaenidae: *Brachypterois serrulifer*, *Dendrochirus zebra*, *Macroscorpius pallidus*, *Scorpaenodes parvipinnis*, *Pterois radiata*, *Sebastiscus marmoratus*, *Setarches guentheri.*

Intrinsic Gasbladder Muscles

Dissections revealing gasbladders containing fully intrinsic gasbladder muscles were made on two species, *Leptotrigla alata* (Triglidae) and *Apistes* species (Scorpaenidae). Intrinsic gasbladder muscles have been widely examined in triglids (Tower, 1908; Fish, 1954; Tavolga, 1964; Evans, 1973), and Matsubara (1943) in his review of Japanese scorpaenids reported intrinsic musculature for *Apistes carinatus*. Figure 4B is a diagram of an *Apistes* gasbladder.

Cranioclavical Muscle Systems

The muscles of this group, found in members of the suborder Cottoidei, are stout cylindrical muscles connecting the pectoral girdle to the occipital region of the skull (fig. 4C). The point of attachment to the skull seems to correspond to the point of attachment of the extrinsic gasbladder muscles described for scorpaenids. Likewise, the point of attachment to the pectoral girdle seems to correspond to that in the scorpaenids. Species dissected are as follows:

Zaniolepididae: *Zaniolepis latipinnis*
Cottidae: *Clinocottus analis*, *Cottus asper*, *Hemilepidotus jordani*, *Leptocottus armatus*, *Myoxocephalus quadricornis*, *Scorpaenichthys marmoratus*
Cottuniculidae: *Cottunculus thompsoni*
Agonidae: *Occella verrucosa*
Cyclopteridae: *Liparis florae*.

Discussion

Taxonomic value of gasbladder muscle systems. In all rockfish species examined, only one mode of origin for the gasbladder muscles was observed, that being on the occipital region of the cranium. In some species fibers of the striated muscle tissue attached to the supracleithral bone as the gasbladder muscles passed posteriorly, while in others no such attachment occurred. Two major muscle categories were recognized on the basis of the presence (Type I) or absence (Type II) of a pectoral girdle attachment. A total of seven subdivisions were recognized, three for Type I and four for Type II, on the basis of additional structural variations.

Because of the high degree of intraspecific variability (see table 2) and interspecific overlap in insertion sites (see table 1), these muscles were in most cases not useful in species delineations. However, of the 82 species examined, four had unique muscle types. These species are *Sebastes serriceps*, (Type I), *S. marinus* (Type I), *S. paucipinis* (Type II), and *S. taczanowskii* (Type II), and could easily be separated from other species on the basis of the morphology of their gasbladder muscles.

The use of these various muscle types in conjunction with other characters as a means of delineating subgenera seems in some instances useful. For example, in the eastern Pacific subgenus *Pteropodus*, all species with the exception of one, had gasbladder muscles that were found only in this small group (*atrovirens-vexillaris* subdivision of Type II). Muscle morphology seems to support the subgeneric classification for the *Pteropodus* group. The one species in the *Pteropodus* complex that did not possess an atrovirens-vexillaris muscle system was *S. rastrelliger.* It had instead the more common aleutianus-zacentrus bladder muscles (Type I). Workers dealing with phylogenetic relationships in *Sebastes* should perhaps consider separating *S. rastrelliger* from the other species (*S. atrovirens*, *S. carnatus*, *S. caurinus*, *S. chrysomelas*, *S. maliger*, *S. nebulosus*, and *S. vexillaris*) in this group.

Two species of the subgenus *Sebastodes*, *S. brevispinis* and *S. paucispinis*, which are usually considered to be closely related, have major differences in the structure of the gasbladder musculature. *Sebastodes brevispinis* has the aleutianus-zacentrus muscles (Type I), and *S. paucispinis* (Type II) possesses a unique form. These species seem to occur in similar habitats, so their general similarity may indicate ecological convergence from different ancestral lines.

The considerations given to the taxonomy of eastern Pacific subgenera in this section are in fact only brief speculations. Rearrangement of eastern Pacific subgenera lies far beyond the scope of this paper. Speculations about Oriental subgenera were completely omitted due to insufficient numbers of dissections on Japanese forms. It is probable that other workers, correlating the structure of gasbladder muscles with a variety of other taxonomic characters, will find the morphology of these gasbladder muscles useful in phylogenetic studies on the rockfish genus *Sebastes*.

ORIGIN AND EVOLUTION OF GASBLADDER MUSCULATURE WITHIN THE GENUS *SEBASTES*. In the course of a study in which one particular character is reviewed throughout a group, it is worthwhile to give consideration to the possible evolutionary origin and diversification of the structure concerned. The first worker to extensively examine the extrinsic gasbladder musculature of scorpaenids was Matsubara (1943). His hypothesis concerning the successive changes of the muscle bands was that ". . . the existence of well developed muscle is a primitive feature in the scorpaenoid fish." Matsubara speculated that species such as *Sebastes taczanowskii* possessing well developed extrinsic gasbladder muscles represented the ancestral muscle condition. Conversely, species having muscles small in size and connected posteriorly to the axial skeleton by tendons as in the aleutianus-zacentrus subdivision were thought by him to possess the more recent evolutionary structure.

It is possible that these structures may have followed a mode of evolutionary differentiation opposite to that shown by Matsubara. This speculation is based upon the preponderance of small gasbladder muscles throughout the order.

If one assumes that the structural condition of the gasbladder muscle occurring most frequently in these rockfishes is the type most likely to be the primitive state for the genus, then the Type I division, found in 62 of the 82 species examined, is representative of the ancestral condition for the genus. The gasbladder muscles in these species are dorsoventrally flattened, originating on the cranium, passing posteriorly to make a strong attachment to the pectoral girdle, and finally inserting by tendons to ribs or vertebrae. The other structural variants (Type II) which occurred much less frequently are probably derived states.

However, another interpretation of the widespread occurrence of the Type I muscle pattern is that this pattern arose originally from one of the less frequently occurring patterns. This seems unlikely, though, in view of the widespread occurrence of this Type I pattern throughout the rest of the family. A total of 24 species belonging to 15 genera in the family Scorpaenidae also display a similar structural condition. This suggests that the pattern did not arise in the genus *Sebastes* and that it is the primitive condition for the family.

The selective pressures that have caused this divergence of gasbladder muscle structure within the rockfishes are unknown. The work of McInerney and Yearsley (in press) indicates that rockfishes possessing the smaller gasbladder muscles that attach only to the ribs or vertebrae produce sounds that are very similar to those produced by rockfishes possessing the larger gasbladder muscles that attach directly to the gasbladder. In light of this information it does not seem probable that selection for increased sound producing ability was an important evolutionary force involved in the divergence of gasbladder muscles within this lineage, although it may have been an important factor in the general elongation of gasbladder musculature in this group. What factors were involved in their subsequent divergence is a question open to speculation.

SPECULATIONS ON THE ORIGIN AND EVOLUTION OF GASBLADDER MUSCULATURE WITHIN THE ORDER SCORPAENIFORMES. It is of interest to look beyond the generic level to speculate on the possible stages of evolution of gasbladder musculature within the order Scorpaeniformes. The muscle pattern of most widespread occurrence in the genus *Sebastes* and the family Scorpaenidae is that in which the muscles are dorsoventrally flattened, inserting on the vertebrae by tendons. This muscle pattern (similar to the *Sebastes* Type I) is found in four of the six suborders recognized by Greenwood *et al.* (1966) for the order Scorpaeniformes. Again if one assumes that the structural condition of the gasbladder muscles that occurs most frequently in this group is the type most likely to be the primitive state for the order, then the dorsoventrally flattened muscles that insert to ribs of vertebrae by tendons are representative of the ancestral condition for the order.

A muscle condition exists within the order, however, that complicates the picture somewhat. All species examined from the suborder Cottoidei were found to possess lateral musculature different in structure from the long gasbladder muscles found in other scorpaeniform fishes. They possess, instead, two stout cylindrical muscles that originate on the occipital portion of the cranium and insert on the pectoral girdle. These structures were referred to by Barber and Mowbray (1956) as cranioclavical muscles (fig. 4c), and these workers demonstrated that sounds are produced when these structures are vibrated. The points of attachment to the cranium and pectoral girdle are similar to those points of attachment of gasbladder muscles in scorpaenids. Both systems seem to have evolved from modifications of the ventral fibers of the epaxialis, the dorsal half of the lateral body musculature. Homologies between the cranioclavical muscles of cottoids and the elongate muscles of other scorpaeniform fishes are not clear.

A variety of possible evolutionary schemes can be envisioned to explain possible differences between cottoid musculature and that found in other scorpaeniform groups. For example, the members of the suborder Cottoidei may have retained muscles similar to original ancestoral structures from which other scorpaeniform groups eventually developed elongate gasbladder muscles. What selection pressures might be involved in this process of muscle elongation are not clear. Perhaps the lengthening of lateral musculature increased mobility of the pectoral girdle in scorpaenidlike fishes, aiding them in movements associated with swimming or moving around on the bottom. After this primary elongation, the gasbladder muscles in some species increased in size possibly to become efficient sound-producing structures.

It is possible, however, that the situation may have been the opposite. The loss of the gasbladder in members of the suborder Cottoidei suggests that they may be derived forms. Perhaps cottoid ancestors once possessed elongate gasbladder muscles similar to those in scorpaenids. With the loss of the gasbladder, this group of benthic fishes may have evolved a modified pair of muscles that are in some way adaptive to a benthic existence. This picture, in which cottids evolved from a scorpaenoid ancestor, coincides with that proposed by Quast (1965) on the basis of osteological evidence.

Another possibility is that the common ancestor of cottoids and scorpaenids had some sort of gasbladder musculature different from that found in either of the present-day groups. It is also possible that this major difference in gasbladder musculature between the cottoids and the scorpaenids reflects different phylogenetic origins for these two groups. In any event, the picture is at present hazy, and none of the previous hypotheses can be firmly defended. For the present this author must agree with the views expressed by Greenwood *et al.* (1966) and Gosline (1971). The former stated, "The scorpaeniform fishes represent a more or less typical example of the work that needs still to be done.";

the latter, "The classification of the group appears to be in an advanced state of confusion."

Function of the extrinsic gasbladder muscle in *Sebastes*. The function of extrinsic and intrinsic gasbladder musculature in a wide variety of fish groups is that of sound production. Two review papers covering sound-producing mechanisms in fishes are those by Tavolga (1971) and Courtenay (1971).

The morphology of extrinsic gasbladder musculature in rockfishes suggests that most species are probably capable of producing sounds. Sound production has been reported for the western Pacific species, *Sebastes schlegeli* (Protasov *et al.*, 1965). Sounds have recently been recorded and analyzed for nine eastern Pacific forms, *Sebastes caurinus*, *S. flavidus*, *S. maliger*, *S. melanops*, *S. mystinus*, *S. nebulosus*, *S. nigrocinctus*, and *S. paucispinis* (McInerney and Yearsley, in press). These workers found that sounds were commonly produced during agonistic encounters between conspecifics, both in the laboratory and under natural conditions in the field. This author has heard sounds produced in the field by *Sebastes atrovirens*, *S. carnatus*, *S. caurinus*, *S. chrysomelas*, and *S. nebulosus*, but only under unnatural conditions of stress.

The morphology of gasbladder musculature in several other scorpaenid species suggests that these fishes may also produce sounds. Sound production has been reported in *Sebastiscus marmoratus* (Dotu, 1951), a species which possesses extrinsic gasbladder muscles that originate on the occipital region of the cranium and insert upon the swimbladder wall (fig. 4A).

The gasbladder muscles of rockfishes and other scorpaenids may also aid in sound reception. This seems possible in view of the large otoliths possessed by rockfishes, as well as the origin of the gasbladder muscles on the cranium in the general proximity of the otoliths. Whether rockfishes are receptive to sounds is not known at this time, and work remains to be done in this regard.

Possible ecological significances of sound production. Field observations made by the author indicate that some species of the subgenus *Pteropodus* are territorial at least part of the year, unlike other rockfishes occurring sympatrically. These species are usually solitary although field observations by the author suggests that they aggregate in pairs or small intraspecific groups during certain times of the year. The work of McInerney and Yearsley (in press) indicates that these territorial, hole-dwelling fishes, which possess the large Type II atrovirens-vexillaris gasbladder muscles (see figs. 2C and 3), produce sound during territorial defense, and as a fright response. Such uses of sound have been demonstrated for squirrelfishes (Winn and Marshall, 1963; Bright, 1972), and toadfishes (Gray and Winn, 1961; Winn, 1964, 1967).

Sounds produced by rockfishes might be species-specific and thus serve as isolating mechanisms between sympatric species. A high degree of congeneric sympatry exists among rockfishes, with as many as 10 species being captured at one collecting station. One method used in species isolation might be species-specific sound emissions. The work of McInerney and Yearsley indicates that this is possible, but interestingly, they found that structurally similar species produce sounds that appear to be indistinguishable from each other. Additional audio-isolation studies by species of *Sebastes* would be valuable.

SUMMARY

Rockfishes from the large scorpionfish genus *Sebastes* have been studied only regionally. One morphological feature that may prove useful for clarification of phylogenetic relationships within *Sebastes* is variation in the structure of extrinsic gasbladder musculature. Eighty-two species of rockfishes were dissected for examination of their gasbladder muscles. For the purpose of clarifying gasbladder muscle relationships within the genus, dissections were made on representatives from 23 other genera in the family Scorpaenidae, and fishes from 9 other families in the order Scorpaeniformes.

Dissections revealed considerable intrageneric variation in gross morphology of the extrinsic gasbladder musculature. On the basis of these structural variations, two major structural divisions in gasbladder musculature have been recognized for the rockfish genus *Sebastes,* and have been designated Type I and Type II. Type I have been divided into 3 subdivisions (aleutianus-zacentrus, serriceps, and marinus) and Type II has been divided into 4 subdivisions, (paucispinis, ijimae-vulpes, atrovirens-vexillaris, and taczanowskii).

In most cases these muscles were not especially useful for characterizing species because of a high degree of intraspecific variability and interspecific overlap in insertion sites. However, four species (*Sebastes marinus*, *S. paucispinis*, *S. serriceps*, and *S. taczanowskii*) had species-specific gasbladder musculature, and therefore could be separated from other rockfish species on the basis of morphology of their gasbladder muscles.

Delineations of subgenera through the use of the various muscle types is in most cases not practical since the muscle patterns exhibit considerable overlap between proposed subgenera. However, in the case of the subgenus *Pteropodus*, gasbladder muscles morphology supports the subgeneric classification of this group.

Within the genus *Sebastes* the presence of large cylindrical gasbladder muscles may represent the more recent evolutionary condition. Conversely, the small dorsoventrally flattened gasbladder muscles found most commonly are probably more representative of the ancestral form for the genus. Possible explanations for the occurrence of cranioclavical muscles in fishes of the suborder Cottoidei are discussed.

The function of the large cylindrical gasbladder muscles found in several

rockfish species seems to be primarily for the production of sound (McInerney and Yearsley, in press). Gasbladder muscles may also be used for sound reception.

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Appendix

Specimens examined in the course of this study are listed below by family. Abbreviations of depositories of specimens are as follows: CAS—California Academy of Sciences, San Francisco, California. BC—University of British Columbia, Vancouver, B.C. UMMZ—University of Michigan Museum of Zoology, Ann Arbor, Michigan. SIO—Scripps Institution of Oceanography, La Jolla, California. SU—Stanford University, collection now incorporated in the CAS collection. ZMK—Zoologisk Museum, Copenhagen, Denmark. The number of specimens examined from a particular lot and standard length in mm. are given in parentheses.

ORDER SCORPAENIFORMES

SCORPAENIDAE

Sebastes

aleutianus: CAS 15271 (1 specimen, 410 mm.), British Columbia, Vancouver Island, 10 September 1972.

alutus: CAS 15314 (1, 227), British Columbia, Vancouver Island, 11 September 1972; CAS 14888 (1, 341), southern Oregon, 26–28 April 1972.

atrovirens: CAS 14861 (1, 280), California, 3 April 1972; CAS 15061 (1, 232), California, 21 August 1972.

auriculatus: CAS 14472 (2, 229–357), California, 20 May 1972; CAS 14870 (1, 284), California, 15 April 1972.

aurora: CAS 15301 (1, 261), British Columbia, 10 September 1972.

babcocki: CAS 15286 (1, 362), British Columbia, 10 September 1972.

baramenuke: CAS 30088 (1, 300), Japan, 12–13 August 1929.

borealis: CAS 15272 (1, 406), British Columbia, 10 September 1972.

brevispinis: CAS 14431 (1, 230), Alaska, Summer 1971.

capensis: CAS 17644 (1, 198), Chile, 21 September 1966.

carnatus: CAS 14732 (1, 249), California, 23 April 1972.

caurinus: CAS 14869 (1, 330), California, 15 April 1972.

chlorostictus: CAS 14705 (1, 269), California, 26 May 1972.

chrysomelas: CAS 14896 (1, 271), California, 30 July 1972.

ciliatus: CAS 30089 (1).

constellatus: CAS 14724 (1, 266), California, 27 May 1972.

crameri: CAS 15292 (1, 258), British Columbia, 11 September 1972.

dallii: CAS 14708 (1, 139), California, 27 May 1972; SU 4377 (1, 159), California, no date.

diploproa: CAS 14889 (1, 284), Oregon, 26–28 April 1972.

elongatus: CAS 14713 (1, 221), California, 26 May 1972.

emphaeus: CAS 15153 (1, 110), Oregon, 21 August 1972; BC66–135 (1, 122), British Columbia, 7 September 1966.

ensifer: CAS 17609 (1, 141, paratype), California, 26 May 1965.

entomelas: CAS 14865 (1, 207), California, 5 March 1972.

eos: CAS 17611 (1, 378), California, 3 August 1968.

exsul: CAS 17605 (1, 191), Gulf of California, 29 April 1969.

flameus: CAS 30090 (1, 290), Japan, Spring 1929.

flavidus: CAS 14880 (1, 343), California, 8 April 1972.

gilli: SIO 65-1-53B (1, 488), California, 9 January 1965.

goodei: SU 87 (1, 161), California, Santa Cruz Island, 7 February 1888.

helvomaculatus: CAS 15302 (1, 256), British Columbia, off Vancouver Island, 10 September 1972; CAS 17606 (1, 180), British Columbia, off Vancouver Island, 9–10 February 1967.

hopkinsi: CAS 15300 (1, 221), California, Santa Monica Bay, 16 September 1972.

hubbsi: CAS 30091 (1, 151), Japan, station H29-240, 9 August 1929.

ijimae: CAS 30080 (1, 192), Japan, no date.

inermis: CAS 30081 (1, 159), Korea, Seiskin, 15 September 1924; SU 7413 (1, 140), Japan, Misaki, no date.

jordani: CAS 26448 (1, 201), California, off Gaviota, 7 June 1953.

joyneri: SU 7604 (1, 133), Japan, Tokyo, no date.

lentiginosus: CAS 17614 (1, 175, paratype), California, Cortes Bank, 16 May 1963.

levis: CAS 26594 (1, 123), California, Santa Monica, 21 June 1953.

longispinis: CAS 14281 (1, 136), Korea, 23 July 1959.

macdonaldi: CAS 17610 (1, 163), Baja California, off west coast, 16 January 1970.

maliger: CAS 14890 (1, 312), California, Farallon Islands, 15 July 1972; CAS 15410 (1, 275), British Columbia, spring 1972.

marinus: SU 34329 (3, 205–232), Nova Scotia, Sable Island Gulley, 18–20 July 1939; SU 1770 (1, 126), no data; SU 9870 (1, 203), Norway, no date.

matsubarae: SU 7393 (1, 231), Japan, Misaki, no date.

melanops: CAS 14726 (1, 332), California, off Point Reyes, 7 June 1972.

melanostomus: SIO 67-79-53 (1,194), Mexico, Baja California, 3 May 1967; SU 2459 (1, 95), southern California, no date.

miniatus: CAS 14878 (1, 396), California, off Farallon Islands, 8 April 1972.

mystinus: CAS 14712 (1, 342), California, off Santa Catalina Island, 26 May 1972; CAS 14474 (1, 222), California, Halfmoon Bay, 20 May 1972; CAS 14712 (1, 258), California, Santa Catalina Island, 26 May 1972; CAS 14717 (3, 231–294), California, Fort Ross Cove, 11 June 1972; CAS 14727 (1, 265), California, Point Reyes, 7 June 1972; CAS 14863 (1, 376), California, Halfmoon Bay, 5 March 1972; CAS 14871 (2, 260–289), California, Halfmoon Bay, 15 April 1972; CAS 14882 (2, 267–275), California, Farallon Islands, 8 April 1972; CAS 14894 (1, 251), California, Farallon Islands, 15 July 1972; CAS 15440 (2, 157–191), California, Santa Rosa Island, 21 September 1972; CAS 25900 (1, 112), California, Monterey Bay, 7 October 1953; SU 15097 (1, 70), California, Pacific Grove, 31 July 1948.

nebulosus: CAS 14720 (2, 277–278), California, Fort Ross Cove, 11 June 1972; CAS 14731 (1, 288), California, Farallon Islands, 8 April 1972.

nigrocinctus: CAS 28877 (1, 224), Canada, British Columbia, 10 June 1963.

nivosus: CAS 30082 (1, 175), Japan, station H29-299, Spring 1929.

oblongus: SU 7421 (1, 202), Japan, Matsushima, no date.

ovalis: CAS 14710 (1, 278), California, off Santa Catalina Island, 26 May 1972.

owstoni: CAS 30083 (1, 145), Japan, Toyama Bay, station H29-249, 12–13 August 1929.

pachycephalus: CAS 30241 (1, 157), Japan, Sea of Japan, station H29-224, 4 August 1929.

paucispinis: CAS 15299 (1, 259), California, Santa Monica Bay, 16 September 1972; CAS 14864 (1, 453), California, Halfmoon Bay, 5 March 1972.

phillipsi: SIO 65-153-53A (1, 320), California, off Newport Beach, 17 June 1965.

pinniger: CAS 15057 (1, 315), Oregon, Stonewall Bank, 21 August 1972.

proriger: CAS 15289 (1, 329), British Columbia, off Vancouver, 11 September 1972.

rastrelliger: CAS 14895 (1, 198), California, Halfmoon Bay, 28 July 1972.

reedi: CAS 15290 (1, 332), British Columbia, off Vancouver, 11 September 1972.

rosaceus: CAS 14875 (1, 227), California, Farallon Islands, 8 April 1972.

rosenblatti: CAS 14703 (1, 347), California, La Jolla, 25 May 1972.

ruberrimus: CAS 14560 (1, 288), California, off Point Reyes, 28 May 1972.

rubrivinctus: CAS 14704 (1, 287), California, La Jolla, 25 May 1972.

rufus: CAS 17612 (1, 339), California, Santa Catalina Island, 3 May 1968.

saxicola: CAS 14885 (1, 269), southern Oregon, 26–28 April 1972.

schlegelii: SU 7428 (1, 223), Japan, Hakodate, no date; SU 6274 (1, 88), Japan, Hakodate, no date.

scythropus: SU 7169 (1, 147), Japan, Misaki, no date.

serranoides: CAS 15806 (1, 285), California, Farallon Islands, 15 July 1972.

serriceps: CAS 17613 (1, 251), California, San Diego, 13 December 1972.

simulator: CAS 17607 (1, 235, paratype), Mexico, Guadalupe Island, 29 August 1956.

sinensis: CAS 17608 (1, 115), Gulf of California, Ballenas Channel, 18 January 1968.

steindachneri: SU 7422 (1, 166), Japan, Hakodate, no date.

taczanowskii: CAS 30084 (1, 122), Japan, Mutsu Bay, summer 1929.

thompsoni: CAS 30085 (1, 188), station H29-185-63.

trivittatus: CAS 30086 (1, 160), Japan, station H29-292C, 1 September 1929.

umbrosis: CAS 14707 (1, 194), California, La Jolla, 25 May 1972.

variegatus: SIO 63-946-53 (1, 220), Gulf of Alaska, 14 August 1960.

vexillaris: CAS 18461 (1, 245), California, La Jolla, 5 April 1945.

vulpes: CAS 30087 (1, 161), Japan, station H29-292C, 1 September 1929.

wilsoni: SU 2443 (1, 116), Oregon, no date.

zacentrus: CAS 15309 (1, 210), British Columbia, off Vancouver Island, 11 September 1972.

OTHER GENERA AND SPECIES

Apistes species: CAS 15975 (1, 109), Hong Kong, off Lema Island, 25 July 1958.

Brachypterois serrulifer: CAS 15973 (1, 79), Hong Kong, off Lema Island, 25 July 1958.

Dendrochirus zebra: CAS 15971 (1, 100), Palau Islands, 23 September 1957.

Dendroscorpaena species: CAS 15965 (1, 107), Gulf of Thailand, 18 June 1961.

Ectreposebastes imus: CAS 30092 (1, 154), 300 miles west of Sumatra, 26 May 1966.

Gymnapistes marmoratus: CAS 30093 (1, 71), Western Australia, 8 February 1970.

Helicolenus dactylopterus: CAS 13941 (1, 137), Morocco, 15 July 1969.

Inimicus cuvieri: CAS 13553 (1, 131), Gulf of Thailand, 17–21 December 1960.

Iracundus signifer: CAS 24990 (1, 93), Hawaiian Islands, Oahu, 20 July 1969.

Macroscorpius pallidus: Fisheries Research Station Hong Kong, uncat. (1, 93), Indonesia, off Borneo, 6 June 1964.

Minous monodactylus: CAS 13907 (1, 79), Gulf of Thailand, 14 December 1960. *M. pictus*: CAS 13894 (1, 89), Hong Kong, 24 July 1958.

Neomerinthe beanorum: CAS 24386 (1, 105), Gulf of Mexico, 4 February 1967.

Parascorpaena armatus: CAS 15967 (1, 100), Gulf of Thailand, 27 May 1960.

Plectrogenium nanum: CAS 15704 (1, 51), Hawaiian Islands, Lanai, November 1967.

Pontinus longispinis: CAS 15968 (1, 157), Gulf of Mexico, off Yucatan Peninsula, 22 January 1969.

Pterois radiata: CAS 15970 (1, 115), Society Islands, Moorea, 15 May 1957.

Scorpaena agassizii: CAS 24380 (1, 127), South Atlantic, 27 April 1966. *S. albobrunnea*: CAS 15969 (1, 46), Palau Islands, 29 September 1958. *S. brasiliensis*: CAS 15964 (1, 119), Colombia, Gulf of Morrosquillo, 28 November 1968. *S. elongata*: CAS 24399 (1, 192), Angola, 18 March 1968. *S. guttata*: CAS 2463 (1, 193), Mexico, Guadalupe, 16 March 1932. *S. mystes*: SU 50171 (1, 106), Mexico, Sonora, 30 December 1955. *S. porcus*: CAS 13924 (1, 153), Yugoslavia, Piran Bay, 5 October to 1 December 1968. *S. russula*: CAS 13955 (1, 116), Peru, 7 September 1966.

Scorpaenodes parvipinnis: CAS 15972 (1, 71), Mariana Islands, Guam, 4 April 1959.

Scorpaenopsis species: CAS 15966 (1, 108), Mariana Islands, Guam, 25 January 1959.

Sebastiscus species: CAS 17643 (1, 186), Taiwan Strait, Formosa Bank, February 1972.

Sebastosemus species: ZMK uncat. (1, 100), Kermadec Island, Galathea-Ekspeditionen 1950–52 Station Number 675, 3 March 1952.

Setarches guentheri: CAS 15974 (1, 101), Caribbean, off San Andrés Islands, 20 November 1968. *S. longimanus*: Fisheries Research Station Hong Kong, uncat. (1, 118), Hong Kong, 23 August 1964.

Synanceia verrucosa: CAS 14966 (1, 134), Mariana Islands, Guam, 26 April 1959.

OTHER SCORPAENIFORM FISHES

TRIGLIDAE

Leptotrigla alata: SU 21270 (1, 142), Japan, Nagasaki, no date.

HEXAGRAMMIDAE

Hexagrammos decagrammus: SU 55245 (1, 194), California, Moss Beach, 3 July 1949.
Ophiodon elongatus: CAS 21750 (2, 187–202), California, San Pablo Bay, 28 July 1953.

ZANIOLEPIDIDAE

Zaniolepis latipinnis: CAS 15979 (1, 160), California, off Avila, 19–20 October 1970.

PLATYCEPHALIDAE

Platycephalus species: SU 60950 (1, 166), Hong Kong, Plover Cove, 6 January 1958.

HOPLICHTHYIDAE

Hoplichthys langsdorfi: SU 49455 (1, 145), Formosa, no date.

COTTIDAE

Clinocottus analis: CAS 15980 (1, 124), California, off Santa Rosa Island, 25 January 1949.
Cottus asper: CAS 20857 (1, 110), California, Waddell Creek, 24 February to 2 March 1935.
Hemilepidotus jordani: CAS 15568 (1, 149), Alaska, Shumagin Island, 10 August 1962.
Leptocottus armatus: CAS 18110 (1, 157), California, Marin County, 27 May 1945.
Myoxcephalus quadricornis: SU 49209 (1, 134), Alaska, near Barrow, 19 July 1951.
Scorpaenichthys marmoratus: SU 19391 (2, 125–198), California, Moss Beach, 27 November 1951.

COTTUNCULIDAE

Cottunculus thompsoni: SU 9458 (1, 131), Off Delaware, no date.

AGONIDAE

Occella verrucosa: CAS 15149 (1, 142), Oregon, 19 August 1972.

CYCLOPTERIDAE

Liparis florae: SU 63602 (1, 153), California, Monterey County, 14 October 1955.

ADDENDUM

Recently William Eschmeyer was able to examine additional specimens from the North Atlantic. He informs me that two structural conditions exist for gasbladder musculature in North Atlantic species of *Sebastes*. The gasbladder muscles pass between ventral ribs 2–3 in *S. marinus* and *S. mentella* and between ventral ribs 3–4 in *S. fasciatus* and *S. viviparus*. Therefore the specimens reported here as *S. marinus* are probably *S. fasciatus*, and the muscle type here referred to as the marinus subdivision should be termed the fasciatus-viviparus subdivision.

PROCEEDINGS
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A NEW GENUS AND SPECIES OF EUBLEPHARINE GECKO (SAURIA: GEKKONIDAE) FROM BAJA CALIFORNIA, MEXICO

By

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Abstract: A new genus and species of eublepharine gecko, *Anarbylus switaki*, from central Baja California, Mexico is described and figured. Karyotype data is given.

During a photographic expedition through Mexico, Mr. Karl H. Switak of the California Academy of Sciences' Steinhart Aquarium, collected an unusual ground gecko in central Baja California, Mexico. Cytological and morphological characters of this specimen are unique among eublepharine geckos. Thus the description of a new genus and species, on the basis of a single specimen, seems justified. All descriptive color references refer to those taken from the living animal and are compared with the standardizations of Ridgeway (1912).

Anarbylus Murphy, new genus

Type-species. *Anarbylus switaki* Murphy.

Definition. A monotypic genus of the subfamily Eublepharinae; moderate in size; body largely covered with granular scales interspaced with enlarged keeled tubercles except on head, limbs, and venter. Skin soft, unattached to bones of skull. Eyes large, pupils vertically elliptical; eyelids well developed and functional, inner surface pigmented with black. All gulars equal in size. Ventral surface of digits sheathed with strongly peaked granular scales, sometimes forming longitudinally parallel rows; claws partially hidden by a pair of lateral scales and a single elongate dorsal terminal scute. Ventral scales flat, imbricate. Preanal pores in angular series. Parietal single; retroarticular process

Figure 1. CAS 139472, the holotype of *Anarbylus switaki*. Copyright photograph reprinted by permission of Karl H. Switak.

recurved. Karyotype composed primarily of metacentric chromosomes; diploid number 24.

Etymology. *Anarbylus* (treated as a masculine noun) from the Greek "without shoes" refers to the lack of transverse lamellae on ventral surface of digits.

Anarbylus switaki Murphy, new species.

Switak's Barefoot Gecko

(Figures 1–2.)

Holotype. CAS 139472, an adult male, from 5.5 miles west of San Ignacio (27° 27′ N., 112° 51′ W.) along Mexican Highway 1, Baja California Sur, Mexico, 500 feet elevation, collected by Karl H. Switak on 20 June 1974.

Diagnosis. Characters of the genus but also having nine crossbands of yellow spots between limb insertions and a single enlarged postnasal scale.

Etymology. This species is named for Karl H. Switak, Supervising Herpetologist of the Steinhart Aquarium, who discovered and collected the sole specimen.

Description. (All bilateral counts are given as left-right.) Head and snout uniformly covered above and below with juxtaposed circular granules which are larger on snout. Rostral pentagonal, two times wider than deep, two short sides contacting first supralabials; longer concave edges contact prenasals and are rounded at apex, in contact with 1 of 2 internasals. One prenasal on each side, convex distally and twice concave proximally to supranasals and nasals; supranasals number 1-1, as long as broad, lateral side concave, medial side convex; postnasals slightly smaller than supranasals, triangular, and numbering 1-1; single nasal scale on either side twice as tall as wide; nostril round; subnasals absent; granules in contact with nasal series from rostral to supralabials number 11-12. Imbricate scales with serrate edges border well developed functional eyelids and number 18-18 above, 19-19 below; inner surface of eyelids black except outer border which is brownish drab with warm blackish brown serrate edges above and pallid neutral gray bordered with brownish drab below; pupils vertically elliptical; in life eye grayish black with dense light speckling on outer and inner area of iris, otherwise speckles few. Ear vertically oval, two times longer than wide, ventral edge anterior to dorsal. Enlarged supralabials number 9-8, decrease in size posteriorly, terminate beneath center of eye, the first two times longer than following scales. Infralabials number 12-12. Mental largest head scale, slightly narrower than rostral, quadrilateral, as wide as deep, posterior side narrower than anterior and comprising a short circular arc contacted by 9 gulars; 14 gulars contact mental plus first infralabials on both sides. First infralabial quadrilateral, longest side along mental, wider and much deeper than succeeding infralabials; remaining infralabials decreasing in size posteriorly.

Dorsum covered by granules of similar size with interspaced enlarged tubercles in irregular rows posterior to head; about 16 tubercles transverse on midbody; about 41 tubercles between limb insertions adjacent to middorsal line; tubercles keeled, increasing in size from neck to tail, some peaked posteriorly.

Dorsal and lateral granules and tubercles replaced ventrally with flat triangular scales, larger posteriorly, slightly larger than dorsal granules; short umbilical line interrupts regularity of adjacent scales; approximately 41 imbricate scales across venter, about 100 midventral scales from center of arm insertion to enlarged preanal scales; scales in preanal region further enlarged with 6 conspicuous preanal pores; pore-containing scales obtusely angular in arrangement, pointing forward, two median scales in contact.

Arm scales juxtaposed, strongly peaked, base size equal to dorsal granules; tubercles absent; dorsum of hand covered with imbricate scales; palmar surface granular; third and fourth fingers longest, equal in length; ventral surface of digits without series of transverse lamellae; slightly enlarged peaked granules in longitudinal parallel rows, except on fifth finger, blend to palmar granules, numbering approximately 14 on fourth finger; fingers terminating in a pair of large shell-like lateral scales, capped by a long wedge-shaped terminal scute; claws clearly evident. Legs covered in granular and imbricate scales; tubercles absent; toes sheathed as fingers; fourth toe longest; 18 scale rows on fourth toe; claws clearly evident.

Bifurcated cloacal spurs placed on each side of and slightly posterior to vent, 1.4 mm. long, 1.4 mm. wide at base; 2 postanal sacs present.

Tail base sheathed dorsally and laterally in granular scales with interspaced tubercles and ventrally in wide imbricate scales; regenerated tail begins 6.5 mm. posterior to vent, round in section, covered both dorsally and ventrally with granular scales of equal size to midbody granules, tubercles lacking.

Pattern and color. (In life.) Anterior portion of head with pallid neutral gray spots on mottled base of warm blackish brown and brownish drab; spots blend to sulphur yellow on head above ears. Lightly pigmented canthal ridges pallid neutral gray; ridges extend from eyes to rostral where they converge; second set of slightly darker snout lines lying adjacent to supralabials and extending from postnasals to below eyes. Supralabials pigmented with alternating bands of warm blackish brown and brownish drab; infralabials identical to supralabials. Two crossbands of sulphur yellow spots transverse on parietal region. Neck lightly mottled with warm blackish brown on brownish drab with 3 distinct crossbands of 8 to 10 sulphur yellow spots. Pallid neutral gray gular and throat scales lack dark pigmentation.

On dorsum between limb insertions nine crossbands of sulphur yellow spots blend to pallid neutral gray laterally with warm blackish brown spots concentrated near crossbands; first 2 crossbands form an 'X' pattern behind arm insertion; fifth crossband located at midbody, composed of fourteen spots. Light middorsal stripe extends from base of parietal to tail. Lateral pallid neutral gray spots form two longitudinal rows; each spot encircled, at least partially, by warm blackish brown pigmentation; some spots blend to venter and are not distinct from it; nine spots in both lateral rows offset anteriorly to nine dorsal crossbands. Ventral scales pallid neutral gray, immaculate.

Tail base with 2 crossbands of spots, one lateral and anterior to cloacal spurs, one adjacent to regenerated portion of tail, coloration identical to body crossbands. Regenerated tail pale purplish gray with randomly dispersed large blackish brown spots.

Hands brownish drab, slightly lighter on tips of fingers; forearms lightly mottled; upper arm identical to lower but with heavier mottling and pallid neutral gray spots at insertion. Feet mottled at region of metacarpals; lower leg heavily mottled, few sulphur yellow spots occur on posterior surfaces; upper leg heavily mottled, containing 3 crossbands of sulphur yellow spots which fade to pallid neutral gray laterally, first crossband at leg insertion, second and third almost equidistant between insertion and knee.

Karyotype. Chromosome pattern (fig. 2) is a diploid complement of 24 chromosomes consisting of a graded series of 22 metacentric and 2 acrocentric chromosomes. When ranked in size sequence each 2 pairs of chromosomes are conspicuously larger than the following pair.

These data represent chromosome complements analyzed from 39 intestinal

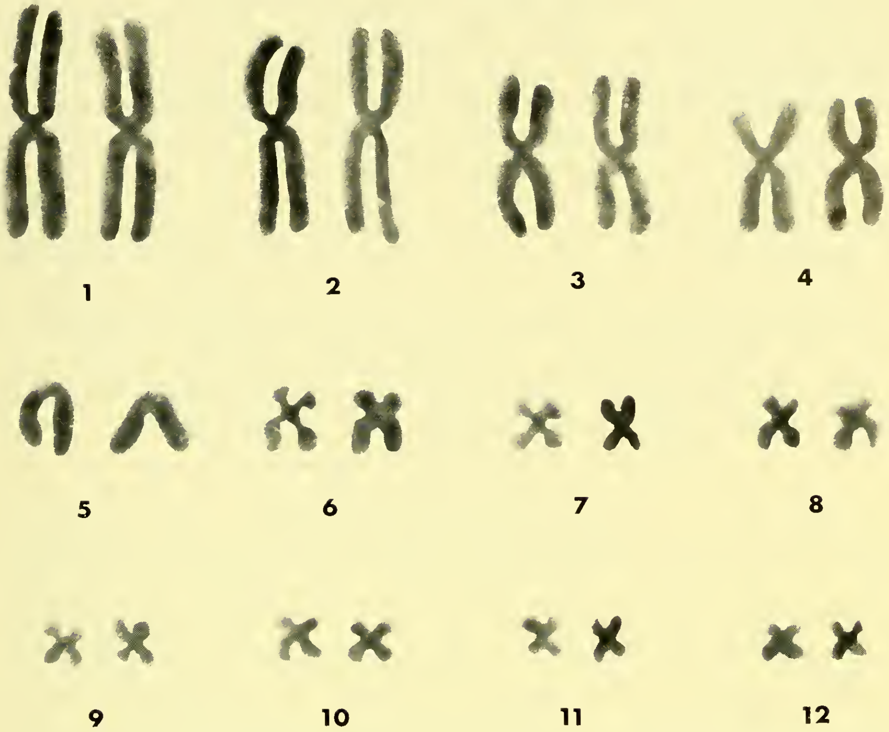

Figure 2. The karyotype of *Anarbylus switaki.* Note the single pair of acrocentric chromosomes (no. 5).

cells taken from the holotype: cells were prepared by colchicine/hypotonic citrate technique. Centromeric position classification follows that of Levan, *et al.* (1964).

Measurements. (In mm.) Snout-vent length, 87; tail length, 48 (regenerated); head width, 16.4; head length, 26.7; width between eyes, 2.8; distance snout to eye, 10.5; distance snout to ear, 20.0; eye width, 5.0; internarial width, 2.9; fourth finger length, 4.3; fourth toe length, 5.3; arm length, 24; leg length, 35.

Range. Known only from type locality.

Remarks. *Anarbylus switaki* is readily distinguished from all other eublepharine geckos in having a single enlarged postnasal scale. It is further distinguished from *Aeluroscalabotes*, *Coleonyx,* and *Eublepharis* in not having enlarged transverse lamellae; from *Aeluroscalabotes*, *Eublepharis*, and *Hemitheconyx* in having numerous small gulars in contact with the mental and infralabials; and from *Holodactylus* and *Coleonyx* (*brevis-variegatus* complex) in having tubercles.

Though the karyotypes of only a few species of gekkonids are known, Gorman (1973) speculated that the "typical karyotype" is sufficient to serve as a cytological definition. Such a definition consists of three elements: 1) a range in diploid number of 32 to 46; 2) a graded series of acrocentric chromosomes with no distinct break between macrochromosomes and microchromosomes; 3) large metacentric elements infrequent with the majority of two-armed chromosomes having subterminal centromeres. The karyotype of *Anarbylus switaki* (fig. 2) does not agree with any criterion of Gorman's definition. Such cytotaxonomic data strongly support the view that this species is neither an aberrant *Coleonyx* nor can it be referred to any currently recognized genus within the subfamily. The preliminary results of a cytotaxonomic study of the eublepharine geckos, in which the karyotypes of *Anarbylus switaki*, *Coleonyx brevis*, *C. variegatus*, *C. elegans*, *C. reticulatus*, *Eublepharis macularius*, and *Hemitheconyx caudicinctus* have been examined, support the above conclusions.

Acknowledgments

My appreciation is due Karl H. Switak for making available this unique gecko for study and for permission to reproduce the copyright photograph of the holotype. Alan E. Leviton and Robert C. Drewes kindly read, criticized, and improved the manuscript and assisted with the karyotyping. James E. Gordon provided radiographs of the specimen and Robert Dempster of the Steinhart Aquarium assisted with the photography of the karyotype.

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TWO NEW BLIND SNAKES (SERPENTES: LEPTOTYPHLOPIDAE) FROM BAJA CALIFORNIA, MEXICO WITH A CONTRIBUTION TO THE BIOGEOGRAPHY OF PENINSULAR AND INSULAR HERPETOFAUNA

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Abstract: Two new subspecies of *Leptotyphlops humilis* from the Gulf of California, Mexico are described. Biogeographical theories explaining the distribution of the herpetofauna of southern insular and peninsular Baja California, Mexico are reviewed. Recent developments in continental drift form the basis of a new interpretation of the distribution of the isolated forms.

Recently two specimens of *Leptotyphlops* which appear to belong to *L. humilis* were received by the California Academy of Sciences. They were collected on Isla Santa Catalina, Gulf of California, Mexico by Bruce Feldhammer in March, 1972. These specimens are of considerable interest because they are the first records for the genus from Isla Santa Catalina which has a highly endemic herpetofauna. Of ten reptiles known on the island, all are endemic, so it is not surprising to find that this is indeed the case for these blind snakes. Another insular representative of *Leptotyphlops* was reported by Soulé and Sloan in 1966. They assigned a single specimen of *L. humilis* from Isla Carmen with seven pigmented rows of median dorsal scales to *L. h. slevini*, a subspecies described by Klauber (1931) as having only five lightly or moderately colored dorsal scale rows. Re-examination of the Soulé-Sloan specimen showed this blind snake to be so unique that reference to a distinct taxon seems justified. I take pleasure in naming the Santa Catalina population for Dr. Alan E. Leviton who has provided me the opportunity to study at the California Academy of Sciences. The Isla Carmen population is named in honor of Dr. George E. Lindsay who, as former Director of the San Diego Society of Natural History and current Director of the California Academy of Sciences, has played a most important role in biological research in Baja California.

The following abbreviations are used in this paper: CAS—California Academy of Sciences; CAS-SU—California Academy of Sciences—Stanford University Collection; LACM—Los Angeles County Museum of Natural History; MVZ—Museum of Vertebrate Zoology, University of California, Berkeley; SDSNH—San Diego Society of Natural History.

Leptotyphlops humilis levitoni Murphy, new subspecies.

Santa Catalina Island Blind Snake.

(Figure 1.)

Holotype. CAS 135146, adult, from Isla Santa Catalina, Gulf of California, Mexico [26° 40′ N., 110° 47′ W.], collected by Bruce Feldhammer on 24 March 1972.

Paratype. CAS 135147, adult, same locality data as the holotype.

Diagnosis. A subspecies of *Leptotyphlops humilis* (Baird & Girard) having a low dorsal scale count, seven pigmented scale rows, 12 scale rows around the tail, a low number of subcaudal scales, and no pigmentation around the mouth.

Description. Snout bluntly rounded; rostral elongate and wedge-shaped with widest point at level of nostrils, in contact with nasals and prefrontal; nasals completely divided; lower nasal elongate, wider dorsally, completely separating rostral and anterior supralabial; upper nasal elongate, wider ventrally, in contact with ocular, rostral, lower nasal, and prefrontal; single anterior supralabial with dorsal edge acutely terminating at lower level of eye; large ocular extending from central dorsal row to the mouth and completely separating supralabials; eye anterior in upper half of ocular; occipital and parietal elongate with the latter in contact with posterior supralabial; temporal smaller than other postoccipitals. First four dorsal median scales are hexagonal, almost as long as broad with approximate order of increasing size being 2nd-1st-4th-3rd; fifth dorsal median scale slightly broader than all others. Head widest at occipitals. Four infralabials, anterior being minute (easily confused with mental) and posterior being largest. Mental very small, approaching triangular shape. Chin shields irregular, blending with ventrals at level of parietals.

Body almost cylindrical; head slightly distinct, narrower than mid-body diameter; tail slightly but distinctly diminished in diameter and terminating in

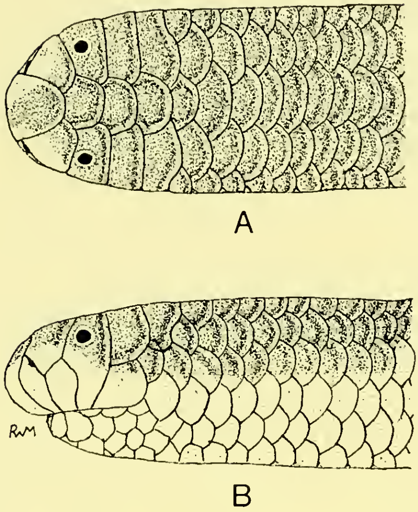

FIGURE 1. *Leptotyphlops humilis levitoni* Murphy, new subspecies. A. Dorsal view of head. B. Lateral view of head.

a laterally compressed sharp spine. Body scales equal in size without conspicuously enlarged dorsal or ventral scales.

Ground color (in 75% ethanol) of cinnamon or medium dark brown present on seven median dorsal scale rows; pigmentation sometimes involves as few as five rows anteriorly and as many as nine posteriorly. Pigmentation is applied evenly as a multiplicity of dots with a greater density on the terminal edge of each pigmented scale. An area surrounding the mouth lacks pigmentation, except for occasional spots, and includes: anterior two-thirds of rostral; lower nasals; lower one-fourth of the upper nasals; anterior supralabials; lower portion of the ocular and posterior supralabials from a line beginning at the top of the anterior supralabial to the angle of the jaw. Infralabials, mental, and chin shields lack pigmentation. Ventral color varies from light brown in the anterior half to cream in the posterior half.

MEASUREMENTS. Total length 212 mm.; tail length 9.6 mm.; body diameter 5.1 mm.; tail length into total length 23.1; average body diameter into total length 42.8. Fourteen scale rows around the body; 12 scale rows around the tail; 249 dorsal scales from rostral to spine; 14 subcaudal scales; anal plate not divided.

RANGE. Known only from type locality.

PARATYPE. The single paratype, an adult, adheres closely to the description of the holotype. Total length 214 mm.; tail length 8.5 mm. (tail somewhat constricted); body diameter 4.8 mm.; tail length into total length 25.2; average body diameter into total length 43.2. Fourteen scale rows around the body; 12 scale rows around the tail; 250 dorsal scales from rostral to spine; 14 subcaudal scales. The first four dorsal scales are hexagonal, almost as long as broad with approximate order of increasing size being 1st-2nd-3rd and 4th. Coloration is identical to the holotype.

REMARKS. A blind snake of the species *Leptotyphlops humilis* (Baird & Girard) which differs from *L. h. humilis*, *L. h. cahuilae*, *L. h. utahensis*, and *L. h. segregus* in having fewer dorsal scale rows; from *L. h. slevini* and *L. h. cahuilae* in having 7 pigmented median dorsal scale rows; from *L. h. segregus* and *L. h. tenuiculus* in having 12 scale rows around the tail; and from *L. h. dugesi* in having fewer subcaudals and no pigmentation around the mouth.

Leptotyphlops h. levitoni appears to be most closely allied to *L. h. dugesi*, and on the basis of the number of dorsal scales, to *L. h. slevini*. However, the character of the number of dorsal scales may be misleading. Fox (1948) showed that temperature may be a major factor in determining the number of scales of *Thamnophis couchi* (= *elegans*) *atratus*. One may observe a similar situation in *Leptotyphlops humilis*, for the number of dorsal scales appears to increase in specimens from south to north (or warm to cold). This trend was noted first by Klauber (1940) and again by Hardy and McDiarmid (1969).

Leptotyphlops humilis lindsayi Murphy, new subspecies.

Lindsay's Blind Snake.

(Figure 2.)

Leptotyphlops humilis slevini KLAUBER (part), 1966, Trans. San Diego Soc. Nat. Hist., vol. 14, no. 11, pp. 137–156.

HOLOTYPE. SDSNH 44386, adult female from Isla Carmen, Gulf of California, Mexico [25° 57′ N., 111° 12′ W.], collected by Charles E. Shaw and George E. Lindsay on 4 April 1962.

DIAGNOSIS. A subspecies of *Leptotyphlops humilis* (Baird & Girard) having a low dorsal scale count, seven pigmented median dorsal scale rows, 12 scale rows around the tail, low number of subcaudal scales, and pigmented supralabials.

DESCRIPTION. Head widest behind occipital; snout bluntly rounded; rostral elongate, widest point at level of nostril, in contact with nasals and prefrontal and terminating at anterior level of eye; lower nasal elongate, wider dorsally, completely separating rostral and anterior supralabial; upper nasal longer than wide with greatest width at level of eye, in contact with ocular, rostral, lower nasal, and prefrontal; single anterior supralabial with dorsal edge acutely terminating; large ocular extending from central dorsal scale row to the mouth, completely separating anterior and posterior supralabials; eye anterior in center of ocular; occipital and parietal elongate with latter in contact with posterior

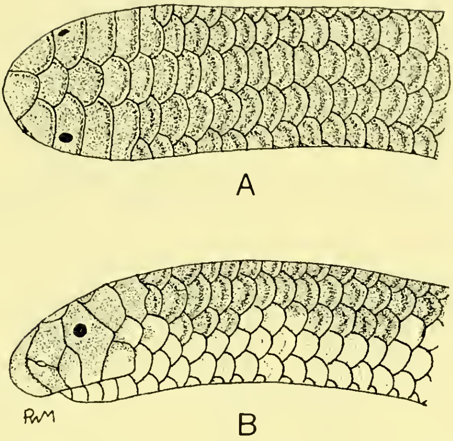

FIGURE 2. *Leptotyphlops humilis lindsayi* Murphy, new subspecies. A. Dorsal view of head. B. Lateral view of head.

supralabial; first three postoculars as elongate scales on right side, first two elongate on left side; temporals smaller than body scales. First four dorsal median scales hexagonal, almost as long as broad and nearly equal in size; fifth dorsal median scale not greatly enlarged. Four infralabials, anterior being greatly reduced, posterior being largest; mental very small, almost triangular in shape; chin shields irregular anteriorly, blending with ventrals behind head.

Body nearly cylindrical, head only slightly distinct; tail slightly, but distinctly, diminished in diameter and terminating in a laterally compressed sharp spine. Body scales equal in size without conspicuously enlarged dorsal or ventral scales.

The ground color (in 75% ethanol) of sayal or medium brown is usually present on seven dorsal median scale rows and occasionally involves as few as five anteriorly and as many as nine posteriorly. Body pigmentation is evenly dispersed as a multiplicity of dots except at the terminal edge of the scales where pigmentation appears denser; lateral rows may appear lighter than dorsal rows. Other body scales are varying shades of cream. Head pigmentation is as follows: posterior one-half of rostral; right lower nasal slightly pigmented; left lower nasal; upper nasals; dorsal one-half of anterior supralabials; oculars; dorsal and anterior portion of posterior supralabials; all dorsal scales. The lower jaw is void of pigmentation.

MEASUREMENTS. Total length 202 mm.; tail length 8 mm.; body diameter 4.9 mm. (may be small since the body cavity is completely opened); tail length into total length 25.3; body diameter into total length 41.2. Fourteen scale rows around the body; 12 scale rows around the tail; 243 dorsal scales from rostral to spine; 14 subcaudal scales; anal plate not divided.

RANGE. Known only from type locality.

REMARKS. A blind snake of the *Leptotyphlops humilis* (Baird & Girard) complex differing from *L. h. humilis*, *L. h. cahuilae*, *L. h. utahensis*, and *L. h. segregus* in having fewer dorsal scales; from *L. h. slevini* and *L. h. cahuilae* in having seven pigmented median dorsal scale rows; from *L. h. segregus* and *L. h. teniculus* in having 12 scale rows around the tail; from *L. h. levitoni* in having pigmented upper lips; and from *L. h. dugesi* in having fewer subcaudals and no pigmentation in lower labials of adults.

One characteristic of *L. h. lindsayi* appears unique. The enlarged right third postocular (or postoccipital) has not been reported for any other subspecies of *L. humilis*. The occurrence of this phenotypic expression within a genetically isolated population seems significant.

In other characteristics, *Leptotyphlops h. lindsayi* is allied to *L. h. levitoni* and *L. h. dugesi*. Similarity between these three forms is seen in low dorsal scale counts, coloration, and similarity of scale patterns.

DISCUSSION

Savage (1960) presented a detailed hypothesis of southern peninsular Baja California invasion by northern herpetofaunal forms. According to Savage, immigration of northern forms, which presumably began in the Pliocene and occurred in four successive waves, replaced the early Tertiary fauna of the area. Savage contended that the first Pliocene wave ultimately formed the basic modern fauna of the Californian and San Lucan areas. A second wave of desert-adapted groups invaded the northern areas as aridity increased during the end of the Pliocene, while at the beginning of the Pleistocene a third wave invaded the northern portion of the peninsula as general temperature drops occurred; this third cluster produced the desert forms of the east and south peninsula. Finally, in the Pleistocene, the fourth or possibly several waves of desert forms invaded from the northeast at times of interglacial conditions. Overlap of San

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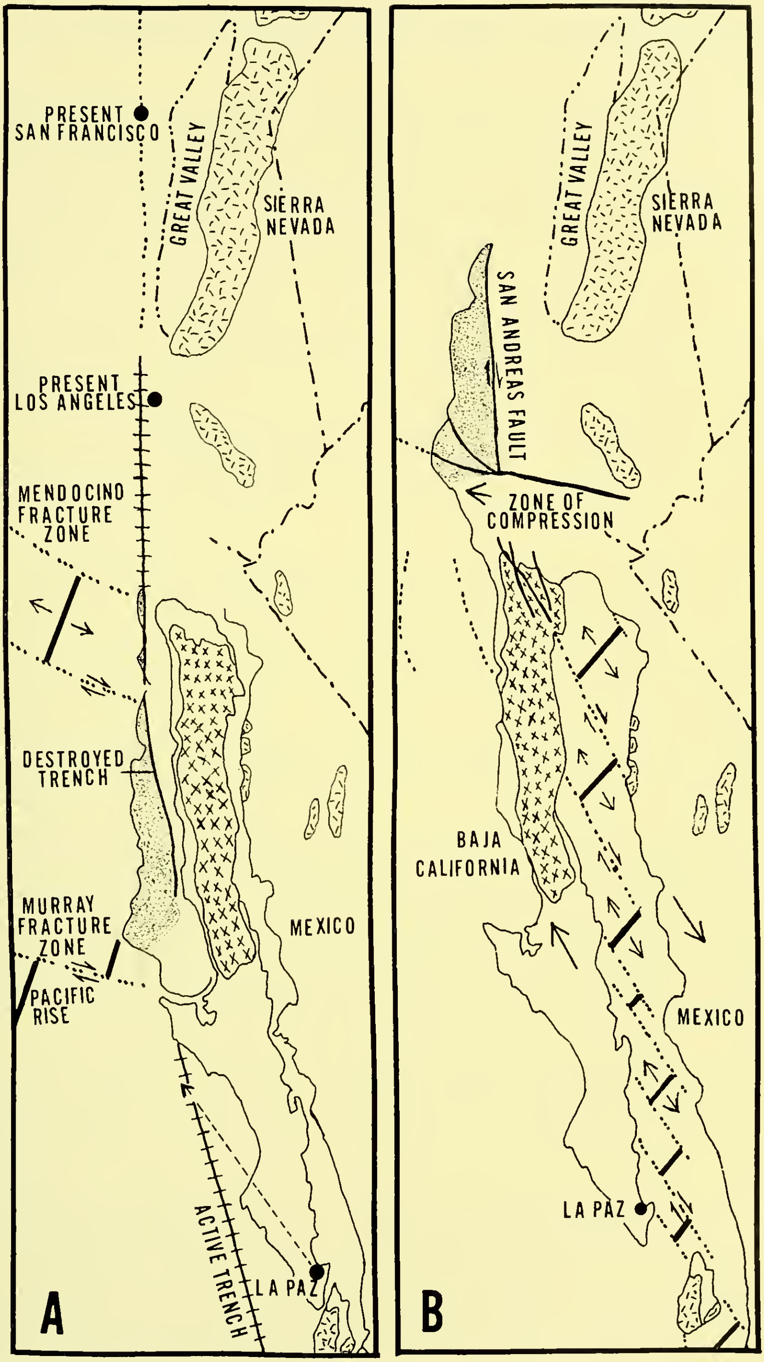
FIGURE 3. Early and late stages in the history of the San Andreas fault. A. twenty-five million years ago Baja California presumably nestled against mainland Mexico. The first section of oceanic rise between the Murray fracture zone and the Pioneer fracture zone has just collided with the continent. Trench deposits are uplifted and become part of the Coastal Ranges of California. The block containing the present San Francisco area (stippled) is about to start its long northward journey. A block immediately to the east (cross-hatched) becomes attached to the Pacific plate and eventually is jammed against the San Bernardino Mountains. B. Three million years ago the Gulf of California has started to open. As the peninsula moves away from mainland Mexico a series of rifts appear, fill with magma, and are offset by numerous fractures. Baja California may have been torn off in one piece or in slivers. (Reprinted from Anderson, *The San Andreas Fault*. Copyright © 1971 by Scientific American, Inc. All rights reserved.)


PRESENT SAN FRANCISCO
GREAT VALLEY
SIERRA NEVADA
PRESENT LOS ANGELES
MENDOCINO FRACTURE ZONE
DESTROYED TRENCH
MURRAY FRACTURE ZONE
PACIFIC RISE
MEXICO
ACTIVE TRENCH
LA PAZ
A
GREAT VALLEY
SIERRA NEVADA
SAN ANDREAS FAULT
ZONE OF COMPRESSION
BAJA CALIFORNIA
MEXICO
LA PAZ
B

Lucan forms moving north and the northern forms moving south then occurred in the central peninsula.

The plate tectonic conception of continental drift was founded in the late 1950's. Many American scientists were reluctant to accept the concept until the late 1960's (Wilson, 1972). This may account for the fact that Savage failed to include the distribution and origin of the insular faunas, which could not be readily explained by his northern origins hypothesis. Thus, Savage overlooked one important possibility, that much of the San Lucan and insular herpetofauna did not arrive by Pliocene and Pleistocene invasion from the north but rather by traversing the Gulf on the Peninsula as the latter broke away from mainland Mexico. In fact, Streets, in 1877 (pp. 41–42), suggested ". . . geological changes . . . since the post-Tertiary period," to explain the insular occurrence of reptiles on Pacific and Gulf islands. This concept is best exemplified by the presence of *Bipes biporus*, *Natrix valida celaeno*, *Ctenosaura hemilopha*, *Pseudemys scripta nebulosa*, and *Eridiphas slevini*, the latter possibly representing a link between *Leptodeira* and *Hypsiglena* (Leviton & Tanner, 1960).

Since the discussion by Savage (1960), Anderson (1971) evaluated current information on the San Andreas Fault and presented his "Two-fault hypothesis" (fig. 3). According to Anderson, before the Pacific plate began moving northwest the "San Francisco" area was located near the present location of Ensenada in northern Baja California and present day "Baja California" presumably nestled against mainland Mexico. Twenty-five million years ago the northern Pacific plate separated from Bahia Sebastian Vizcaino (near Scammon's Lagoon) and began its northwest journey of up to 700 miles. Twenty million years later (four to six million years ago) the southern portion of the Pacific plate was torn from mainland Mexico forming the Gulf of California. Eventually, after 300 miles of northwest migration, the southern Pacific plate rammed into the northern Pacific plate and formed a single unit. It should be noted that the peninsula may have split from mainland Mexico in several fragments. Anderson (1971, p. 60), in illustrating the early and late stages of the history of the San Andreas Fault, pictures the southern tip of Baja California as being a separate land mass as late as three million years ago (fig. 3).

Auffenberg and Milstead (1965) noted that very little taxonomic differentiation occurred between the Pliocene and Recent, particularly at the species level. They further state that the greatest effects of the Pleistocene on Baja California were those of changes in sea-level and not climatic change. The sea-level changes (such as a drop of approximately 110 meters and estimated rise of 30 meters [Flint, 1971]) had little effect on Baja California topography except for creating and drowning many islands (Durham & Allison, 1960). On this basis Soulé and Sloan (1966) placed many islands in a category of probable recent or young shallow-water islands, including therein Tiburon, San Marcos, Coronados, San Jose, San Francisco, and Espiritu Santo as well as many small coastal and satellite islands and possibly Carmen, Monserrate, and Danzante (fig. 4).

In view of recent information and concepts, it is possible to suggest the following interpretation of the distribution and interrelationships of the forms of *Leptotyphlops humilis.* Prior to the separation of Baja California from mainland Mexico *L. humilis,* as well as many other forms of reptiles and amphibians, occurred in both areas. The southern Pacific plate began moving northwest and carried the blind snakes with it. The Cape San Lucan region parted from mainland Mexico, possibly from a location further south, as a separate unit, free of the peninisula, and remained isolated until mid-Pleistocene. The population of *L. humilis* isolated on this island evolved into a group having only five pigmented median dorsal scale rows. This group is presently known as *L. h. slevini.* As the peninsula was torn away from mainland Mexico two southern groups of islands were formed and have remained without further contact: Isla Santa Catalina and islas San Diego and Santa Cruz. Evidence for this is the high percentage of endemic reptiles present on these islands. If these islands had had recent contact with the mainland, then mainland forms would be expected to occur. In addition, the existence of *Crotalus catalinensis,* allied to *C. atrox* (Klauber, 1956, 1972), on Isla Santa Catalina and *C. atrox* on Isla Santa Cruz is better explained by continental drift than by the swimming or rafting suggested by Klauber (1956, 1972). *Sator angustus,* which occurs on San Diego and Santa Cruz presents the same problem [see below]. *Leptotyphlops humilis* is presently known from one of these "old" islands, Isla Santa Catalina.

Another group of islands was formed later. During the Pleistocene, tectonic shifts and sea-level changes formed the young, shallow-water islands (as noted earlier) including Carmen, Monserrate, and Danzante. These islands share a large percentage of their herpetofauna with the Baja California mainland. During Pleistocene glaciation and lower water-levels, reptiles could easily pass from the peninsula to these islands. There is evidence that some of these islands have undergone recent uplifting (Anderson, 1950; Wilson & Rocha, 1955; Soulé & Sloan, 1966) indicating recent faulting and instability. If this dual theory of island formation is true then *L. h. levitoni* has remained isolated from the parental stock since mid-Pliocene, *L. h. lindsayi* being isolated sometime during the Pleistocene.

The presence of *Sator grandaevus* on Isla Cerralvo and its absence from the San Lucan region of mainland Baja California has been a subject for interesting speculation for a long time. On those islands on which *Sator* occurs, no other sceloporine lizards are known. The occurrence of the old southern forms of reptiles, as *Eridiphas slevini,* on both Isla Cerralvo (Soulé, 1961) and the southern tip of mainland Baja California, would seem to indicate that these two regions had

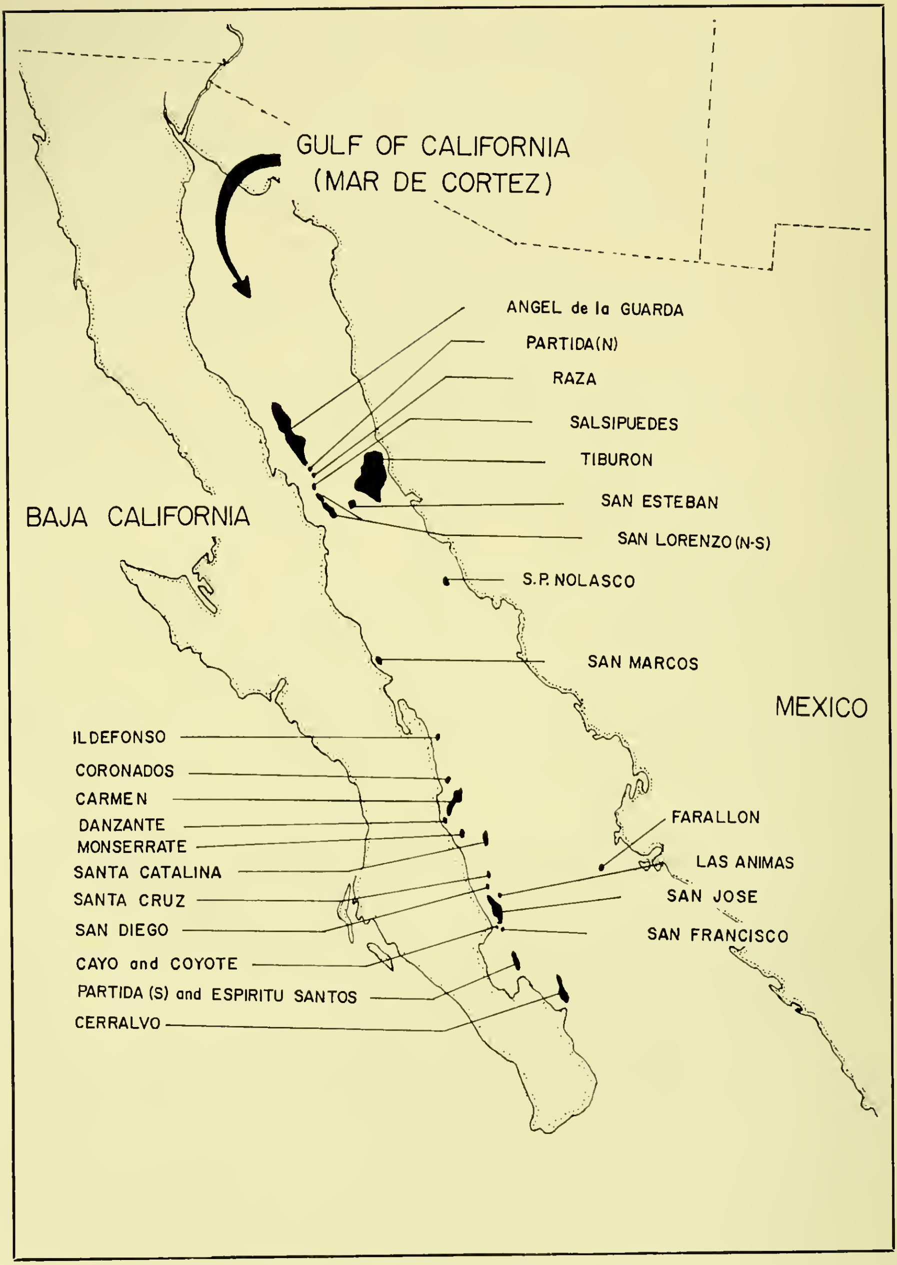


FIGURE 4. A map of the Gulf of California indicating the islands discussed in this paper.

a similar origin. Seemingly, Isla Cerralvo was separated from the San Lucan region before the San Lucan plate joined with the southern Pacific plate in the mid-Pleistocene. When these two plates joined, the sceloporine lizards of the north invaded the San Lucan region and pressured the San Lucan form of *Sator* to extinction. After the San Lucan plate joined the Pacific plate, the sea-level dropped briefly allowing invasion of Isla Cerralvo by northern iguanids. However, the length of time for invasion was not sufficient to allow invading sceloporines to overrun the Cerralvo populations of *Sator*. Islas San Diego and Santa Cruz may have had a similar southern origin and have been moving northwest since the San Lucan plate rammed the southern Pacific plate.

The relationships between Isla Cerralvo and islas San Diego and Santa Cruz have never been understood. If these islands had a similar southern origin, and if they were only recently separated, it seems reasonable to expect that any *Leptotyphlops* discovered would be of similar origin and therefore would have only five pigmented median dorsal scale rows. Unfortunately, we have no evidence at this time to test this speculation.

Leptotyphlops humilis slevini, as mentioned earlier, was long separated from other populations of *L. humilis*. By the time the San Lucan plate joined the rest of the peninsula, the local population of *L. humilis* had undergone a substantial change, that of reduction in the number of pigmented median dorsal scale rows. The occurrence of this subspecies on Isla Cerralvo (Banks & Farmer, 1963) provides further evidence that this island is part of the San Lucan plate.

Only one other subspecies, *L. h. cahuilae*, is known to have five pigmented median dorsal scale rows. Klauber (1940) postulated that the Sonoran *L. h. cahuilae* became isolated for a considerable length of time, possibly by Lake Cahuilla, and then remet and interbred with *L. h. humilis*. He also noted that different desert-dwelling populations of *L. h. cahuilae*, as that of the Vizcaino Desert in central Baja California, either evolved parallelly with Sonoran *L. h. cahuilae* or represent a residue of a former intrusion from Sonora. Continental drift adds two additional possibilities; either the Vizcaino Desert population traversed the gulf or immigrated from the south. Two specimens of *L. h. cahuilae* (CAS 103465 and LACM 2167) from Bahia de Los Angeles, Baja California Norte, [28° 55′ N., 113° 32′ W.], indicate that the ranges of Sonoran and Vizcaino Desert *L. h. cahuilae* are continuous. Seemingly this would eliminate Klauber's anticipation of the isolated Vizcaino Desert population. However, current data are not adequate to determine the *"slevini-cahuilae"* subspecies relationships.

Of the nine subspecies of *L. humilis* currently recognized two are definitely allied; *L. h. utahensis* is certainly derived as a northern extension of *L. h. humilis*, *L. h. utahensis* being distinct in having a divided fourth and an enlarged fifth anterior median dorsal scale. The occurrence of five *L. h. humilis* × *utahensis* intergrades (CAS 89570, 89577, 89591–89593) from Inyo County, California extends the expected range of intergradation, as predicted by Klauber (1940), by approximately 100 miles.

As noted earlier, *L. h. dugesi*, *L. h. levitoni*, and *L. h. lindsayi* also appear to be quite closely related for all three share the characteristics of a low number of dorsal scales, 12 scale rows around the tail, a low ratio of body length to body diameter, 7 pigmented median dorsal scale rows, and a medium to dark brown coloration. *L. h. slevini* shares some of these characteristics but differs in having 5 pigmented median dorsal scale rows and a light brown coloration. Based on the transgulfian migration theory, *L. h. slevini* forms a unique taxon within the *L. humilis* complex and, though closely related, is not a member of the *"dugesi-levitoni-lindsayi"* combination.

In their discussion of the biogeography and distribution of the herpetofauna on the islands in the Gulf of California Soulé and Sloan (1966) commented on two trends of insular reptiles; gigantism in lizards and dwarfism in snakes (with noted exceptions). The ratio of body length to body diameter for *L. h. levitoni* and *L. h. lindsayi* is less than those of any other subspecies of *L. humilis*. Such a low ratio of body length to body diameter indicates that the two insular worm snakes have heavier bodies than their mainland relatives. Once the population structure is better known these statistics can be further interpreted as being attributable to gigantism, an effect of dwarfism, or the result of insufficient data.

A REVISED KEY TO THE SUBSPECIES OF THE WESTERN BLIND SNAKE, *LEPTOTYPHLOPS HUMILIS*

1a. Five pigmented dorsal median scale rows 2
b. Seven to nine pigmented dorsal median scale rows 3

2a. Dorsal scale rows less than 270; Cape region of Baja California Sur; Isla Cerralvo, Gulf of California, Mexico .... *L. h. slevini* Klauber
b. Dorsal scale rows more than 280; central Baja California north to southern California and Arizona; northern Sonora, Mexico .... *L. h. cahuilae* Klauber

3a. Ten scale rows around tail 4
b. Twelve scale rows around tail 5

4a. Dorsal scale rows less than 250; San Luis Potosi .... *L. h. tenuiculus* (Garman)
b. Dorsal scale rows more than 250; central Coahuila, Mexico north to southeastern Arizona and through trans-Pecos Texas .... *L. h. segregus* Klauber

5a. Dorsal scale rows more than 280; fourth mid-dorsal scale often divided; fifth dorsal much wider than sixth; southwestern Utah .... *L. h. utahensis* Tanner
b. Dorsal scale rows less than 280; fifth mid-dorsal scale not much wider, if any, than sixth 6

6a. Dorsal scale rows greater than 257; central Baja California, Mexico north to southern Nevada southeast to south-central Arizona; Cedros Island .... *L. h. humilis* (Baird and Girard)
b. Dorsal scale rows less than 257 7

7a. Lower nasals pigmented 8
b. Lower nasals not pigmented; Isla Santa Catalina, Gulf of California, Mexico .... *L. h. levitoni* Murphy

8a. Subcaudals 15 or less; infralabials not pigmented in adults; Isla Carmen, Gulf of California, Mexico .... *L. h. lindsayi* Murphy

b. Subcaudals usually more than 15; infralabials of adults often pigmented; southern Sonora southeast to Colima; Guanajuato, Mexico .... *L. h. dugesi* (Bocourt)

Material Examined

L. h. cahuilae (13). California. Imperial Co.: 5 mi. N. Winterhaven (MVZ 63562); Riverside Co.: Palm Springs, China Canyon (MVZ 71090). ARIZONA: Yuma Co., (CAS-SU 5697). MEXICO. Baja California del Norte: 5 mi. N. San Felipe, Playa del Sol Camp (CAS 136368-136369); 6 mi. N. San Felipe (LACM 36504); Puncta San Felipe, ± 50 ft. (MVZ 50168); Bahia de Los Angeles (CAS 103465, LACM 2167); Sierra Juarez (CAS 85069); Base of grade below Alaska (CAS-SU 11567); San Jose, 2300 ft. (MVZ 9637). Sonora: 56 mi. E. San Luis (LACM 9033).

L. h. dugesi (12). MEXICO. Sinaloa: Mazatlan (CAS-SU 1776); 11 mi. N. Culiacan (LACM 6773); 20 mi. S. Culiacan, Mexico Highway 15 (LACM 51564); 0.5 mi. N. Terroros (LACM 6773). Nayarit: Tepic, LaLoma Motel (CAS-SU 19243); 5 mi. E. Santa Cruz (CAS 134054); between San Blas and Mexico Highway 15 (LACM 8730–8731); 18.5 mi. E. (by road) San Blas (MVZ 71333). Jalisco: Jocotepec (CAS 85470); 14.5 mi. E. Tapalpa (LACM 37327–37328).

L. h. humilis (28). California. San Diego Co.: (CAS 58160, 62992, 64442); Palomar Mountain (CAS 58132); Ladrillo Station (Rose Canyon, CAS 53933); Scissors Crossing, Highway 78 (MVZ 64478); 1.2 mi. E. Scissors Crossing (CAS-SU 19763); 2 mi. E. Scissors Crossing (CAS-SU 19766); 0.5 mi. E. Scissors Crossing (CAS-SU 19764–19765); 1 mi. ENE. Scissors Crossing, 2200 ft., San Felipe Valley (MVZ 79215); Lemon Grove (MVZ 10189). San Bernardino Co.: 9 mi. W. Earp (MVZ 51268); Twenty-nine Palms (MVZ 56491). Inyo Co.: Inyo Mountains, N. side of Daisy Canyon, 3900 ft. (CAS 89594); Nelson Mountains, Grapevine Canyon, 4500 ft. (CAS 89568). Los Angeles Co.: near mouth of Big Santa Anita Canyon (MVZ 74653). Riverside Co.: mouth of Whitewater Canyon, E. canyon wall (MVZ 80920). Arizona. Pima Co.: Tucson (CAS 33525, 33835–33836, 91533); Santa Catalina Mountains (CAS 35849). Pinal Co.: S. Florence Junction (CAS 84135). MEXICO. Baja California del Norte: San Ignacio, 500 ft. (MVZ 10667); 15 mi. E. San Telmo de Arriba (CAS 123717); 7 mi. S. Tecate (CAS 134800). Chihuahua: 3 mi. NW. Chilmahma, 0.5 mi. W. main highway (MVZ 57331).

L. h. levitoni (2). MEXICO. Gulf of California, Isla Santa Catalina (CAS 135146–135147).

L. h. lindsayi (1). MEXICO. Gulf of California, Isla Carmen (SDSNH 44386).

L. h. slevini (16). MEXICO. Baja California Sur: Gulf of California, SW. side of Isla Cerralvo (CAS 93009); La Paz (CAS 129644–129645, 134772–134223; MVZ 45386; LACM 25061); 7 km. S. La Paz (CAS 134801–134802); Eureka (MVZ 11850–11851); San Jose del Cabo (CAS-SU 4118, paratype); vicinity of Cabo San Lucas (CAS-SU 14032–14033); Santa Anita (CAS-SU 6025); vicinity of Cape San Lucas (CAS-SU 16061).

L. h. humilis × *cahuilae* intergrades (191). California. Imperial Co.: Colorado River, Laguna Dam (MVZ 63543–63548, 63550–63556, 63560–63561, 70457); Laguna Dam, Laguna

Island (MVZ 105162–105172, 85237–85238, 93113, 93115); Laguna Dam, Potholes (MVZ 63549, 50228–50233; CAS 80392–80459, 80461–80468, 80470–80532); 3 mi. S. Laguna Dam (MVZ 93114); about 15 mi. E. Glamis on Highway 78-S (MVZ 84701). Riverside Co.: 1 mi. SE. Cabazon, base of San Jacinto Mountains (MVZ 74652); 1.5 mi. ENE. Cabazon, base of San Jacinto Mountains (MVZ 74647–74651); Palm Springs, China Canyon (MVZ 70458). Inyo Co.: Death Valley, Coweruls, 4 mi. N. Furnace Creek Dam, 150 ft. (MVZ 19284); Death Valley, Cow Creek (MVZ 35360). San Bernardino Co.: Merango Valley, 4 mi. N. Riverside Co. line (MVZ 63571). MEXICO. Sonora: 136 mi. E. Mexicali, Mexico Highway 2 (LACM 20309); 23 mi. SSE. Sonoyta (LACM 25168–25169).

L. h. humilis × *utahensis* intergrades (5). California. Inyo Co.: Nelson Mountains, Grapevine Canyon, 4630 ft. (CAS 89592–89593); Nelson Mountains, Grapevine Canyon, 4480 ft. (CAS 89570); Saline Valley, S. end, Racetrack Valley Road, 2100 ft. (CAS 89591); Saline Valley, S. end, Lower Grapevine Canyon, 4000 ft. (CAS 89577).

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THE ROCKFISHES, GENUS *SEBASTES* (SCORPAENIDAE), OF THE GULF OF CALIFORNIA, INCLUDING THREE NEW SPECIES, WITH A DISCUSSION OF THEIR ORIGIN

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Abstract: Seven species of *Sebastes*, herein described and compared, occur in the Gulf of California at the near-tropical fringe of the range of the genus in the northeastern Pacific. Six of the species are endemic to the Gulf. Three of these, (*S. spinorbis*, *S. varispinis*, and *S. peduncularis*) are described as new. Only *S. macdonaldi* occurs also on the outer coast of Baja California.

Sebastes sinensis and *S. cortezi* are mesopelagic as well as benthic. *Sebastes cortezi*, like *S. diploproa* of the outer coast, inhabits floating vegetation as prejuvenile; it undergoes extreme morphological change on leaving its surface habitat.

The distribution pattern of these seven species seems to be related to water temperature and dissolved-oxygen level.

Multiple invasion from the outer coast and subsequent radiation within the Gulf may both have contributed to the species diversity within the Gulf. *Sebastes diploproa* of the outer coast probably came from reciprocal invasion by *S. cortezi* from the Gulf.

Introduction

The rockfish genus *Sebastes* is represented by many species in the North Pacific. Only a few others are known from the North Atlantic and from the southern hemisphere. Chen (1971) listed 65 species of the genus for the American coast of the North Pacific. Since then there have been three additions: *S. borealis* Barsukov (1970), *S. variegatus* Quast (1971), and *S. rufinanus* Lea and Fitch (1972).

The first species of *Sebastes* recorded from the Gulf of California were described as *Sebastichthys sinensis* in 1890 and *Scorpaenodes cortezi* in 1938. Lavenberg and Fitch (1966) reported specimens from the Gulf but did not assign species names. The next record was that of Chen (1971), who reported the occurrence of *S. macdonaldi* and described *S. exsul* from the Gulf. I here report seven species from the Gulf, of which three are described as new (two of these three were included, but not specifically named, in my 1971 list of 65 American North Pacific species).

With these additions, with another new species to be described by Lea and Fitch (personal communication), and with the placement of *S. vexillaris* in the synonymy of *S. caurinus* (Chen, in preparation), the number of known species of *Sebastes* in the eastern North Pacific is now 69.

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Methods

The terminology and methods in this report follow those of Chen (1971).

Abbreviations for the listed collections are: CAS, California Academy of Sciences; LACM, Los Angeles County Museum; SDSC, San Diego State University; SIO, Scripps Institution of Oceanography; UCLA, University of California, Los Angeles.

Key to the Rockfishes, Genus *Sebastes*, of the Gulf of California

1a Lower edge of lachrymal with three or four small, spinelike projections; lateral-line pores more than 50; second anal spine shorter than third; lateral surface of lachrymal with a spine in specimens longer than 10 cm. (fig. 1a) .... *S. macdonaldi*

1b Lower edge of lachrymal with only two projections which may be spinelike and sometimes split; lateral-line pores fewer than 50; second anal spine longer than third; lateral surface of lachrymal without a spine (except in *S. spinorbis*) 2

2a Supraocular spines present 3

2b Supraocular spines absent 4

3a Lateral surface of lachrymal and/or orbital edge of first and/or second suborbital with spines; P_1 18; rakers on first gill arch 29–33 (fig. 1b) .... *S. spinorbis*

3b Lateral surface of lachrymal and orbital edge of first and second suborbitals without spines; P_1 17; rakers on first gill-arch 32–37 (fig. 1c) .... *S. exsul*

4a Scales mostly cycloid, occasionally with weakly developed ctenii; dorsal soft-rays more often 11 than 12 (mouth and gill-cavity linings dusky in specimens 4 or 5 cm. long, jet-black in larger ones; ventral lachrymal projections pointing backward; rakers on first gill-arch 29–33) (figs. 1d and 2b) .... *S. sinensis*

4b Scales mostly ctenoid, with ctenii evident in specimens 4 or 5 cm. long; dorsal soft-rays more often 12 than 11 5

5a Mouth and gill-cavity linings black; lower jaw slightly projecting; dorsal spines sometimes 12 (20%); (rakers on first gill-arch 30 or more) (fig. 2a) .... *S. varispinis*[1]

5b Mouth and gill-cavity linings may be dusky, never black; jaws subequal; dorsal spines almost always 13 6

6a Head width in S.L. 6.5 or less; (rakers on first gill-arch 30 or fewer; anterior lachrymal projection directed forward in specimens longer than 6 cm.) (figs. 1e, 2c, and 2d) .... *S. cortezi*

6b Head width in S.L. more than 6.5 (fig. 2e) .... *S. peduncularis*[1]

Sebastes exsul Chen, 1971.

(Figure 1c.)

Sebastes exsul Chen, 1971, p. 27 (type locality: Gulf of California, at 28° 59′ N., 113° 25.5′ W.)

Diagnosis. *Sebastes exsul* can be differentiated from all other species of *Sebastes* by the following combination of characters: (1) the color pattern of the subgenus *Sebastomus* (body pink or red, with white blotches at tip of opercle, bases of fourth, eighth, and last dorsal spines and last dorsal ray, and also one below ninth dorsal spine just above lateral line); (2) the cranial spine pattern (with nasal, preocular, supraocular, postocular, tympanic, and parietal spines); (3) the meristics (D. XIII, 12–13; A. III, 6; P_1 17; rakers on first gill-arch 32–37; lateral-line pores 35–43); (4) a nearly vertical anal profile; (5) a narrow interorbital divided by frontal ridges into three grooves; (6) the oral and the gill-cavity linings white; (7) subequal jaws; (8) scaled mandibles; (9) short dorsal spines (orbit length in fourth dorsal spine less than 1.2); and (10) absence of spines on the lateral surface of lachrymal and the orbital edge of the first and second suborbitals.

Description. A detailed description was given by Chen (1971) and is supplemented here.

Principal caudal rays 14; vertebrae (in 8 specimens) 26 (11 + 15). Each one of the two extrinsic gas-bladder muscles (2 specimens examined) extends backward from an origin on or near the opisthotic, passes medial to the cleithrum to which it has a membranous connection, then splits into three tendons which pass between the second and third ribs, running straight along the inner side of succeeding ribs and inserting respectively on the parapophyses of the 7th, 8th, and 9th centra. The last tendon is split in one specimen, with the additional branch attached to the parapophysis of the 10th centrum. There is no direct connection between the tendons and the gas-bladder wall.

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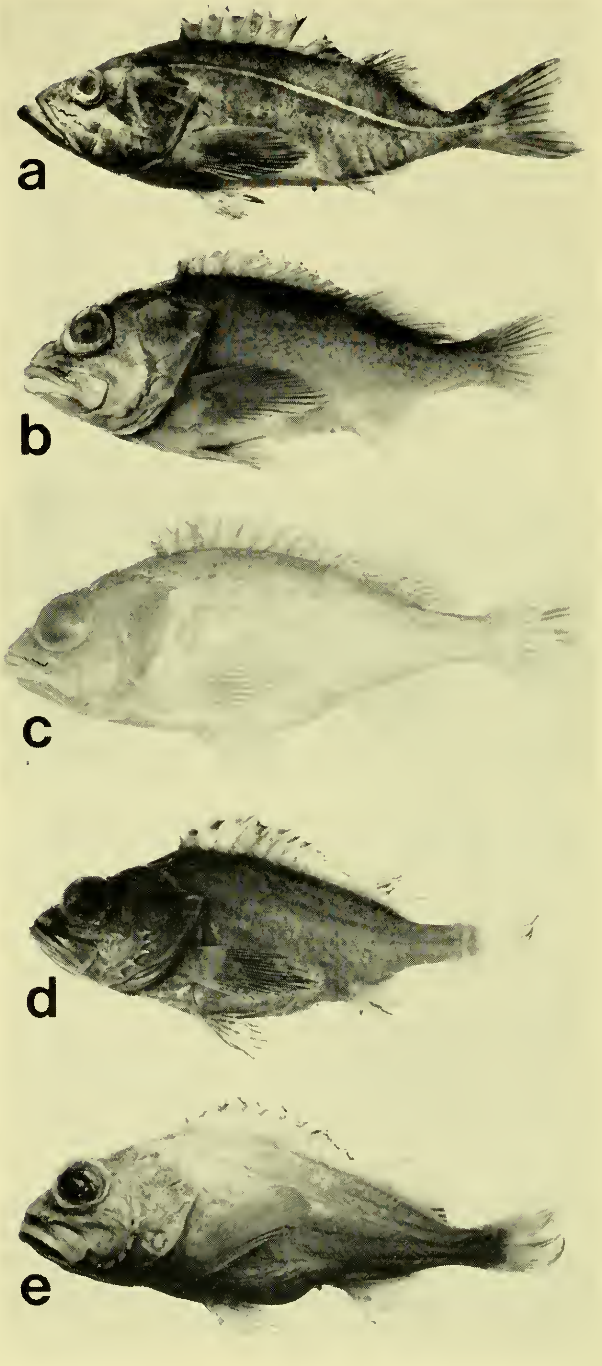
[1] 3–5 cm. juveniles only.


a
b
c
d
e

For morphometrics and meristics, see tables 1, 7, 8, and 9.

Remarks. This species is most likely to be confused with *S. umbrosus*, *S. rosenblatti*, and *S. spinorbis*. It can be distinguished from *S. umbrosus* by its lack of the conspicuous honeycomblike color pattern, from *S. rosenblatti* by its higher average number of gill rakers, and from both by its short dorsal spines. From *S. spinorbis*, *S. exsul* can be distinguished by the lack of spines on the lateral surface of the lachrymal and the orbital edge of the first and second suborbitals, by having only 17 pectoral rays, by having more rakers on the first gill-arch (32–37 instead of 29–33), by lacking spines on the lower edge of the gill-cover, and by having clear fin membranes and white oral and gill-cavity linings.

Since describing the species in 1971, I have acquired 21 additional specimens, all from the type locality. Of these specimens, one (SIO 69-437, 180 mm.) resembles *S. spinorbis* in having a spine on the lateral surface of each lachrymal, but it is regarded as *S. exsul* because the spine is weak and because it agrees with *S. exsul* in having 16–17 pectoral rays, 33–34 rakers on the first gill-arch, no spines on the lower edge of gill-cover, the fin membranes clear, and the oral and the gill-cavity linings white.

Range. Known only from the vicinity of the type locality, 28° 59′ N., 113° 25.5′ W.

Material examined. A total of 36 specimens, 150–212 mm.

Holotype. SIO 68-1, 171 mm., adult female, from 28° 59′ N., 113° 25.5′ W., 2.5 miles N. of Punta Roja, Bahía de los Angeles.

Paratypes. All from vicinity of the type locality. SIO 62-241, 7 (158–212); SIO 68-3, 7 (150–202).

Other specimens. All from vicinity of the type locality. SIO 69-318, 12 (170–188); SIO 69-437, 14 (156–197); CAS 17605, 1 (184).

Sebastes spinorbis Chen, new species.

(Figure 1b.)

Diagnosis. *Sebastes spinorbis* can be differentiated from all other species of *Sebastes* by the following combination of characters: (1) the color pattern and the cranial spine pattern of the subgenus *Sebastomus* (see diagnosis of *S. exsul*); (2) presence of a spine on the lateral surface of the lachrymal and/or the orbital edge of the first and second suborbitals; (3) 18 pectoral rays; (4) 29–33 gill-rakers; and (5) dusky to black pectoral membrane.

←

Figure 1. a). *Sebastes macdonaldi*, adult male, 412 mm., SDSC 74-12. b). *S. spinorbis*, holotype, adult male, 225 mm., SIO 69-318. c). *S. exsul*, holotype, adult female, 171 mm., SIO 68-1. d). *S. sinensis*, adult female, 149 mm., LACM 30065-1. e). *S. cortezi*, adult female, 207 mm., LACM 33939-1.

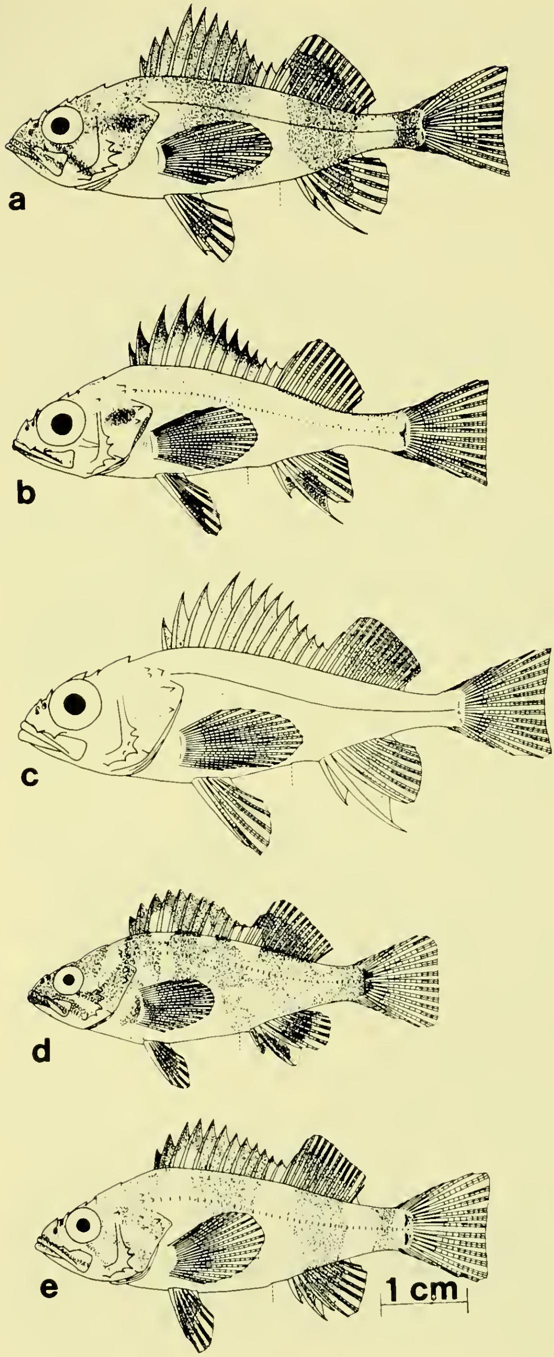

a
b
c
d
e
1 cm

Table 1. *Morphometrics (standard length/body part measurement) of* Sebastes exsul *and* Sebastes varispinis. *Characters are in sequence as given for the subgenus* Sebastomus *by Chen (1971), with the most frequently negatively allometric one placed above and the most frequently positively allometric one placed below.* "+" *means significant positive allometry and* "–" *means significant negative allometry.*

Character		*S. exsul*	*S. varispinis*
	size range, mm.	151–212	33–53
	no.	36	20
2nd anal spine		5.1 – 6.3	4.3 – 5.5
Gill-raker at angle		18 – 31	15 – 21
3rd anal spine		6.1 – 7.6	5.6 – 7.5
2nd dorsal soft-ray		5.7 – 6.9	5.1 – 7.4
1st anal spine		10.0 –12.8	8.4 –11.3
Orbit length		7.1 – 8.4	8.4 –10.0
Total length		0.81– 0.84	0.80– 0.83
4th dorsal spine		6.6 – 8.1	4.6 – 6.2
1st anal soft-ray		4.7 – 5.4	5.0 – 6.2
Anal-fin base		6.6 – 8.1	5.9 – 7.5
Pelvic-fin length		4.1 – 4.9	4.2 – 4.9
Predorsal length		2.5 – 2.8	2.8 – 3.2
Pectoral-fin length		3.1 – 3.7	3.3 – 3.8
Lower peduncle length		4.8 – 5.6	4.8 – 5.9
Soft-dorsal base		4.4 – 5.0	4.1 – 5.1
Dorsal-fin incision		12 – 16	7.6 –13.8
Caudal-peduncle depth		9.5 –11.2	10.2 –11.6
Upper peduncle length		6.6 – 8.4	6.2 – 7.6
Spinous-dorsal base		2.5 – 2.9	2.8 – 3.3
Snout length		8.7 –11.4 (+)	11.0 –13.2
Prepelvic length		2.1 – 2.5 (+)	2.3 – 2.7
Head length		2.3 – 2.4 (+)	2.6 – 3.0
Upper-jaw length		4.6 – 5.1 (+)	5.6 – 6.8
Preanal length		1.4 – 1.5	1.4 – 1.5
Body depth		2.4 – 2.8 (+)	3.2 – 3.6
Head width		4.6 – 5.4 (+)	6.3 – 8.0
Lachrymal width		27 – 38	50 – 62
Interorbital width		13 – 17 (+)	14 – 16

Description. D. XIII, 13–14; A. III, 6; P_1 18 (16–18); C. 14; rakers on first gill-arch 29–33 (9–10 + 20–23); lateral-line pores 33–41; vertebrae (in 4 specimens) 26 (11 + 15).

Base of skull straight. Interorbital concave, divided by frontal ridges into

←

Figure 2. a). *Sebastes varispinis*, holotype, subsurface juvenile, 49 mm., LACM 8821-11. b). *S. sinensis*, juvenile, 46 mm., LACM 30064-3. c). *S. cortezi*, transformed juvenile, 51 mm., SIO 68-90. d). *S. cortezi*, surface prejuvenile, 38 mm., SIO 62-239. e). *S. peduncularis*, holotype, juvenile, 43 mm., LACM 8818-6.

three grooves. Nasal, preocular, supraocular, postocular, tympanic, parietal, and, frequently, nuchal spines present, sharp, and strong. Parietal ridges well developed, elevated. Lower edge of gill-cover where interopercular and subopercular meet often with one or two spines. Preopercular spines equally spaced, the upper two directed backward, the lower two or three downcurved. Lachrymal projections two, spinelike, directed backward, sometimes bifurcate; lateral surface of lachrymal above and between lachrymal projections and orbital edge of first and second suborbitals each often bearing a sharp, backward-directed spine. Supracleithral, cleithral, and the two opercular spines well developed.

Symphyseal knob round, directed downward; jaws subequal. Maxillary reaching to vertical from posterior edge of orbit.

Scales ctenoid. Upper and lower lips and snout between and before nasal spines scaleless; branchiostegals with or without scales, head scaled elsewhere. Fin rays scaled; fin membranes scaled basally, most extensively on anal and caudal.

Dorsal spines increasing in length to 4th, then decreasing gradually to 12th, 13th spine longer than 12th; soft dorsal high, with the short posterior rays when depressed reaching to about midpoint of caudal peduncle. Second anal spine stronger and longer than third, its tip extending to about two-thirds the length of first anal soft-ray when depressed; tips of posterior anal soft-rays, when depressed, exceeded by tips of anterior anal soft-rays. Profile of anal nearly vertical. Caudal truncate. Origin of pectoral below third or fourth dorsal spines; pectoral pointed, with longest ray (usually 11th) notably longer than adjacent rays; pectoral extending beyond tip of pelvic to above anus. Origin of pelvic below 4th dorsal spine; tip of pelvic reaching to anus or falling short by one-fifth of pelvic-to-anal distance. Origin of anal below 3rd or 4th dorsal soft-ray, insertion of anal below 9th to 11th dorsal soft-ray.

Extrinsic gas-bladder muscles (one paratype examined) as in *S. exsul*.

Color in life pink to red. Body with six white blotches as in *S. exsul*. Dark green dusky patches on top and sides of head, above lateral line, and along basal part of dorsal fin, those on the back sometimes disrupted into vermiculations. Fins pink, conspicuously dusky on membranes of pectoral, soft-dorsal, and caudal. Scales on side of body with dusky margin. Gill cavity and mouth lining dusky. Peritoneum blackish. In preserved condition dusky marks become black and pink or red fade.

For morphometrics and meristics, see tables 2, 7, 8, and 9.

Etymology. The name *spinorbis*, from the Latin, refers to the spines along the lower edge of the orbit.

Discussion. Because only four specimens are available and because the several distinguishing characteristics are subject in the genus to some variation, it is difficult on the basis of single characters to differentiate *S. spinorbis* from *S. exsul*. The spine on the lateral surface of lachrymal, although not found

Table 2. *Morphometrics (standard length body part measurement), meristics ("*" signifies left and right counts), and head spines of* Sebastes spinorbis.

Character	Holotype	Paratypes		
	SIO 69-318	SIO 69-437	CAS 30689	
Standard length (mm.)	225	259	241	213.5
Morphometrics:				
2nd anal spine	5.9	5.9	5.9	5.6
Gill-raker at angle	27	24	25	25
3rd anal spine	6.4	6.9	6.4	7.1
2nd dorsal soft-ray	5.9	6.5	6.1	6.0
1st anal spine	11.1	11.2	11.0	11.4
Orbit length	8.7	8.2	8.7	8.1
Total length	0.83	0.83	0.83	0.81
4th dorsal spine	8.0	7.9	7.7	7.4
1st anal soft-ray	4.6	5.0	4.7	4.7
Anal-fin base	7.5	7.6	7.5	7.4
Pelvic-fin length	4.2	4.5	4.2	4.2
Predorsal length	2.7	2.6	2.6	2.6
Pectoral-fin length	3.3	3.4	3.1	3.3
Lower peduncle length	5.2	5.8	5.1	5.3
Soft-dorsal base	4.8	4.8	4.8	4.5
Dorsal-fin incision	15.3	15.0	15.8	14.6
Caudal-peduncle depth	9.9	10.4	9.9	9.7
Upper peduncle length	7.6	8.0	7.7	7.3
Spinous-dorsal base	2.7	2.8	2.7	2.7
Snout length	10.1	10.0	9.2	9.7
Prepelvic length	2.6	2.4	2.5	2.4
Head length	2.4	2.3	2.3	2.3
Upper-jaw length	4.8	4.4	4.7	4.6
Preanal length	1.40	1.34	1.41	1.39
Body depth	2.6	2.4	2.6	2.5
Head width	4.6	4.1	4.5	4.3
Lachrymal width	30	30	28	30
Interorbital width	15	14	13	16
Meristics:				
Lateral-line pores *	38–38	37–36	33–35	41–40
Dorsal soft-rays	13	14	13	13
Pectoral rays *	18–18	18–18	18–18	16–18
Anal soft-rays	6	6	6	6
Gill-rakers *	30–31	31–32	33–32	29–29
Head spines *:				
Nuchal	1–1	0–0	0–1	0–0
Edge of lower gill cover	2–2	1–0	2–2	2–2
Lateral surface of lachrymal	1–1	1–1	1–1	0–1
Orbital edge of 1st suborbital	0–1	0–0	1–0	0–0
Orbital edge of 2nd suborbital	1–1	0–0	0–0	0–0

in any other species of subgenus *Sebastomus*, is variably present in *Sebastiscus marmoratus* (personal data), and does not develop in *Sebastes macdonaldi* until the fish reaches 10 cm. The spines along the orbital edge of the first and second suborbitals develop only in adults in *Sebastes aleutianus*. The higher pectoral-ray count (significantly different from that of *S. exsul* at 0.01 level, rank-sum test), the lower gill-raker number (significantly different from that of *S. exsul* at 0.002 level, rank-sum test), the presence of spine(s) on lower edge of gill cover, and the dusky fin membranes, all are variable and overlap with *S. exsul*. The separation of the two species is based on: (1) the non-obligatory correlation of the above characters (higher pectoral-ray count and wider pectoral base, or larger eye and narrower lachrymal would be obligatorily correlated); (2) the larger size of the specimens of *S. spinorbis*; and (3) the co-occurrence of the two forms (taken at the same stations from the same depths.)

MATERIAL EXAMINED. Four specimens, 214–259 mm., two males and two females, all mature, but with gonads in resting stage.

Holotype. SIO 69-318, 225 mm., male, from 28° 58.5′ N., 113° 26.5′ W., 2.5 miles NE. of Punta Rojas, Bahía de los Angeles, collected by hook and line from bottom at 130–160 m., by H. G. Moser on 29 April 1969.

Paratypes. All from the type locality at depths between 130–160 m. SIO 69-437, 1 (259); CAS 30689, 2 (214–241).

Sebastes sinensis (Gilbert, 1890).

(Figures 1d and 2b.)

Sebastichthys sinensis GILBERT, 1890, p. 81 (type locality: *Albatross* Station 3015, at 29° 19′ 00″ N., 112° 50′ 00″ W.).

Pteropodus sinensis: EIGENMANN & BEESON, 1893, p. 670 (relationships); 1894, p. 397 (species analysis).

Sebastodes sinensis: CRAMER, 1895, p. 600 (species analysis). JORDAN & EVERMANN, 1896, p. 431 (placed in subgenus *Hispaniscus*); 1898, pp. 1776 & 1813 (key and description). HUBBS, 1951, p. 129 (designated as type species of subgenus *Allosebastes*).

Hispaniscus sinensis: JORDAN, EVERMANN, & CLARK, 1930, p. 368 (name only).

Sebastes sinensis: CHEN, 1971, pp. 63 & 77 (meristics and distribution).

REMARKS. M'Clelland (1843) described *Sebastes sinensis* from China. The '*sinensis*' of M'Clelland is now considered to be a junior synonym of *Sebastiscus marmoratus* and is not to be confused with the present species. Since the '*sinensis*' of Gilbert has been placed into the genus *Sebastes* previously (Chen, 1971), according to the subsection (ii) added in 1972 to the Article 59 (b) of the International Code of Zoological Nomenclature, the '*sinensis*' of Gilbert is not to be rejected for its secondarily homonymous condition.

DIAGNOSIS. *Sebastes sinensis* can be differentiated from all other species of *Sebastes* by the following combination of characters: (1) the cranial spine pattern (with sharp nasal, preocular, postocular, tympanic, parietal, and occasionally nuchal spines); (2) the meristics (D. XIII, 11 (11–13); A. III, 5–6; P_1 18 (17–19); rakers on first gill-arch 29–33); (3) division of the interorbital by frontal ridges into three shallow grooves; (4) sharp, spinelike, backward-directed lachrymal projections; (5) the oral and the gill-cavity linings jet-black; and (6) predominantly cycloid rather than ctenoid squamation.

Description. D. XIII, 11 (11–13); A. III, 6 (5–6); P_1 18 (17–19); C. 14; rakers on first gill-arch 29–33 (8–10 + 20–23); lateral-line pores 38–43 (36–46); pyloric caeca (in 6 specimens) 9–12; vertebrae (in 25 specimens) 26 (11 + 15).

Base of skull straight. Interorbital concave, divided by frontal ridges into three shallow grooves. Nasal, preocular, postocular, tympanic, parietal, and occasionally nuchal spines present, sharp, and moderately strong. Parietal ridges well developed and elevated. Lower edge of gill-cover spineless. Upper three or four preopercular spines parallel, pointing straight backward or obliquely upward, lower one or two preopercular spines tend to point downward and be more widely spaced. Lachrymal projections two, spinelike, directed backward, occasionally bifurcate. Supracleithral, cleithral, and the two opercular spines well developed.

Symphyseal knob inconspicuous in small specimens, directed downward in large ones; jaws subequal. Maxillary ending behind vertical from posterior edge of pupil but before margin of orbit.

Most scales cycloid, occasionally with weakly developed ctenii. Lips and snout between and before nasal spines scaleless; mandibles and maxillaries scaleless or rarely with patches of fine scales, skin smooth to touch; branchiostegals scaleless; head scaled elsewhere. Fin rays scaled; fin membranes scaled basally, most extensively on anal and caudal.

Dorsal spines increasing in length to 4th, then decreasing gradually to 12th, 13th spine longer than 12th; soft dorsal high, with the short posterior rays when depressed reaching to near midpoint of caudal peduncle. Second anal spine stronger and longer than third, its tip often reaching to or beyond tip of first anal soft-ray when depressed; tips of posterior anal soft-rays, when depressed, exceeded by tips of anterior anal soft-rays Profile of anal nearly vertical. Caudal truncate. Origin of pectoral below 3rd or 4th dorsal spines; margin of pectoral fin rounded, 9th to 11th rays longest; pectoral extending beyond tip of pelvic to above anus. Origin of pelvic below 4th or 5th dorsal spine; tip of pelvic reaching to anus (small specimens) or falling short by one-fourth of pelvic-to-anal distance (large specimens). Origin of anal below 4th or 5th dorsal soft-ray, insertion of anal below 9th to 10th dorsal soft-ray.

Extrinsic gas-bladder muscles (7 specimens examined) as in *S. exsul*, except that each muscle sometimes splits into only two instead of three tendons, inserting respectively on parapophyses 8 and 9, 9 and 10, or 8, 9, and 10.

Color in life pink or red, with light to heavy dusky patches on back and sides. Membranes of the edge of spinous dorsal and distal part of pectoral

Table 3. *Morphometrics of* Sebastes sinensis. *Explanations as table 1.*

Character	size range mm.	44–49	51–99	102–152
	no.	6	25	27
2nd anal spine –		3.8 – 4.4	3.6 – 4.5	4.1 – 5.2
Gill-raker at angle –		18 – 23	17 – 23	18 – 32
3rd anal spine –		4.8 – 5.7	4.7 – 5.6	4.8 – 5.8
2nd dorsal soft-ray –		5.0 – 5.8	5.1 – 6.2	5.5 – 6.5
1st anal spine		8.8 –10.8	8.2 –10.9	8.4 –11.5
Orbit length +		6.9 – 7.3	6.8 – 8.1	6.3 – 8.1
Total length –		0.78– 0.81	0.79– 0.83	0.80– 0.84
4th dorsal spine –		4.4 – 5.2	4.1 – 5.3	4.6 – 5.6
1st anal soft-ray		4.7 – 5.9	4.7 – 5.7	4.6 – 5.5
Anal-fin base –		5.9 – 7.3	6.3 – 7.6	6.7 – 8.8
Pelvic-fin length –		4.1 – 4.5	4.0 – 4.5	4.1 – 4.7
Predorsal length		2.6 – 2.7	2.6 – 2.8	2.5 – 2.9
Pectoral-fin length –		3.4 – 3.6	3.2 – 3.7	3.2 – 3.8
Lower peduncle length –		4.9 – 5.5	4.8 – 5.8	5.1 – 6.2
Soft-dorsal base		4.7 – 5.4	4.4 – 5.8	4.4 – 5.6
Dorsal-fin incision –		7.0 – 8.0	6.4 – 9.9	7.7 –10.1
Caudal-peduncle depth		11.4 –12.5	10.8 –13.1	10.2 –13.1
Upper peduncle length –		6.7 – 7.5	6.2 – 7.5	6.6 – 8.0
Spinous-dorsal base		2.7 – 3.0	2.6 – 3.0	2.6 – 3.2
Snout length +		11.6 –13.0	10.5 –12.4	9.8 –11.8
Prepelvic length +		2.4 – 2.6	2.4 – 2.7	2.3 – 2.6
Head length +		2.4 – 2.5	2.4 – 2.5	2.3 – 2.5
Upper-jaw length +		5.3 – 5.8	5.0 – 5.7	4.8 – 5.6
Preanal length +		1.5	1.4 – 1.5	1.3 – 1.4
Body depth +		3.0 – 3.2	2.7 – 3.3	2.7 – 3.1
Head width +		5.6 – 6.6	5.4 – 6.6	5.0 – 6.5
Lachrymal width +		46 – 53	41 – 52	39 – 52
Interorbital width +		16 – 17	15 – 19	14 – 17

relatively clear in juveniles but becoming conspicuously black in adults; other fin membranes dusky over pink. Specimens in alcohol pale, with dusky to black patches on the back and on various fin membranes and on the edge of the dorsal. Peritoneum and oral and gill-cavity linings jet-black.

For morphometrics and meristics, see tables 3, 7, 8, and 9.

Range. The range of this species is rather limited. In spite of the numerous collections, *S. sinensis* is definitely known only within a range of about one degree square (28° 35′ to 29° 49′ N., 112° 50′ to 113° 59′ W., see Material examined). The only exception is from a questionable record (CAS SU 123, 31° 22′ N., 114° 07′ 45″ W., 34 m., 18.4° C., 25 March 1889).

Size. *S. sinensis* is a small fish. Females as small as 99 mm., collected 18 January 1968, carry eyed embryos. The largest female examined measures 152 mm. and the largest male 147 mm.

DEPTH. Most specimens examined were collected with otter trawls at depths ranging from 290 m. to 654–670 m. Some of the specimens, however, were collected with midwater trawls far above the bottom (in one case at a depth of less than 500 m. where the bottom is at 1400 m. The circumstance that these specimens, both juveniles and adults, possess characteristics not normal to epipelagic prejuveniles of *Sebastes*, indicates that *S. sinensis* occurs mesopelagically.

MATERIAL EXAMINED. A total of 102 specimens from 46 to 150 mm.

Holotype. USNM 43085, 150 mm., adult male, from *Albatross* Station 3015, 29° 19′ 00″ N., 112° 50′ 00″ W., 290 m.

Other material. SDSC 72-28, 10 (59–133), 29° 48.7′ N., 113° 57.2′ W. SIO 68-89, 5 (104–135), 29° 43.9′ N., 113° 58.0′ W. to 29° 40.2′ N., 113° 55.4′ W. SIO 68-90, 26 (94–149), 29° 39.5′ N., 113° 55.5′ W. to 29° 43.5′ N., 113° 59.0′ W. SIO 68-102, 5 (55–62), 29° 00.5′ N., 113° 17.5′ W., to 28° 56.1′ N., 113° 12.1′ W., to 28° 47.4′ N., 113° 08.0′ W. LACM 8821-12, 5 (58–117), 28° 58′ N., 113° 11.4′ W. LACM 8818-8, 12 (106–156), 28° 55′ N., 112° 50.5′ W. LACM 30064-3, 14 (46–128), 28° 46′ 45″ N., 113° 06′ 00″ W., to 28° 35′ 36″ N., 112° 52′ 56″ W. LACM 30065-1, 22 (47–148), 28° 35′ N., 112° 52′ W., to 29° 03′ 00″ N., 113° 21′ 30″ W. CAS SU 123, 1 (119), *Albatross* Station 3026 (31° 22′ N., 114° 07′ 45″ W.).

Sebastes cortezi (Beebe and Tee-Van).

(Figures 1e, 2c, and 2d.)

Scorpaenodes cortezi BEEBE & TEE VAN, 1938, p. 304 (type locality: 24° 55′ N., 110° 20′ W.).

Sebastes cortezi was first described on the basis of suface-living prejuveniles. In the original description the species was assigned to the genus *Scorpaenodes* because of the poorly developed palatine teeth in the type. The pointed posterior end of the suborbital stay, however, indicates clearly that the species is of the genus *Sebastes*, and it was so listed by Chen (1971).

DIAGNOSIS. The combination of the cranial spine pattern (with sharp nasal, preocular, postocular, tympanic, parietal, and occasionally nuchal spines) and the forward direction of the spinous lachrymal projection in adults differentiates this species from all other species of the genus except *S. diploproa*. This species is most similar to *S. diploproa* and *S. sinensis*. It differs from the former in lacking dentigerous knobs and a conspicuous symphyseal knob and in having fewer rakers on the first gill-arch (31 or fewer). From *S. sinensis* it differs in having an anteriorly directed, spinelike lachrymal projection, a dusky rather than jet-black gill-cavity lining, ctenoid rather than cycloid scales, and more often 12 rather than 11 dorsal soft-rays.

Surface-living prejuveniles of *S. cortezi* can be distinguished from those of other species of *Sebastes* by the following combination of characters: (1)

the cranial spine pattern (with skin-covered and therefore blunt-looking spines); (2) flat or slightly concave interorbital with inconspicuous frontal ridges; (3) the meristics (D. XIII, 12 (11–12); A. III, 6 (5–6); P_1 18 (17–19); rakers on first gill-arch 27–31); (4) small eyes (8.4–10.0 in SL in 28–43 mm. specimens); and (5) a distinctive color pattern (fig. 2d).

Description. D. XIII, 12 (11–12); A. III, 6 (5–6); P_1 18 (17–19); C. 14; rakers on first gill-arch 27–31 (8–10 + 18–22), with the first 3–8 rakers on each limb of first arch often rudimentary; lateral-line pores 33–45; pyloric caeca (in 3 specimens) 9–10; vertebrae (in 33 specimens) 26 (11 + 15).

Base of skull straight. Nasal, preocular, postocular, tympanic, parietal, and occasionally nuchal spines present. Parietal ridges well developed and elevated. Lower edge of gill-cover spineless. Supracleithral, cleithral, and both opercular spines well developed.

Symphyseal knob inconspicuous; jaws subequal. Maxillary ending behind vertical from posterior edge of pupil but before margin of orbit.

Scales ctenoid. Lips and snout between and before nasal spines scaleless; mandibles and maxillaries scaleless or with patches of fine scales, skin smooth to touch; branchiostegals scaleless; head scaled elsewhere. Fin rays scaled; membranes scaled basally, most extensively on anal and caudal.

Dorsal spines increasing in length to 4th or 5th, then decreasing gradually to 12th, 13th spine longer than 12th; soft dorsal high, with the short posterior rays when depressed reaching to only about midpoint of caudal peduncle. Second anal spine stronger and longer than third, its tip reaching to tip (transformed juveniles) or falling short by one-fourth of the length (surface-living prejuveniles and large adults) of first anal soft-ray when depressed. Caudal truncate. Origin of pectoral below 2nd or 3rd dorsal spine; margin of pectoral fin rounded, 9th to 11th rays longest; pectoral extending beyond tip of pelvic to near anus. Origin of pelvic below 3rd or 4th dorsal spine; tip of pelvic reaching to anus (transformed juveniles) or falling short by one-fourth of pelvic-to-anal distance (surface-living prejuveniles and large adults). Origin of anal below 2nd dorsal soft-ray, end of anal below 10th to 11th dorsal soft-ray.

Extrinsic gas-bladder muscles (4 specimens examined) as in *S. exsul*, except that each muscle splits variably into three to six tendons, with variable insertions. Of the four specimens examined, the tendons insert on parapophyses 8, 9, 10; 4, 6, 7, 8; 4, 6, 7, 8, 9; and 5, 6, 5, 6, 7, 8 respectively.

In other respects the surface-living prejuveniles differ from the transformed stages that live below the surface. The interorbital is flat rather than being concave and divided by frontal ridges into three grooves. Cranial and fin spines are so well covered with skin to appear blunt, rather than being superficially sharp. The preopercular spines are spaced equally and radiate, rather than having the two upper ones directed backward and the three lower ones down-curved. The two lachrymal projections are blunt rather than becoming spine-

Table 4. *Morphometrics of* Sebastes cortezi. "*" *signifies significant difference (analysis of covariance, $P < .005$) between prejuveniles and transformed specimens. Other explanations as table 1.*

	Prejuveniles	Transformed specimens			
size range mm.	28–40	51–91	104–144	160–198	208–255
Character no.	20	4	5	4	2
2nd anal spine * –	5.8 – 8.1	4.0 – 5.0	4.4 – 5.9	5.1 – 6.4	5.9 – 6.9
Gill-raker at angle –	18 – 27	19 – 23	20 – 34	23 – 42	34 – 42
3rd anal spine * –	7.0 – 9.6	4.9 – 7.0	5.2 – 6.7	6.0 – 7.3	6.5 – 7.6
2nd dorsal soft-ray –	5.3 – 6.7	5.7 – 6.0	5.8 – 6.3	6.3 – 6.6	5.9 – 6.7
1st anal spine * –	10.5 –19.3	8.6 –10.3	8.8 –11.2	10.0 –13.1	11.8 –17.5
Orbit length * –	8.4 –10.1	6.6 – 7.1	6.6 – 8.0	7.3 – 7.6	8.4 – 8.5
Total length –	0.78– 0.81	0.79– 0.81	0.80– 0.81	0.81– 0.82	0.82– 0.84
4th dorsal spine * –	6.3 – 7.7	5.0 – 5.8	5.6 – 7.4	6.6 – 7.3	7.1 – 7.4
1st anal soft-ray *	5.2 – 6.7	4.7 – 6.0	4.9 – 5.5	4.9 – 5.7	5.3
Anal-fin base –	6.1 – 7.2	6.0 – 8.1	7.2 – 8.9	7.6 – 8.5	7.5 – 7.6
Pelvic-fin length –	4.5 – 5.2	4.2 – 5.0	4.5 – 5.4	4.9 – 5.3	4.9 – 5.2
Predorsal length	2.7 – 3.0	2.7 – 2.8	2.5 – 2.8	2.6	2.6 – 2.7
Pectoral-fin length *	3.6 – 4.3	3.4 – 3.7	3.3 – 3.6	3.4 – 3.7	3.6 – 3.7
Lower peduncle length *	4.5 – 5.1	5.1 – 5.7	4.7 – 5.6	5.2 – 5.5	5.2
Soft-dorsal base	4.1 – 5.0	4.7 – 4.9	4.4 – 5.3	4.6 – 4.9	4.8 – 4.9
Dorsal-fin incision * –	12 – 22	8.9 –11	11 – 17	11 – 15	12 – 14
Caudal-peduncle depth *	8.7–10.3	11.5 –12.6	11.3 –13.0	11.4 –12.2	10.9 –11.7
Upper peduncle length	6.1 – 7.5	6.8 – 7.8	7.0 – 8.0	7.1 – 8.0	7.1 – 7.5
Spinous-dorsal base +	2.7 – 3.0	2.9 – 3.1	2.6 – 2.9	2.6 – 2.8	2.5 – 2.8
Snout length	9.3 –11.4	10.2 –12.4	9.5 –11.9	10.1 –11.4	9.9 –10.7
Prepelvic length	2.4 – 2.7	2.4 – 2.5	2.4 – 2.7	2.4 – 2.7	2.4 – 2.5
Head length *	2.6 – 2.8	2.4	2.3 – 2.5	2.4 – 2.5	2.2 – 2.5
Upper-jaw length	5.5 – 6.3	5.1 – 5.5	4.9 – 5.8	5.0 – 5.3	4.7 – 5.2
Preanal length	1.5 – 1.6	1.4 – 1.5	1.3 – 1.5	1.4 – 1.5	1.4
Body depth * +	2.8 – 3.3	3.0 – 3.1	2.8 – 3.1	2.7 – 2.8	2.6 – 2.8
Head width +	5.1 – 6.5	5.6 – 5.8	5.5 – 5.8	4.8 – 5.2	4.2 – 4.7
Lachrymal width +	36 – 55	40 – 51	35 – 42	38 – 41	31 – 40
Interorbital width *	13 – 16	15 – 19	15 – 20	14 – 17	13 – 15

like, with the anterior one directed forward and both occasionally bifurcate. Tips of posterior anal soft-rays, when depressed, exceed rather than are exceeded by tips of anterior anal soft-rays. Profile of anal slanting slightly posteriorly, rather than being vertical.

Life color of surface juveniles, as quoted from the original description: "Body dark reddish-brown with a yellowish tinge, paler below, the entire body covered with black punctulations and irregular greenish-yellow blotches, the latter especially marked posteriorly. Dorsal fin dark brown, the membranes of the spinous dorsal black, the soft dorsal irregularly blotched with lighter. Caudal fin yellowish-green, without pattern. Pectoral fin brownish, yellow

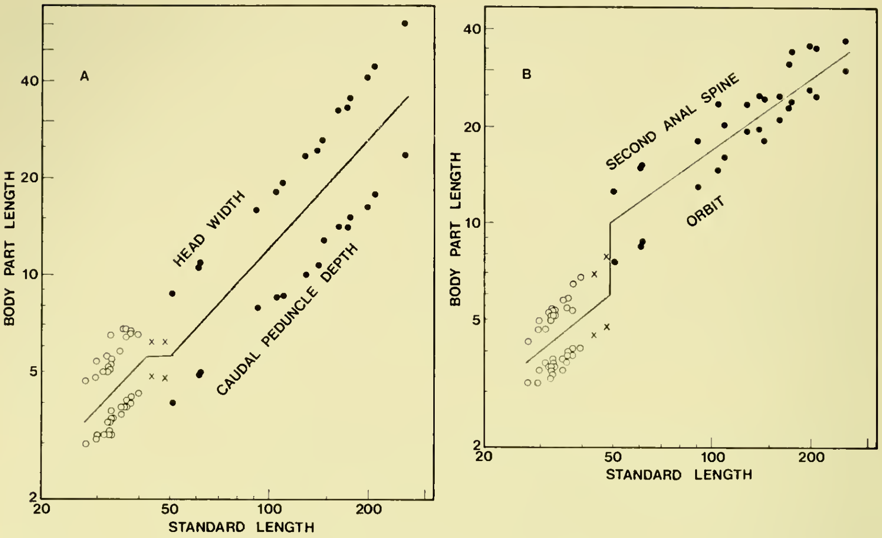


FIGURE 3. A) Head width and caudal peduncle depth and B) second anal spine length and orbit length of *Sebastes peduncularis* (x), and prejuvenile (open circles) and transformed (solid dots) *S. cortezi.*

toward the tip and dusky at the base. Pelvic fins black at base, yellow at tips and with scarlet along the anterior edge. Anal fin black at base, yellow on outer half and with a small scarlet patch at base of the first spine." Specimens in alcohol light brown, with dusky marks in pattern as illustrated (fig. 2d). Peritoneum and oral and gill-cavity linings slightly dusky.

Life color of adults pink, with trace of dusky. Specimens in alcohol pale, with trace of dusky on back, on various fin membranes, and on edge of dorsal. Peritoneum dusky to jet-black. Oral and gill-cavity linings slightly dusky.

For morphometrics and meristics, see tables 4, 7, 8, and 9.

DISCUSSION. In fishes, transition from epipelagic to benthic stages often is associated with a growth infection, resulting in altered body form, as demonstrated in *Pseudupeneus maculatus* by Caldwell (1962) and in *Sebastolobus* species by Moser (1974). The surface-living prejuveniles (28–43 mm.) and the transformed specimens (51–255 mm.) of *Sebastes cortezi* differ markedly in appearance, as is indicated in the species description. In addition, the surface-living prejuveniles have a number of significantly different morphometrics, particularly the heavier caudal peduncle, the smaller eye, and the shorter dorsal and anal spines (table 4, fig. 3). Many of the same differences, however, also exist (personal observation and George Boehlert, personal communication) between epipelagic prejuveniles and benthic forms in *S. diploproa*, a species the adults of which are most similar to the 15 transformed specimens herein called *S. cortezi*. It is on the basis of the known ontogenetic changes in the closely related *S. diploproa* and the identical meristics (tables 7, 8, and 9) that I consider the 15 specimens to be the older stage of *S. cortezi*.

Range. Chen (1971) in giving the range of this species as 26° N., 111° 49′ W. to 29° N., 113° 30′ W., overlooked the type locality and listed the transformed specimens of the species as species "a." The corrected range of *S. cortezi* should be 24° 55′ N., 110° 20′ W. to 29° 43.9′ N., 113° 58.0′ W.

Depth. Ten of the 15 transformed specimens examined, including the several largest and the several smallest, were collected by otter or beam trawls at depths ranging from 200–270 to 800–1100 m. The other five specimens (91–160 mm. long), however, were collected with midwater trawls in areas with 1000–1060 and 1400–1700 m. of water. The exact depth of capture of these specimens cannot be determined but presumably they were mesopelagic.

Size. The largest male examined measures 255 mm.; the largest female examined, 207 mm. This 207 mm. female was collected on 2 December 1967; its ovary contains large ova.

Material examined. A total of 93 specimens.

Surface-living prejuveniles: 78 (15.5–43).

Holotype. CAS SU 46503 (formerly Dept. Trop. Res. N. Y. Zool. Soc. 24889-A), 43.4 mm., taken at surface in weed, at 24° 55′ N., 110° 20′ W., 8 April 1936.

Other specimens. SIO 62-239, 77 (15.5–39.8), 29° N., 113° 30′ W., also taken at surface in weed.

Transformed specimens: 15 (51–255).

SIO 68-89, 2 (61), 29° 43.9′ N., 113° 58.0′ W. to 29° 40.2′ N., 113° 55.4′ W. SIO 68-90, 5 (51–198), 29° 39.5′ N., 113° 55.5′ W. to 29° 43.5′ N., 113° 59′ W. SIO 59-205, 4 (91–139), 28° 45.0′ N., 113° 03.4′ W. LACM 33939-1, 2 (144–207), 28° 38′ N., 113° 00′ W. to 28° 33′ N., 112° 50′ W. LACM 30065-6, 1 (160), 28° 35′ 26″ N., 112° 52′ 56″ W. to 29° 03′ 00″ N., 113° 21′ 30″ W. LACM 8837-3, 1 (255), 26° 59.1′ N., 111° 48.9′ W.

Sebastes varispinis Chen, new species.

(Figure 2a.)

Diagnosis. *Sebastes varispinis* can be differentiated from all other eastern North Pacific species of *Sebastes* by the following combination of characters: (1) the cranial spine pattern (with sharp nasal, preocular, postocular, tympanic, parietal, occasionally nuchal, and, rarely, coronal spines); (2) presence of frontal ridges; (3) the meristics (D. XII–XIII, 11–12 (11–13); A. III, 5–6 (5–7); P_1 18 (17–19); rakers on first gill-arch 29–33); (4) slightly protruding lower jaw; (5) small eyes (orbit 8.4–10.0 in S. L. in 33–53 mm. specimens); (6) slender caudal peduncle (peduncle depth 10.3–11.6 in S. L. in 33–53 mm. specimens); (7) the oral and the gill-cavity linings black; and (8) a color pattern as illustrated (fig. 2a).

Although the present species description is based on juveniles and no adults are known, the black oral and gill-cavity linings and the protruding lower jaw (two characters that are believed to persist into the adult stage), together with the tendency for reduction of the number of dorsal spines from 13 to 12, and the ctenoid rather than cycloid scales will differentiate adults of this species from those of other species of *Sebastes* in the Gulf.

Description. D. XII–XIII, 11–12 (11–13); A. III, 5–6 (5–7); P_1 18 (17–19); C. 14; rakers on first gill-arch 29–33 (8–10 + 20–23); lateral-line pores 37–44; pyloric caeca (in 2 specimens) 9; vertebrae (in 32 specimens) 26 (11 + 15).

Base of skull straight. Interorbital divided by frontal ridges into three shallow grooves. Nasal, preocular, postocular, tympanic, parietal, occasionally nuchal, and rarely coronal spines present, sharp, and moderately strong; many of the specimens have pterotic spines although this is probably a juvenile characteristic (Moser, 1972). Parietal ridges well developed and elevated. Lower edge of gill-cover spineless. Upper four preopercular spines directed backward, lowermost preopercular spine directed downward and often more widely spaced. Lachrymal projections two, spinelike, directed downward and backward. Supracleithral, cleithral, and the two opercular spines well developed.

Symphyseal knob inconspicuous. Tip of lower jaw projecting beyond that of upper. Maxillary reaching to between verticals from mid-orbit and posterior margin of pupil.

Scales ctenoid, many of the specimens examined have scales with a single spine. Mandibles, maxillaries, branchiostegals, and the head before eyes scaleless; head scaled elsewhere.

Dorsal spines increasing in length to 4th or 5th, then decreasing gradually to 11th, 12th spine often slightly longer than 11th, 13th spine nearly twice as long as 11th; soft dorsal high, with the short posterior rays when depressed reaching to near midpoint of caudal peduncle. Second anal spine stronger and longer than third, its tip nearly reaching to tip of first anal soft-ray when depressed; tips of posterior anal soft-rays, when depressed, sometimes exceeded by tips of anterior anal soft-rays. Profile of anal nearly vertical. Caudal truncate. Origin of pectoral below 2nd to 4th dorsal spine; margin of pectoral fin rounded, 8th to 11th rays longest; tip of pectoral extending to anus. Origin of pelvic below 3rd and 4th dorsal spines; tip of pelvic reaching to three-fourths to four-fifths of the length of the pelvic-to-anal distance. Origin of anal below 3rd or 4th dorsal soft-ray, insertion of anal below 9th to 11th dorsal soft-ray.

Extrinsic gas-bladder muscles (2 specimens examined) as in *S. exsul,* except that each muscle splits into only two instead of three tendons and these insert respectively on the parapophyses of the 9th and 10th centra.

Specimens in alcohol light brown, with dusky to black patches on body and various fins (fig. 2a). Pectoral and caudal membranes clear. Peritoneum jet-black. Oral and gill-cavity linings black.

For morphometrics and meristics, see tables 1, 7, 8, and 9.

ETYMOLOGY. The name *varispinis*, from the Latin, refers to the variation in the number of dorsal spines.

MATERIAL EXAMINED. A total of 61 specimens, 33–56 mm., all juveniles collected with midwater trawls between surface and 500 m. (bottom at 1400 m.).

Holotype. LACM 8821-11, 49 mm., 28° 58′ N., 113° 11.4′ W.

Paratypes. LACM 8821-8, 60 (33–56) collected with the holotype.

Sebastes peduncularis Chen, new species.

(Figure 2e.)

DIAGNOSIS. Juveniles of *S. peduncularis* can be differentiated from those of other eastern North Pacific species of *Sebastes* by the following combination of characters: (1) the cranial spine pattern (with sharp nasal, preocular, postocular, tympanic, and parietal spines); (2) the meristics (D. XIII, 12–13; A. III, 6; P_1 18; rakers on first gill arch 29–30); (3) presence of frontal ridges; (4) subequal jaws; (5) small eyes (orbit length 8.0–10.0 in S. L. in 43–47 mm. specimens); (6) deep caudal peduncle (peduncle depth 9.0–10.0 in S. L. in 43–47 mm. specimens); (7) narrow body (head width 7.1–7.7 in S. L. in 43–47 mm. specimens); and (8) a color pattern as illustrated (fig. 2e).

DESCRIPTION. D. XIII, 12–13; A. III, 6; P_1 18 (17–18); C. 14; rakers on first gill arch 29–30 (8–9 + 21); lateral-line pores 39–43; vertebrae (in 2 specimens) 26 (11 + 15).

Base of skull straight. Interorbital slightly concave, divided by frontal ridges into three concave grooves. Nasal, preocular, postocular, tympanic, and parietal spines present, sharp, and moderately strong. Parietal ridges well developed and elevated. Lower edge of gill cover spineless. Upper four preopercular spines directed backward, lowermost preopercular spine directed downward and spaced wider. Lachrymal projections two, sharp but not spine-like. Supracleithral, cleithral, and the two opercular spines well developed.

Symphyseal knob inconspicuous; jaws subequal. Maxillary reaching to beyond vertical from posterior margin of pupil.

Scales ctenoid, with 2–3 ctenii on the scales of both specimens.

Dorsal spines increasing in length to 4th, then decreasing gradually to 11th, 12th spine nearly as long as 11th, 13th spine longer than 12th; soft dorsal high, with the short posterior rays when depressed reaching to near midpoint of caudal peduncle. Second anal spine stronger and longer than third, its tip reaching to about three-fourths the length of first anal soft-ray when depressed; tips of posterior anal soft-rays, when depressed, exceed tips of anterior soft-rays. Profile of anal slanting somewhat posteriorly. Origin of pectoral below 3rd dorsal spine;

TABLE 5. *Morphometrics (standard length/body part measurement) and meristics ("*" signifies left count and right count) of* Sebastes peduncularis.

Character	Paratype LACM 8818-11	Holotype LACM 8818-6
Standard length	48.0	44.0
Morphometrics:		
2nd anal spine	6.1	6.3
Gill-raker at angle	25	24
3rd anal spine	7.4	7.1
2nd dorsal soft-ray	6.2	5.3
1st anal spine	13.0	12.6
Orbit length	10.0	9.8
Total length	0.84	0.79
4th dorsal spine	6.9	6.5
1st anal soft-ray	5.8	5.9
Anal-fin base	6.7	6.3
Pelvic-fin length	4.8	4.6
Predorsal length	3.1	2.9
Pectoral-fin length	4.2	3.9
Lower peduncle length	5.1	4.9
Soft-dorsal base	4.7	5.2
Dorsal-fin incision	16	13
Caudal-peduncle depth	10.0	9.0
Upper peduncle length	7.6	6.1
Spinous-dorsal base	3.0	2.9
Snout length	12.0	11.6
Prepelvic length	2.6	2.6
Head length	2.8	2.7
Upper-jaw length	6.9	6.1
Preanal length	1.48	1.49
Body depth	3.0	3.0
Head width	7.7	7.1
Lachrymal width	60	55
Interorbital	15.5	14.2
Meristics:		
Lateral-line pores *	43–40	39––
Dorsal soft-rays	13	12
Pectoral rays *	18–18	18–17
Anal soft-rays	6	6
Gill-rakers *	30–30	29–29

margin of pectoral fin rounded, 10th ray longest; tip of pectoral extending to near anus. Origin of pelvic below 4th dorsal spine; tip of pelvic reaching to two-thirds the length of the pelvic-to-anal distance. Origin of anal below 3rd or 4th dorsal soft-ray, end of anal below 10th or 11th dorsal soft-ray.

Specimens in alcohol light brown with faint marks in pattern as illustrated (fig. 2e). Peritoneum dusky. Oral and gill-cavity linings slightly dusky.

For morphometrics and meristics, see tables 5, 7, 8, and 9.

Discussion. Considering the morphological changes involved in metamorphosis from the surface-living prejuvenile stage to the juvenile stage in *S. cortezi,* it is very difficult to establish the validity of *S. peduncularis* without a series of specimens of different sizes. Meristics do not differentiate this form from *S. cortezi, S. varispinis,* or *S. sinensis.* The two specimens of *S. peduncularis* agree with prejuveniles of *S. cortezi* in having short dorsal and anal spines and pectoral fins, small eyes and head, deep caudal peduncle, and broad interorbital (fig. 3); and agree with transformed juveniles of *S. cortezi* in having frontal ridges and sharp cranial and fin spines. These two specimens are intermediate in size between specimens of *S. cortezi* of the the two contrasting stages. Since the two specimens were captured in a midwater trawl and as they show only a trace of the dark vertical bands characteristic of surface-living juveniles, they probably were in the process of transforming to the juvenile stage. However, although the two specimens have a mixed combination of the prejuvenile and juvenile characteristics of *S. cortezi,* none of the characteristics are intermediate between the two stages. That the two specimens of *S. peduncularis* are specifically distinct from *S. cortezi* is suggested by their characteristic color pattern (fig. 2e) not intermediate between the two stages of *S. cortezi,* by their narrow head (fig. 3), and by the dorsal soft-ray count of 13 and the gill-raker count of 30 in the paratype, two rather unusual counts for *S. cortezi.*

The distinction between *S. peduncularis* and *S. varispinis* is much more apparent, as the specimens of the two species available are probably in a similar stage of development. Compared with juveniles of *S. varispinis,* the two specimens of *S. peduncularis* have shorter fin spines, gill-rakers, and pectoral fins; deeper caudal peduncle and body; and much lighter pigmentation in the gill cavity and oral linings. Furthermore, they lack the protruding lower jaw of *S. varispinis.*

From *S. sinensis, S. peduncularis* can be distinguished by having ctenoid rather than cycloid scales.

Etymology. The name *peduncularis,* from the Latin, refers to the deep caudal peduncle of this species.

Material examined. Only two specimens are known.

Holotype. LACM 8818-6, 43 mm., juvenile, collected with midwater trawl from 28° 55′ N., 112° 50.5′ W., midway between southern tip of Tiburon Island and Angel de la Guarda Island, the water depths were 440–450 m. and the trawl was operated between bottom and surface (Lavenberg & Fitch, 1966).

Paratype. LACM 8818-11, 47 mm., collected together with the holotype.

Sebastes macdonaldi (Eigenmann & Beeson).

(Figure 1a.)

Sebastodes proriger (not of Jordan & Gilbert): EIGENMANN & EIGENMANN, 1890, p. 15 (description).

Acutomentum macdonaldi EIGENMANN & BEESON, 1893, p. 669 (type locality: San Diego). JORDAN, EVERMANN, & CLARK, 1930, p. 366 (name only).

Sebastodes macdonaldi: CRAMER, 1895, p. 594 (species analysis). JORDAN & EVERMANN, 1898, p. 1786 (species analysis, description). PHILLIPS, 1957, p. 90 (key, description, range, depth, size).

Sebastes macdonaldi: CHEN, 1971, p. 75 (range). MOSER, 1972, pp. 941–958 (development, distribution).

DIAGNOSIS. The presence of a spine on the lateral surface of lachrymal (in specimens larger than 10 cm.) and three or four spines on the lower edge of lachrymal and the high lateral-line pore count (> 50) differentiate this species from all other species of *Sebastes*.

DESCRIPTION. D. XIII, 13 (12–14); A. III, 7; P_1 19 (18–20); C. 14; rakers on first gill-arch 36–42 (10–13 + 25–29); lateral-line pores 52–58; pyloric caeca (in 3 specimens) 8–11; vertebrae (in 12 specimens) 26 (12 + 14).

Base of skull straight. Interorbital flat in juveniles, slightly convex in adults, without frontal ridges. Nasal, preocular, postocular, tympanic, parietal, and frequently supraocular (nearly 50%) and nuchal (nearly 30%) spines present, sharp, and moderately strong but recumbent. Parietal ridges well developed, low. Lower edge of gill-cover spineless. Preocular spines equally spaced, the two upper ones directed backward, the three lower ones downcurved. Lachrymal projections three or four, spinelike; lateral surface of lachrymal with a retrorse spine above the second lachrymal projection near edge of orbit in specimens longer than 10 cm. Upper edge of second suborbital with a small spine in specimens less than 5 cm. Supracleithral, cleithral, and the two opercular spines well developed.

Symphyseal knob conspicuous and directed forward in juveniles, inconspicuous in adults; lower jaw definitely projecting, entering dorsal profile of head. Maxillary ending behind vertical from posterior edge of pupil but before margin of orbit.

Scales ctenoid, small. Head fully scaled, with the exception of the lips. Fin rays scaled; membranes scaled basally, most extensively on anal and caudal.

Dorsal spines increasing in length to 4th, then decreasing gradually to 12th, 13th spine longer than 12th; soft dorsal high, with the short posterior rays when depressed reaching to only about one-third the distance between dorsal insertion and caudal base. Second anal spine shorter than 3rd, tip of 3rd spine reaching to about one-fifth (large specimens) to one-half (small specimens) the length of first anal soft-ray when depressed; tips of posterior anal soft-rays reaching to about one-third the distance between anal insertion and caudal base, exceed-

Table 6. *Morphometrics of* Sebastes macdonaldi. "*" signifies significant difference *(Analysis of covariance, $P < .005$) between the Gulf and the outer coast samples. Other explanations as table 1.*

Character		Outer coast					Gulf
	size range mm.	55–85	145–238	275–319	379–396	476–513	135–227
	no.	6	9	6	2	3	7
2nd anal spine * –		6.9 – 8.9	8.9 –10.9	10.6 –13.8	13.1 –15.5	13.0 –15.7	7.7 –10.2
Gill-raker at angle –		17 – 20	18 – 22	18 – 27	24 – 29	20 – 43	18 – 20
3rd anal spine * –		7.9 – 9.3	8.8 –10.5	10.7 –12.7	12.0 –13.5	12.5 –13.0	7.5 – 9.5
2nd dorsal soft-ray		6.2 – 7.9	6.7 – 8.3	6.9 – 7.9	6.8 – 7.1	7.0 – 7.9	6.8 – 8.1
1st anal spine * –		11 – 18	16 – 23	18 – 23	22	21 – 28	13 – 23
Orbit length –		8.8 – 9.6	8.3 –10.3	9.4 –10.4	10.9 –11.1	11.2 –11.7	8.6 – 9.4
Total length –		0.79– 0.82	0.81– 0.84	0.81– 0.84	0.82– 0.84	0.79– 0.83	0.81– 0.85
4th dorsal spine –		6.0 – 6.7	7.2 – 8.5	7.3 – 9.4	7.8	7.5 – 8.1	6.7 – 7.3
1st anal soft-ray		5.5 – 6.7	6.4 – 7.6	6.1 – 6.8	5.7 – 6.7	6.0 – 6.4	6.1 – 6.8
Anal-fin base –		6.7 – 7.0	7.0 – 8.1	7.9 – 8.3	7.4 – 8.0	7.8 – 8.1	7.3 – 7.9
Pelvic-fin length –		4.4 – 5.0	5.1 – 5.6	5.3 – 5.5	5.0	5.2 – 5.6	5.1 – 5.6
Predorsal length		2.8 – 3.0	2.8 – 2.9	2.8 – 3.0	2.8 – 2.9	2.9	2.8 – 2.9
Pectoral-fin length –		3.1 – 3.9	3.5 – 4.1	3.8 – 3.9	3.6 – 3.8	3.8 – 4.0	3.5 – 3.8
Lower peduncle length		5.0 – 5.5	4.8 – 5.5	5.0 – 5.9	4.9 – 5.0	5.2 – 5.6	5.0 – 5.3
Soft-dorsal base +		4.6 – 5.1	4.6 – 5.4	5.0 – 5.4	5.1 – 5.2	4.9 – 5.3	4.7 – 5.7
Dorsal-fin incision		13 – 21	14 – 19	14 – 22	17 – 18	13 – 20	15 – 19
Caudal-peduncle depth +		11 – 13	12 – 14	12 – 13	12	11 – 12	12 – 14
Upper peduncle length		6.5 – 7.9	6.5 – 7.4	5.2 – 6.7	6.4 – 7.0	6.9 – 7.0	6.5 – 7.6
Spinous dorsal base +		2.8 – 3.0	2.7 – 3.0	2.7 – 2.8	2.6 – 2.9	2.6 – 2.8	2.5 – 2.9
Snout length +		10 – 12	11 – 12	10 – 12	10	9.2 –10.0	10.4 –11.3
Prepelvic length		2.4 – 2.6	2.5 – 2.8	2.4 – 2.5	2.5 – 2.6	2.4 – 2.5	2.4 – 2.5
Head length +		2.4 – 2.7	2.4 – 2.5	2.4 – 2.6	2.4 – 2.5	2.4 – 2.5	2.4 – 2.5
Upper-jaw length * +		5.7 – 6.4	5.3 – 5.7	5.3 – 5.5	5.2 – 5.3	5.2 – 5.3	5.1 – 5.4
Preanal length +		1.4 – 1.5	1.4 – 1.5	1.4	1.4	1.3 – 1.4	1.4 – 1.5
Body depth +		3.1 – 3.2	3.0 – 3.3	2.9 – 3.3	2.9 – 3.0	2.8 – 2.9	2.8 – 3.2
Head width +		6.0 – 7.2	5.5 – 6.6	5.2 – 6.5	5.7 – 6.1	4.9 – 5.8	5.5 – 6.5
Lachrymal width +		43 – 62	36 – 42	31 – 37	27 – 29	28 – 30	35 – 41
Interorbital width +		13 – 14	13 – 15	13 – 14	12	12	13 – 14

ing tips of anterior anal soft-rays when fin depressed. Profile of anal slightly slanting posteriorly. Caudal slightly forked. Origin of pectoral below 3rd or 4th dorsal spine; pectoral pointed; 10th or 11th ray longest; pectoral extending to beyond tip of pelvic, with tip reaching to anus in small specimens but not in large specimens; origin of pelvic below 3rd to 4th dorsal spine; tip of pelvic extending to one-half (large specimens) to three-fourths (small specimens) of pelvic-to-anal distance; origin of anal below 2nd to 3rd dorsal soft-ray, insertion of anal below 10th to 11th dorsal soft-ray.

Extrinsic gas-bladder muscles (2 specimens examined) as in *S. exsul*, except that each muscle splits into four tendons which insert respectively on parapophyses 6, 7, 8, and 9.

Color in life chocolate brown on back, grading to dull red beginning from below the conspicuous light lateral line. Cheek with three oblique dark bands, one behind eye, one below eye, and one on posterior part of maxillary. Dorsal and caudal fin membranes wholly dark brown; pectoral membrane black, mixed with trace of red; pelvic and anal membranes red, with trace of black. Peritoneum black. Oral and gill-cavity linings slightly dusky. Juveniles smaller than 10 cm. have conspicuous dark vertical bands on body in pattern similar to that of the other species illustrated in figure 2.

For morphometrics and meristics, see tables 6, 7, 8, and 9.

RANGE. *S. macdonaldi* occurs from 36° 18′ N., 122° 04′ W. to 23° 24.0′ N., 111° 11.5′ W. along the outer Pacific coast (Chen, 1971) and from 26° 59.1′ N., 111° 48.9′ W. to 28° 58′ N., 113° 11.4′ W. in the Gulf of California (Moser, 1972). It is the only species of *Sebastes* known to occur both inside and outside the Gulf of California. Chen (1971) suggested that the distribution of the species may be continuous around the tip of Baja California. A comparison made between materials from the two sides of Baja California (tables 6, 7, 8, and 9), however, discloses significant differences in a number of characters. The Gulf sample has longer lower jaw and anal spines ($p << 0.005$, analysis of covariance) and a higher frequency of 20 pectoral rays and 12 dorsal soft-rays ($p < 0.01$, Chi-square test). These suggest isolation of the two populations.

DEPTH AND SIZE. Phillips (1957) gave the maximum depth for the species as 65 fms. (130 m.) and (1968) the maximum size for the species as 26 in. ($\simeq$ 53 cm. S. L.). I herein report a new depth record of 350 m. (SIO 65-64).

MATERIAL EXAMINED. A total of 84 specimens, 33-532 mm.

Gulf of California. LACM 8821-9, 6 (33–46); LACM 8837-4, 1 (227); SIO 73-1, 3 (135–176); SIO 73-2, 3 (174–180).

Outer coast. SIO 54-153, 2 (310–318); SIO 65-126, 4 (478–532); SIO 65-194, 8 (272–322); SIO 65-217, 9 (258–316); SIO 65-227, 11 (60–72); SIO 65-230, 2 (385–405); SIO 68-5, 1 (307); SDSC 72-52, 1 (85); SDSC 72-30, 33 (145–238).

Table 7. *Pectoral-ray, dorsal-soft-ray, and anal-soft-ray counts of the rockfishes of the Gulf of California.*

	Pectoral (left + right)								Dorsal soft-rays				Anal soft-rays			Dorsal spines			
	33	34	35	36	37	38	39	40	11	12	13	14	5	6	7	12	13	14	15
S. spinorbis		1		3							3	1		4			4		
S. exsul	2	29	3	2						18	18		3	32			35		1
S. macdonaldi																			
Gulf						7	2	4		5	5	2			12		12		
Outer coast				1	3	34	7	1		4	37	3		2	42	2	41	1	
S. cortezi																			
Prejuveniles		3	4	12	1				4	16			5	15		1	20		
Older stages			2	7	4	2			3	12			1	14			15		
S. sinensis		2	6	52	5	2			41	26	1		24	43	1	3	62	3	
S. varispinis		2	3	20	1	2			17	29	2		10	37	1	10	38		
S. peduncularis			1	1						1	1			2			2		

TABLE 8. *Total gill-raker counts (left + right) of the rockfishes of the Gulf of California.*

	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82
S. spinorbis					1			1		1		1																	
S. exsul										1	4	5	8	6	3	4	2	2		1									
S. macdonaldi																													
Gulf																				1	5	2	1	2					
Outer coast																				1	7	15	11	5	2	3	1	0	1
S. cortezi																													
Prejuveniles	1	1	7	3	5	3																							
Older stages	2		4		2	2	3	1	1																				
S. sinensis					3	7	11	12	20	7	4	3	1																
S. varispinis					2		2	8	10	2	3		1																
S. peduncularis					1		1																						

Table 9. *Lateral-line-pore counts (left + right) of the rockfishes of the Gulf of California.*

	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91
S. spinorbis	1					1			1					1										
S. exsul			3	1			3	3	5	5	4	4	4		2			1						
S. cortezi																								
Prejuveniles					1					1	2			4	2	3	3	1	1					
Older stages		1								1		1		2	4						1			
S. sinensis								1	2	3	2	7	1	7	3	3	2	1	3	1				1
S. varispinis										1	4			1	2		1	1						
S. peduncularis																1								
	105	106	107	108	109	110	111	112	113	114	115	116												
S. macdonaldi																								
Gulf			1	1			2			1														
Outer coast	1	1	1	3	1	6	3	1	3	1		1												

RELATIONSHIPS, ZOOGEOGRAPHY, AND SPECIATION

Although at least seven species of *Sebastes* have been recognized there, with but a few exceptions their known occurrence in the Gulf of California is restricted to the area between 27° N. and 30° N., centering around the vicinity of Canal de las Ballenas west of Isla Angel de la Guarda and Isla Tiburón (fig. 4). Within this area, however, some of the species, such as *S. macdonaldi*, occur in great abundance, as is found in the catches of the 1972 FAO Hake Resource Survey of the *Alejandre Humboldt* (AH 72-03, David Kramer, personal communication). Walker (1960) listed a number of temperate species restricted to, or most common in, this area.

This pattern of distribution seems to be related to the distribution of water temperature and dissolved oxygen in the Gulf of California. At the tip of Baja California there is an oceanic front, at times with a sharp temperature gradient of from 20° C. in the northwest to 27° C. in the southeast across a distance of only one degree of latitude (Cromwell & Reid, 1956; Griffiths, 1965; and Reid *et al.*, 1958). As the warmest water in which pelagic *Sebastes* larvae have been found is 18.08° C. (CCOFI 5604, 127G. 40, Scripps Inst., Oceanogr., 1963; Oceanic observations of the Pacific, 1956), this oceanic front forms a surface barrier probably not transgressible by *Sebastes*. The surface temperature southeast of the front fluctuates seasonally, with a minimum consistently above 18° C. This condition usually extends northward into the Gulf, with the exception of the vicinity of Canal de las Ballenas where the winter surface temperature (14° C.) is significantly lower, probably caused by the strong local tidal mixing (Roden, 1964). This appears to be the only area in the Gulf where conditions favor the survival of *Sebastes* during their pelagic juvenile stage.

Although most parts of the Gulf have surface water too warm for *Sebastes*, adults of *Sebastes* capable of submerging should find suitable temperatures at depth from Ballenas Channel to the south. South of a submarine ridge south of the Ballenas Channel, however, an oxygen-minimum layer extends in from the North Pacific between 200 m. and 1000 m., with an oxygen concentration of from 0.5 ml./l. to as low as < 0.1 ml./l. (Roden, 1964), lower than the lethal limit for most of the fishes as compiled by Doudoroff and Shumway (1970). This makes deep-water transgression from the outer coast into the upper Gulf also a difficult task for *Sebastes*. The only area in the Gulf with habitats favorable to *Sebastes* is thus the vicinity of Ballenas Channel where surface water is cold enough in the winter to allow a successful pelagic life for the larvae and where at depth (150–600 m.) the temperature is probably low enough (12–16° C.) throughout the year for the adults, and the oxygen level (> 1.0 ml./l.) is adequate.

The high surface temperature and the oxygen-minimum layer in deep water in the south not only limit the distribution of *Sebastes* in the Gulf but probably also create a dispersal barrier contributing to speciation in *Sebastes*. Recent

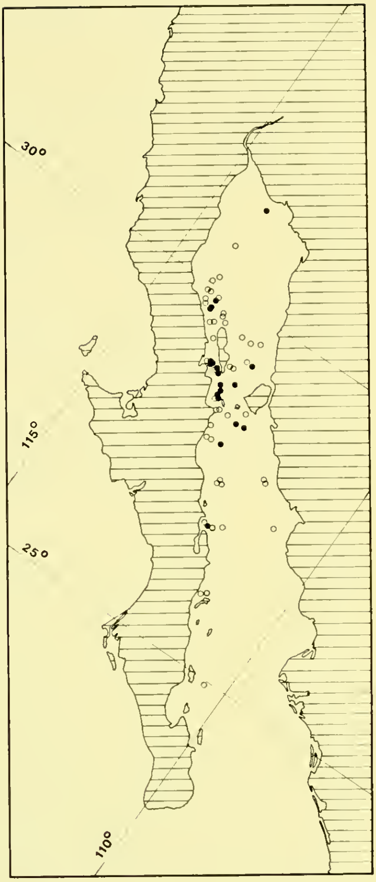


Figure 4. Distribution of *Sebastes* in the Gulf of California. Open circles: surface collections, included are a number of collections from CCOFI (courtesy of H. G. Moser) and UCLA not listed in this report. Solid dots: mesopelagic or benthic collections.

geological studies (Larson, 1972; and Elders *et al.*, 1972) suggest that the Gulf of California originated about four million years ago as a result of northwestward rifting of Baja California and southern and central California along the San Andreas Fault. The first successful invasion of the Gulf by *Sebastes* was apparently a much more recent event, after the development of an area in the Gulf such as the present Ballenas Channel, with conditions favorable to *Sebastes* and during a period of oceanic cooling allowing surface transgression (rather than bottom, assuming the oxygen-minimum layer has existed since the origin of the Gulf). Repeated Pleistocene glaciation is an apparent mechanism providing opportunities for such invasion from the outer coast into the Gulf and the reciprocal events, contributing to the diversity of *Sebastes* both inside and outside the Gulf. An analysis of the relationships among the species will shed some light on the history of such events.

The seven species in the Gulf seem to represent three sets of species. *S. macdonaldi* is an independent lineage and is represented also by population(s) in the outer Pacific waters. The low degree of differentiation of the population of this species in the Gulf from its parental population(s) on the outer coast suggests that the present disjunction in distribution originated rather recently. *S. macdonaldi* is the species of *Sebastes* with the southernmost known limit (23° 24.0′ N.) (Chen, 1971).

The other six species are all Gulf of California endemics. Of the six, *S. exsul* and *S. spinorbis* form a pair, with vermiculations and/or dusky marks on the back and with dusky scale margins characteristic of the *umbrosus-lentiginosus* and the *chlorostictus-rosenblatti-eos* complexes of the subgenus *Sebastomus* recently reviewed by Chen (1971). The close relationship between *S. exsul* and *S. umbrosus* is also supported by the identical hemoglobin electropherograms demonstrated by Sharp (1973). At the present, off southern California, *Sebastomus* is represented by four sets of species (*constellatus*, *rosaceus-helvomaculatus-simulator*, *ensifer-notius*, and *umbrosus-lentiginosus-chlorostictus-rosenblatti-eos*, three of which contain shallow water species (*constellatus*, *rosaceus*, and *umbrosus*) which are more likely to accomplish surface transgression. The present number of species in these species groups suggests that group divergence is not a very recent event. The *exsul-spinorbis* pair does not represent a separate species group but rather belongs to one of the four sets, suggesting that this lineage was distinct prior to the invasion of the Gulf. *Sebastes exsul* and *S. spinorbis* seem more similar to each other than to any other species outside the Gulf, suggesting that the two had a common immediate ancestor. This, if true, would suggest that this lineage represents a single invasion of the Gulf, and thus, the divergence of the two species took place in the Gulf after the invasion. It is interesting to note that the *S. capensis* complex in the southern hemisphere also shares with the *umbrosus-eos* complex the characteristic vermiculations or dusky marks on the back and the dusky scale margins. Although it is possible that the *exsul-spinorbis* and the *capensis* complexes have the same origin, and that successful invasion of the Gulf and crossing of the tropics by *Sebastomus* were accomplished by the same ancestor species using the same climatic event, multiple crossings cannot be ruled out.

The four remaining species are related to the eleven species that I regard as comprising the subgenus *Allosebastes* Hubbs, 1951, namely *S. diploproa*, *S. saxicola*, *S. semicinctus*, *S. dallii*, *S. zacentrus*, *S. wilsoni*, *S. emphaeus*, *S. variegatus*, *S. rufinanus*, and *S. proriger* of the outer coast and *S. scythropus* of the western North Pacific. Shared characters are nasal, preocular, postocular, tympanic, parietal, and occasionally nuchal spines present; a characteristic banded color pattern (fig. 2), at least during the juvenile stage of their life (except perhaps *S. scythropus*), and a pair of extrinsic gas-bladder muscles which originates near the opisthotic, passes medial to the cleithrum to which it has a membranous connection, then each member of the pair splits typically into two or three tendons which pass between the second and third ribs, run straight along the inner side of succeeding ribs, and insert respectively on the parapophyses of the 8th to 10th centra, without any direct connection between the tendons and the gas-bladder wall.

Of these four species, *S. cortezi* and *S. sinensis*, which together with *S. diploproa* of the outer coast form a species group, all have rather similar body configuration, large eyes, uniformly red body with some dusky on back, and epipelagic juveniles charcterized by blunt cranial spines. In this group, *S. cortezi* and *S. diploproa* may be called a species pair; both have anteriorly-directed lachrymal projections (not found in any other species of *Allosebastes*), and both have extra tendons in the extrinsic gas-bladder muscles in addition to the typical *Allosebastes* pattern. *S. sinensis* probably is the species bridging the gap between the *cortezi-diploproa* pair and the closest species of the outer coast, probably *S. saxicola*.

The affinities of the two remaining species, *S. varispinis* and *S. peduncularis*, cannot be ascertained but they both are definitely close to the *sinensis-diploproa-cortezi* complex. It is clear that the history of the four species of *Allosebastes* in the Gulf is more complex than that of the two referred to *Sebastomus*, and suggests a possible multiple invasion of *Allosebastes* species from the outer coast into the Gulf, either by the same ancestral stock at different periods, or by different parental species either simultaneously or not; after successful invasion(s), it appears that radiation took place in the Gulf and there probably was (were) successful reciprocal invasion(s) from the Gulf to the outer coast, as suggested by the *cortezi-diploproa* pair.

The relationships and zoogeographic history outlined above are very speculative. If further studies support the hypothesis that species differentiation took place within a limited area in the Gulf, it would suggest that speciation in *Sebastes* does not necessarily require the presence of a geographic barrier. This helps to explain the origin of the high diversity of *Sebastes* in the North Pacific, with approximately 100 species, most of which are extensively sympatric (Chen, 1971).

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PROCEEDINGS
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THE LARGER MOTHS OF THE GALÁPAGOS ISLANDS (GEOMETROIDEA: SPHINGOIDEA & NOCTUOIDEA)

By

Alan H. Hayes

British Museum (Natural History)

FRONTISPIECE. *Manduca rustica calapagensis* Holland. Three females, Santa Cruz, February 1965, CDRS; photographs by R. Perry. Larvae, Floreana, April 1970; photograph by R. Silberglied.

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THE LARGER MOTHS OF THE GALÁPAGOS ISLANDS (GEOMETROIDEA: SPHINGOIDEA & NOCTUOIDEA)[1]

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ABSTRACT: Eighty-eight of the 90 species of Epiplemidae, Sphingidae, Arctiidae, and Noctuidae now known to occur on the Galápagos Islands are illustrated. Twelve of these are described as new. Four new subspecies are described and six species-group names are newly placed in synonymy. The world distribution of the species is summarized and new biological data is given for some of the species.

INTRODUCTION

The Galápagos were discovered by Fray Tomás de Berlanga, Bishop of Panama, on a voyage to Peru in 1535. Thereafter, for nearly three centuries, the islands received only occasional or temporary visitors, becoming successively the haunt of buccaneers, whalers, and sealers. In 1832, with the dissolution of the Spanish-American Empire, the archipelago was annexed by Ecuador and the first settlement was established, on Floreana Island. Today, the southern slopes of the islands of San Cristóbal, Santa Cruz, and Isabela are inhabited and a small colony continues on Floreana. Altogether over five thousand people live in the islands, mainly engaged in fishing or subsistence farming, or connected in one way or another with tourism.

The Galápagos Islands have a unique place in the history of science because of the visit of Charles Darwin in 1835 and the subsequent role his observations there played in the formulation of his ideas on organic evolution, which culminated in 1859 with the publication of the *Origin of Species*. The extraordinary indigenous wildlife of the islands suffered a rapid decline in the years

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[1] Contribution No. 171 of the Charles Darwin Foundation.

following their settlement, as a result both of exploitation and of introduction of plants and animals brought by man. These threats continue, although they are being alleviated by protective legislation and programs.

In 1959, all uninhabited areas of the islands were declared territory of a National Park by the Government of Ecuador and the current protection laws were brought into force. At the same time, a newly created international organization, the Charles Darwin Foundation for the Galápagos Isles, was entrusted with the task of coordinating scientific research in the islands and advising the Government on conservation policy and the development of the National Park.

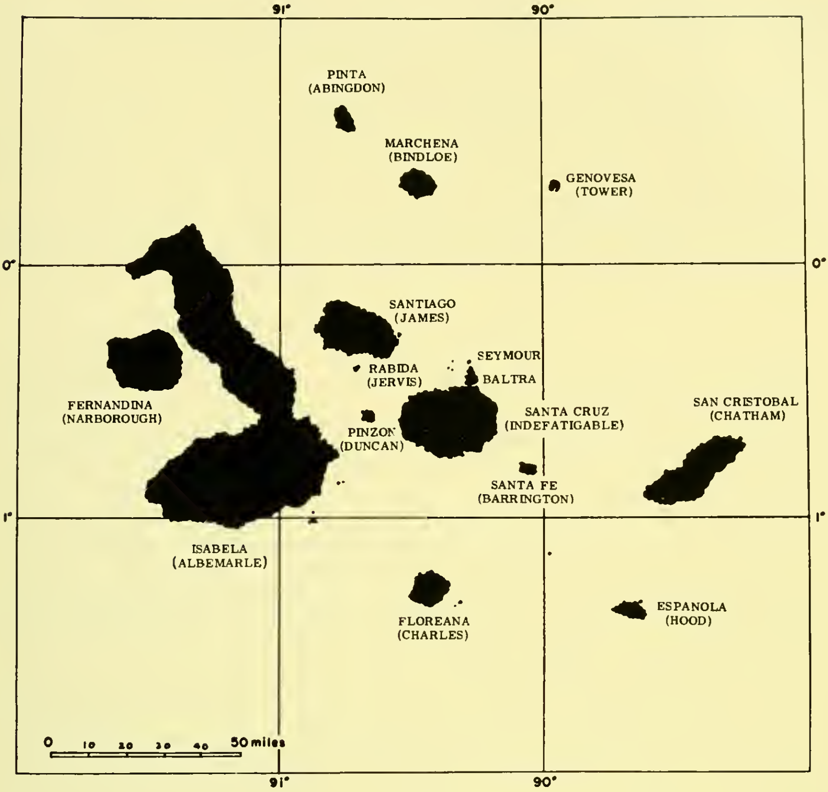
The Galápagos Islands are the tops of huge shield volcanos composed mainly of basalt. Dating studies have shown that the majority of lavas on the surface today came from eruptions during Pleistocene and Recent times. Volcanic activity continues and there have been eruptions on five of the islands in the past hundred years.

Approximately two-thirds of the land area are lava-strewn wastelands with a sparse xerophytic vegetation dominated by cacti and thorn-scrub. Only near the summits and on humid southern slopes of the higher islands does dense vegetation occur, composed typically of *Scalesia* woodland, a lush although somewhat seasonal undergrowth, and a limited number of epiphytic species. Rainfall is irregular, but in most years there is the possibility of heavy showers during the hot season, January to April, when daytime temperatures reach 35° C. on the coast. The cool, or *garúa*, season, lasting for the remaining months of the year, is characterized by generally more cloudy weather and steady southeasterly winds, when corresponding temperatures drop to 22° C. or even lower.

The names of the islands have been a source of confusion. Ecuadorian names (used in this paper) and the equivalent English names are shown on the map. In fact, some of the islands have several names (see Bowman, 1966, p. xvii).

Recent collecting has yielded many additions to the species recorded in *Insects of the Galápagos Islands* by Linsley and Usinger. Dr. F. H. Rindge of the American Museum of Natural History has recently published on the Geometridae and a check list is included here. The Pyralidae and Microlepidoptera of the islands await further study.

An attempt has been made to include all known museum material. Forewing measurement is taken from the center of the mesothorax to the apex of the forewing. Species identifications are based as far as possible on comparisons between Galápagos specimens and the type material. Where the type of a particular species has not been traced the identifications have been made by comparing Galápagos examples with material from the type-locality as far as this is known. The heading 'Distribution' refers to distribution within the



Map 1. Main group of islands forming the Galápagos Archipelago. Darwin (Culpepper) and Wolf (Wenman) lie to the northwest.

islands based on material studied by the author. A proportion of the species under consideration are widespread in distribution and reference to other faunistic works yields useful data; as these works may not be available to readers I have abstracted much of this data. The bibliography lists all publications referred to in the text and in addition cites other scientific and general works relevant to the study of the Galápagos fauna.

Of the 90 species dealt with in this paper 28 are endemic. However, Galápagos populations of the 62 remaining species often differ from those of the mainland and 16 are sufficiently distinct to warrant subspecific status.

The following abbreviations have been used for depositories: AMNH—American Museum of Natural History, New York; BMNH—British Museum (Natural History), London; CAS—California Academy of Sciences, San Francisco; CMP—Carnegie Museum, Pittsburgh; CU—Cornell University, Ithaca; IRSNB—Institut Royal des Sciences Naturelles de Belgique, Brussels; IZ—

Institute of Zoology, University of Uppsala; LACM—Los Angeles County Museum; LS—Linnean Society, London; MCZ—Museum of Comparative Zoology, Boston; MNHN—Museum National d'Histoire Naturelle, Paris; NM—Naturhistorisches Museum, Vienna; NR—Naturhistoriska Riksmuseum, Stockholm; RSM—Royal Scottish Museum, Edinburgh; UM—University Museum, Oxford; USC—University of Southern California, Los Angeles; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.; ZSBS—Zoologische Sammlung des Bayerischen Staates, Munich. Unless otherwise stated all figured specimens are in the BMNH.

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Thanks to the tremendous efforts made in rearing and collecting specimens for the British Museum (Natural History) by Dr. R. Perry (formerly Director of the Charles Darwin Research Station) and Dr. Tj. de Vries (of the Zoölogisch Museum, Amsterdam on grants from the Netherlands Foundation for the advancement of Tropical Research and the World Wildlife Fund) excellent series have been built up to complement the historic material studied by Walker, that collected by Rollo H. Beck for Lord Rothschild, and the St. George Expedition material collected by C. L. Collenette and Miss C. E. Longfield. Through the kindness of L. A. Berger I have examined the Institut Royal des Sciences Naturelles de Belgique material collected by J. and N. Leleup. I am most grateful to Dr. P. H. Arnaud, Jr. who made available to me the 11,387 specimens in the collections of the California Academy of Sciences amassed by D. Q. Cavagnaro, F. (P) Leon, E. G. Linsley, R. O. Schuster, D. W. Snow, I. L. Wiggins, F. X. Williams, and M. Willows (Jr.). E. C. Pelham-Clinton of the Royal Scottish Museum has been of great assistance in the identification of the Edinburgh University Expedition (1968) material. The material deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; the American Museum of Natural History, New York; the Museum of Comparative Zoology, Boston (collected by Dr. R. Silberglied); and the Carnegie Museum, Pittsburgh, has also been examined. J. P. Donahue, Los Angeles County Museum of Natural History, has mailed me material from that institution and has also been kind enough to examine and photograph relevant Allan Hancock Foundation material studied by Prof. A. G. Richards, Jr. at the University of Southern California, Los Angeles. Dr. P. I. Persson of the Naturhistoriska Riksmuseum, Stockholm, and Dr. W. Dierl of the Zoologische Sammlung des Bayerischen Staates, Munich, loaned me their Galápagos material. Special thanks are due to Dr. E. L. Todd, United States Department of Agriculture, and Prof. J. G. Franclemont, Cornell University, for their great help and advice concerning identification of Noctuidae. Dr. Perry and Dr. Tj. de Vries have placed their comprehensive notes concerning early stages and foodplants with me. I wish to acknowledge the extensive help given by my

colleagues at the British Museum (Natural History). I am indebted to P. V. York of this museum for taking the photographs.

Check-List of Species

Epiplemidae

Epiplema becki Hayes, new species.

Geometridae

(recently covered by Dr. F. H. Rindge (1973) and not included in the present work)

Cyclophora impudens (Warren)
Disclisioprocta stellata (Guenée)
Hydria affirmata (Guenée)
Eupithecia leleupi Herbulot
E. perryvriesi Herbulot
Perizoma (?) perryi Rindge
Semiothisa cruciata cruciata Herbulot
S. cruciata isabelae Rindge
S. cerussata Herbulot
Thyrinteina infans Herbulot
T. umbrosa Herbulot
Sphacelodes vulneraria (Hübner)
Oxydia lignata (Warren).

Sphingidae

Agrius cingulatus (Fabricius)
Manduca sexta leucoptera (Rothschild & Jordan), new combination
M. rustica calapagensis (Holland), new combination
Erinnyis alope dispersa Kernbach
E. ello encantada Kernbach
E. obscura conformis Rothschild & Jordan
Enyo lugubris delanoi (Kernbach), new combination
Pachygonia drucei Rothschild & Jordan
Eumorpha fasciata tupaci (Kernbach), new combination
E. labruscae yupanquii (Kernbach), new combination
Xylophanes norfolki Kernbach
X. tersa (Linnaeus)
Hyles lineata florilega (Kernbach), new combination.

Arctiidae

Utetheisa ornatrix (Linnaeus)
U. devriesi Hayes, new species
U. galapagensis (Wallengren)
U. perryi Hayes, new species.

Noctuidae

Noctuinae

Agrotis consternans Hayes, new species
A. ipsilon (Hufnagel)

A. subterranea williamsi (Schaus), new combination
Peridroma saucia (Hübner)
Psaphara conwayi (Richards), new combination
P. interclusa Walker, revived combination
Anicla oceanica (Schaus), new combination.

HELIOTHINAE
Heliothis cystiphora (Wallengren)
H. virescens (Fabricius).

HADENINAE
Mythimna solita (Walker)
M. latiuscula (Herrich-Schäffer)
Pseudaletia sequax Franclemont
P. cooperi (Schaus).

ACRONICTINAE
Magusa erema Hayes, new species
Trachea cavagnaroi Hayes, new species
Cropia infusa (Walker)
Callopistria floridensis (Guenée)
Catabena seorsa Todd
Neogalea esula longfieldae Hayes, new subspecies
Spodoptera eridania (Stoll)
S. latifascia (Walker)
S. dolichos (Fabricius)
S. frugiperda (Smith)
S. roseae (Schaus)
Elaphria encantada Hayes, new species
Platysenta mobilis (Walker), revived species
P. sutor (Guenée)
P. ruthae (Schaus)
Agrotisia williamsi (Schaus).

ACONTIINAE
Ozarba consternans Hayes, new species
Bagisara repanda (Fabricius), new combination
Eublemma recta (Guenée), new combination
Amyna insularum Schaus
Heliocontia margana (Fabricius)
Spragueia creton Schaus
Ponometia indubitans (Walker).

EUTELIINAE
Paectes arcigera (Guenée).

SARROTHRIPINAE
Characoma nilotica (Rogenhofer).

CATOCALINAE
Mocis incurvalis Schaus
M. latipes (Guenée)
Celiptera remigioides (Guenée)
Zale obsita (Guenée), revived species.

Plusiinae

Autoplusia egena galapagensis (Schaus)
Argyrogramma verruca (Fabricius)
Pseudoplusia includens (Walker).

Ophiderinae

Melipotis acontioides producta Hayes, new subspecies
M. indomita (Walker)
M. harrisoni Schaus
Ascalapha odorata (Linnaeus)
Letis mycerina (Cramer)
Rivula asteria Druce, new combination
Glympis toddi Hayes, new species
Anomis editrix (Guenée)
A. illita Guenée
A. luridula professorum Schaus, new status
A. erosa Hübner
Plusiodonta clavifera (Walker)
Gonodonta biarmata evadens Walker, new status
G. fulvangula Geyer
Metallata absumens contiguata Hayes, new subspecies
Bendis formularis Geyer
Anticarsia gemmatalis Hübner
A. prona (Möschler)
Psorya hadesia Schaus
Epidromia zetophora Guenée
E. zephyritis Schaus.

Hypeninae

Sorygaza variata Hayes, new species
Hypena vetustalis (Guenée)
H. microfuliginea Hayes, new species
Peliala fuliginea Hayes, new species
Ophiuche lividalis (Hübner)
O. minualis constans Hayes, new subspecies.

Family Epiplemidae

Epiplema becki Hayes, new species.

(Figures 16, 17, 168–170.)

Description. Male 8.5 mm. Patagia brown. Ground color of forewing white; costal margin and spot on posterior margin brown; fringes and traces of reticulate pattern brown; undersurface brown. Outer margin of hindwing with two short pointed processes; fringes brown; postmedial line brown; undersurface white. Does not resemble any American species known. Superficially resembles the Samoan *Epiplema amygdalipennis* Warren. Genitalia as figured.

Female 9.5 mm. Similar to but larger than male. Reticulate brown pattern prominent. The star shaped signum on the bursa is a distinctive feature of the genitalia.

DISTRIBUTION. Endemic species.

HOLOTYPE. Male. Fernandina (Narborough), 2–5 April 1906, F. X. Williams. CAS.

PARATYPES. 'Isabela (Albemarle)', Volcan Sierra Negra (= Santo Tomas), Corazon Verde, 360 m., January 1971. R. Perry & Tj. de Vries, BMNH; '(N. Albemarle) Isabela', 11 April 1902, R. H. Beck ex. Rothschild Bequest, BMNH. Both specimens are females.

BIOLOGY. No data available.

Family SPHINGIDAE

Agrius cingulatus (Fabricius).

(Figure 1.)

Sphinx cingulata FABRICIUS, 1775, Systema Entomologiae, p. 545. Type material: America (not found by Zimsen, 1964, p. 519).

Herse cingulata (Fabricius): KERNBACH, 1962, Opuscula Zoologica, München, vol. 63, p. 1.

Kernbach did not separate Galápagos specimens as a subspecies.

DISTRIBUTION. Widely distributed in the neotropics. *Galápagos Islands*: Baltra, April; Floreana, March, April; Isabela, March–May, August; San Cristóbal, February, March; Santa Cruz, January–June, October–December; Wolf, February. AMNH, BMNH, CAS, CMP, IRSNB, MCZ, NR, ZSBS.

BIOLOGY. Found from sea-level to summits of principal volcanos; visits flowers of *Opuntia*, *Ipomoea*, and *Cacabus miersii* during the day. *Foodplants*. *Ipomoea* species occur in the archipelago, upon which the larvae feed in the U.S.A. *Larvae*. Not reared by Perry and de Vries but a description appears in Williams (1911).

Manduca sexta leucoptera (Rothschild & Jordan), new combination.

(Figure 2.)

Protoparce leucoptera ROTHSCHILD & JORDAN, 1903, Novitates Zoologicae, vol. 9, Suppl., p. 79. Holotype, female (examined): Galápagos: Chatham [San Cristóbal], BMNH.

Protoparce sexta leucoptera Rothschild & Jordan: KERNBACH, 1962, Opuscula Zoologica, München, vol. 63, p. 2.

The stronger yellow lateral areas on the abdomen and the less conspicuous reniform spot separate this insect from the lighter forms of *Manduca rustica calapagensis*.

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FIGURE 1. *Agrius cingulatus* (Fabricius), female, Santa Cruz (× 1). FIGURE 2. *Manduca sexta leucoptera* (Rothschild & Jordan), female, Santa Cruz (× ¾). FIGURE 3. *M. rustica calapagensis* (Holland), male, Santa Cruz (× ¾). FIGURE 4. *Eumorpha labruscae yupanquii* (Kernbach), male, Santa Cruz (× ¾). FIGURE 5. *Erinnyis alope dispersa* Kernbach, female, paratype, Santa Cruz (× 1). FIGURE 6. *Eumorpha fasciata tupaci* (Kernbach), female, Santa Cruz (× 1).

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Distribution. Endemic subspecies of the widespread neotropical insect. *Galápagos Islands*: Floreana, January, February; Isabela, March–May; San Cristóbal, March; Santa Cruz, January–June. AMNH, BMNH, CAS, CMP, IRSNB, MCZ, ZSBS.

Biology. Common in years with prolonged rainy season; wings when at rest held higher above body than in *M. rustica calapagensis*. *Foodplant. Physalis pubescens. Larva.* Green, pale to white dorsally; seven oblique lateral stripes blackish followed by yellow; anal horn red.

Manduca rustica calapagensis (Holland), new combination.

(Frontispiece and figure 3.)

Protoparce calapagensis Holland, 1889, Proc. U.S. Nat. Mus., vol. 12, p. 195. Holotype (examined): Galápagos: Charles [Floreana]; USNM.

Protoparce rustica calapagensis Holland: Rothschild & Jordan, 1903, Novitates Zoologicae, vol. 9, Suppl., p. 85.

Protoparce rustica calapagensis ab. *nigrita* Rothschild & Jordan, 1903, Novitates Zoologicae, vol. 9, Suppl., p. 86.

Protoparce postscripta Clark, 1926, Proc. New Eng. Zool. Club, vol. 9, p. 70.

Protoparce rustica calapagensis Holland: Kernbach, 1962, Opuscula Zoologica, München, vol. 63, p. 4.

This insect exhibits considerable variation ranging from dark brown through gold to white in basic coloration. Williams (1911) and Kernbach (1962) give excellent coverage concerning this and other Galápagos Sphingidae.

Distribution. Endemic subspecies of the widespread neotropical insect. *Galápagos Islands*: Baltra, April; Española, February; Floreana, January–April; Genovesa, February–April; Isabela, February–April, July; San Cristóbal, February–April; Santa Cruz, January–July. AMNH, BMNH, CAS, CMP, IRSNB, MCZ, NR, USNM, ZSBS.

Biology. Widespread, usually the most abundant sphingid. *Foodplants. Clerodendrum molle, Cordia lutea, Cordia leucophlyctis. Larva.* Variable; green to purplish with yellow granules; oblique stripes purple edged with white; anal horn yellowish green. The darker forms appear to be prevalent at times of great abundance of these larvae, when foodplants are virtually stripped of foliage (see frontispiece).

Erinnyis alope dispersa Kernbach.

(Figure 5.)

Erinnyis alope dispersa Kernbach, 1962, Opuscula Zoologica, München, vol. 63, p. 9. Paratype female (examined): Galápagos: Santa Cruz; BMNH.

Although very close to the mainland species I have found that aedeagus differences mentioned by Kernbach separate it.

Distribution. Endemic subspecies of the widespread neotropical insect. *Galápagos Islands*: Santa Cruz, March–May. BMNH, CAS, ZSBS.

Biology. A single adult was taken on Santa Cruz on 1 March 1967. Subsequently, a mature larva was found on 16 March, and the adult reared from this emerged on 5 April 1967. *Larva.* Buff, darker above with indistinct transverse markings; pink between 1st and 2nd segments; prominent dark spot with inner, lighter ring on 3rd; stigmata with yellowish discs; anal horn short, slightly curved, buff. *Foodplants. Carica papaya*, species of *Jatropha* and *Allamanda* are listed as foodplants by Hodges (1971) and Kimball (1965).

Erinnyis ello encantada Kernbach.

(Figures 13 & 14.)

Erinnyis ello encantada Kernbach, 1962, Opuscula Zoologica, München, vol. 63, p. 10. Paratype female (examined): Galápagos: Santa Cruz; BMNH.

Sexually dimorphic. Kernbach states this subspecies is smaller and lighter in coloration than mainland representatives.

Distribution. Endemic subspecies of the widespread neotropical insect. *Galápagos Islands*: Floreana, March, May; Isabela, March–May; San Cristóbal, February–March, July; Santa Cruz, January–June, August, October. AMNH, BMNH, CAS, CMP, IRSNB, MCZ, RSM, ZSBS.

Biology. *Foodplant. Hippomane mancinella. Larva.* From the Galápagos Islands Curio (1965) describes 3 types of larva of this subspecies which vary in color, pattern, and behavior.

Erinnyis obscura conformis Rothschild & Jordan.

(Figure 12.)

Erinnyis obscura conformis Rothschild & Jordan, 1903, Novitates Zoologicae, vol. 9, Suppl., p. 369. Holotype, male (examined): Galápagos: Albemarle [Isabela]; BMNH.

The males lack the dark line on the forewing found in *Erinnyis obscura obscura* Fabricius.

Distribution. Endemic subspecies of the widespread neotropical insect. *Galápagos Islands*: Baltra, April; Floreana, March–May; Isabela, January–June, August; Pinzón, April; Santa Cruz, January–April, June, August–October. AMNH, BMNH, CAS, CMP, IRSNB, MCZ, NR, RSM, ZSBS.

Biology. *Foodplant. Sarcostemma angustissima. Larva.* Gray; anal horn short. Williams (1911) refers to a second type which is pale green.

Enyo lugubris delanoi (Kernbach), new combination.

(Figures 7 & 8.)

Epistor lugubris delanoi Kernbach, 1962, Opuscula Zoologica, München, vol. 63, p. 11. Paratype male (examined): Galápagos: Santa Cruz; BMNH.

A smaller insect than the nominate subspecies.

Distribution. Endemic subspecies of the widespread neotropical insect.


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Galápagos Islands: Isabela, no month; Santa Cruz, January–June, December. AMNH, BMNH, CAS, MCZ, ZSBS.

BIOLOGY. A species more of the damper inland regions of the islands. *Foodplant. Cissus sicyoides* from Williams (1911).

Pachygonia drucei Rothschild & Jordan.

(Not figured.)

Pachygonia drucei ROTHSCHILD & JORDAN, 1903, Novitates Zoologicae, vol. 9, Suppl., p. 411. Holotype, male (examined): [Panama]: Chiriqui; BMNH.

Doubtfully included, based on the specimen mentioned below which may well have been taken on the Cocos Islands.

DISTRIBUTION. Ecuador, Panama, and Honduras. Included here on the basis of one male specimen labeled Galápagos & Cocos Islands. A. J. Drexel. BMNH.

BIOLOGY. No data available.

Eumorpha fasciata tupaci (Kernbach), new combination.

(Figure 6.)

Pholus fasciatus tupaci KERNBACH, 1962, Opuscula Zoologica, München, vol. 63, p. 12. Holotype (photograph examined): Galápagos: Santa Cruz; ZSBS.

Kernbach states that the forewing stripes show a more conspicuous pink tinge in this subspecies.

DISTRIBUTION. Endemic subspecies of the widespread neotropical insect. *Galápagos Islands*: Santa Cruz, February, April–May. BMNH, CAS, ZSBS.

BIOLOGY. Two fresh adults were taken on Santa Cruz in February 1967; there were no subsequent records for this species. Onograceae are listed as foodplants in the U.S.A.

Eumorpha labruscae yupanquii (Kernbach), new combination.

(Figure 4.)

Pholus labruscae yupanquii KERNBACH, 1962, Opuscula Zoologica, München, vol. 63, p. 13. Holotype (photograph examined): Galápagos: Santa Cruz; ZSBS.

As stated by Kernbach the male genitalia are more heavily chitinized than those of the nominate subspecies.

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FIGURE 7. *Enyo lugubris delanoi* (Kernbach), male, Santa Cruz (× 1). FIGURE 8. *E. lugubris delanoi* (Kernbach), female, Santa Cruz (× 1). FIGURE 9. *Xylophanes tersa* (Linnaeus), male, Santiago (× 1). FIGURE 10. *X. tersa* (Linnaeus), melanic male, Santiago (× 1). FIGURE 11. *X. norfolki* Kernbach, female, Santa Cruz (× 1). FIGURE 12. *Erinnyis obscura conformis* Rothschild & Jordan, male, Santa Cruz (× 1). FIGURE 13. *E. ello encantada* Kernbach, male, Santa Cruz (× 1; CAS). FIGURE 14. *E. ello encantada* Kernbach, female, Santa Cruz (× 1).

Distribution. Endemic subspecies of the widespread neotropical insect. *Galápagos Islands*: Floreana, February, November; Santa Cruz, January–June, August. AMNH, BMNH, CAS, IRSNB, MCZ, RSM, ZSBS.

Biology. Adults not uncommon; inland and coastal regions of main islands. Larvae were not found by Perry and de Vries.

Xylophanes norfolki Kernbach.

(Figure 11.)

Xylophanes norfolki Kernbach, 1962, Opuscula Zoologica, München, vol. 63, p. 14. Holotype, male (photograph examined): Galápagos: Santa Cruz; ZSBS.

The characteristic forewing pattern of this endemic species readily separates it from *Xylophanes tersa.*

Distribution. Endemic species. *Galápagos Islands*: Santa Cruz, January–June, July. AMNH, BMNH, CAS, IRSNB, ZSBS.

Biology. Adults have so far only been taken on Santa Cruz where the species is generally scarce and mainly restricted to inland regions. Larvae were not found by Perry and de Vries.

Xylophanes tersa (Linnaeus).

(Figures 9 & 10.)

Sphinx tersa Linnaeus, 1771, Mantissa Plantarum, vol. 2, p. 538. Type material: Maryland, Jamaica, Antigua; not traced.

One female reared by F. X. Williams and located in the California Academy of Sciences was the only known specimen. Dr. Tj. de Vries has recently taken specimens on Santiago including melanic examples (figure 10).

Distribution. Widespread neotropical species. *Galápagos Islands*: San Cristóbal, February; Santiago, November. BMNH, CAS.

Biology. Kimball lists *Spermacoce* (Rubiaceae) as foodplant in Florida.

Hyles lineata florilega (Kernbach), new combination.

(Figure 15.)

Celerio lineata florilega Kernbach, 1962, Opuscula Zoologica, München, vol. 63, p. 16. Holotype (photograph examined): Galápagos: Santa Cruz; ZSBS.

A small but strikingly marked subspecies.

Distribution. Endemic subspecies of the almost cosmopolitan insect. *Galápagos Islands*: Baltra, April; Española, April; Floreana, January, March–May; Isabela, April; San Cristóbal, February; Santa Cruz, January–June, October; Santiago, February, March. AMNH, BMNH, CAS, CMP, IRSNB, MCZ, RSM, USNM, ZSBS.

Biology. Adults. Widespread, diurnal, seasonally common. *Foodplants.*

Portulaca oleracea, Commicarpus tuberosus. Larva. Green with variable black and yellow markings; some purple near spiracles; anal horn long, curved, yellowish to red.

Family ARCTIIDAE

Utetheisa ornatrix (Linnaeus).

(Figures 18 & 19.)

Phalaena (*Noctua*) *ornatrix* LINNAEUS, 1758, Systema Naturae (10th Ed.), vol. 1, p. 511. Type material: America; IZ.

This day-flying species is, I believe, the insect mentioned by Eibl-Eibesfeldt (1960, p. 99).

DISTRIBUTION. Widespread neotropical species. *Galápagos Islands*: Gardner near Española, April; Isabela, April, June, August; San Cristóbal, January, February, April–June; Santa Cruz, January–April, June, September, October, December; Santiago, March, April. AMNH, BMNH, CAS, IRSNB, MCZ, RSM, USNM, ZSBS.

BIOLOGY. More restricted than *U. galapagensis* yet conspicuous and abundant at times in open, moister areas. Larvae were not collected by Perry and de Vries, but species of *Crotalaria*, the host-plants elsewhere, are widespread in the archipelago.

Utetheisa devriesi Hayes, new species.

(Figures 24–26, 175, & 176.)

DESCRIPTION. Male 20.5 mm. Antenna bipectinate. Palpus dark brown with some gray scaling. Forewing gray with dark brown scaling at margin and on median line. Hindwing gray with brown scaling at margin. Genitalia: the uncus structure distinguishes this species.

Female 22 mm. Antenna simple. Similar to male in maculation but with broader forewing. Genitalia: the considerable spicular ornamentation at the base of the ductus bursae distinguishes the genitalia.

Larger than, but closely related to *U. galapagensis*. The prominent darker shade on the median line also separates this species. Lacks the yellowish buff coloration of *U. perryi.*

DISTRIBUTION. Endemic species.

HOLOTYPE. Male. Pinta, Highlands, southern slope at approximately 500 m.; *Zanthoxylum* forest with undergrowth of *Tournefortia* shrub; 13–15 October 1973. BMNH.

PARATYPES. Same data, BMNH (27 specimens).

OTHER MATERIAL. A melanic male with the same data as the types (BMNH) although excluded from the type-series is tentatively placed here (fig. 26).

BIOLOGY. No data available.


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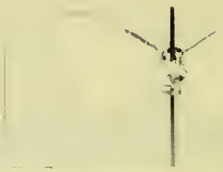
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Utetheisa galapagensis (Wallengren).

(Figures 22 & 23.)

Euchelia galapagensis WALLENGREN, 1860, Wiener entomologische Monatschrift, vol. 4, p. 161. Holotype, female (examined): Galápagos; NR.

The more grayish coloration and genitalic differences separate this species from *U. perryi.* A smaller moth than *U. devriesi.*

DISTRIBUTION. Endemic species. *Galápagos Islands*: Baltra, April; Fernandina, February; Floreana, January, February, July; Isabela, January, March, April, August; Pinta, September, October; San Cristóbal, February, September; Santa Cruz, January–December; Santiago, January, July, November, December. AMNH, BMNH, CAS, CU, IRSNB, MCZ, RSM, USNM.

BIOLOGY. Adults. Abundant generally in coastal and upland regions of main islands. On Santa Cruz often flying before dusk around plants of *Scalesia affinis. Foodplants. Tournefortia pubescens, T. psilostachya. Larva.* Grayish and brownish black with buff markings shading to pale buff below.

Utetheisa perryi Hayes, new species.

(Figures 20, 21, 171, & 172.)

DESCRIPTION. Male 16.5 mm. Antenna bipectinate. Palpus covered with dark brown and yellowish buff scales. Head, thorax, and forewing yellowish buff. Forewing irroration dark brown and black. Two such areas forming reniform spot. Hindwing yellowish cream, margin with dark brown markings and strongly marked discal spot. Genitalia: the uncus formation is diagnostic.

Female 16 mm. Antenna simple. Similar to male in basic coloration. Scaling on forewing forming longitudinal streak in some specimens.

The yellowish buff coloration separates this species from *U. devriesi* and *U. galapagensis.*

DISTRIBUTION. Endemic species.

HOLOTYPE. Male. Santiago, 580 m., November/December 1970. J. Villa & J. Black. BMNH.

PARATYPES. Isabela, January, February, October; Santiago, November, December; Santa Cruz, February, March, June. AMNH (2 specimens), BMNH (43 specimens), CAS (5 specimens).

BIOLOGY. Collected in transition and humid zones.

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FIGURE 15. *Hyles lineata florilega* (Kernbach), male, Santa Cruz (× 2). FIGURE 16. *Epiplema becki* Hayes, new species, holotype, male, Fernandina (× 2; CAS). FIGURE 17. *E. becki* Hayes, new species, paratype, female, Isabela (× 2). FIGURE 18. *Utetheisa ornatrix* (Linnaeus), male, Santa Cruz (× 2). FIGURE 19. *U. ornatrix* (Linnaeus), female, Santa Cruz (× 2).

Figure 20. *Utetheisa perryi* Hayes, new species, holotype, male, Santiago (× 2). Figure 21. *U. perryi* Hayes, new species, paratype, female, Santiago (× 2). Figure 22. *U. galapagensis* (Wallengren), male, Santiago (× 2). Figure 23. *U. galapagensis* (Wallengren), female, Santiago (× 2). Figure 24. *U. devriesi* Hayes, new species, holotype, male, Pinta (× 2). Figure 25. *U. devriesi* Hayes, new species, female, paratype, Pinta (× 2). Figure 26. *U. devriesi* Hayes, new species, melanic male, Pinta (× 2).

Family Noctuidae

Noctuinae

Agrotis consternans Hayes, new species.

(Figures 27, 28, 173, & 174.)

Description. Male 15 mm. Antenna strongly bipectinate. Palpus dark brown. Thorax dark brown. Forewing midbrown with basal, antemedial, and postmedial lines buff edged with black. A broad black streak runs from the reniform through the orbicular spot. Hindwing cream with gray postmedian line and marginal shade. Genitalia as figured.

Female 16.5 mm. Similar to male in basic coloration. Costal margin yellowish buff, prominent.

Allied to *A. bosqi* Kohler, *A. fasicola* Dyar, and *A. lutescens* Blanchard, the orbicular and reniform spot and the strongly bipectinate male antenna separate this species.

Distribution. Endemic species.

Holotype. Male. Pinta, 630 m., November 1970. BMNH.

Paratypes. Isabela, August; Pinta, October, November; San Cristóbal, April; Santa Cruz, March–June, November; Santiago, November. BMNH (92 specimens), CAS (29 specimens), MCZ (2 specimens), ZSBS (1 specimen).

Biology. No data available.

Agrotis ipsilon (Hufnagel).

(Figures 31 & 32.)

Phalaena ipsilon Hufnagel, 1766, Berlinisches Magazin, vol. 3, p. 416. Type material: Germany: Berlin; not traced.

A well known species.

Distribution. Almost cosmopolitan. *Galápagos Islands*: Isabela, March; San Cristóbal, April; Santa Cruz, January–July. AMNH, BMNH, CAS, MCZ.

Biology. Not reared on the Galápagos Islands. Another general feeder. Kimball and Zimmerman give good coverage of crop damage, etc. Known as the Greasy Cutworm in the U.S.A.

Agrotis subterranea williamsi (Schaus), new combination.

(Figures 29 & 30.)

Euxoa williamsi Schaus, 1923, Zoologica, vol. 5, p. 32. Lectotype female (examined): Galápagos: Indefatigable [Santa Cruz]; USNM.

Feltia annexa (Treitschke): Richards, 1941, Allan Hancock Pacific Expedition, vol. 5, p. 235.

Scotia galapagosensis Köhler, 1961, Anales de la Sociedad Cientifica Argentina, vol. 172, pp. 71–72. New synonym.

The strongly pectinate male antenna and very dark forewing of the female separate this subspecies. Hindwing of both sexes with some brown scales.

Distribution. Endemic subspecies of the widespread new world species.

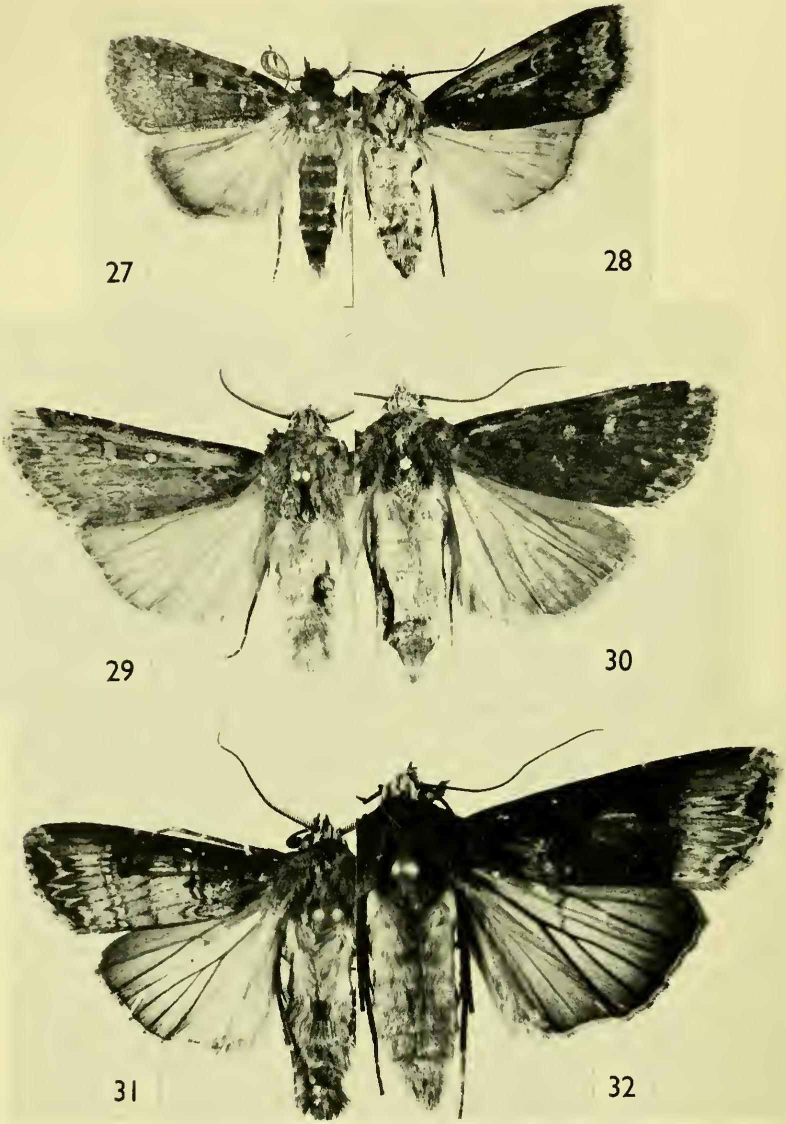

Figure 27. *Agrotis consternans* Hayes, new species, holtype, male, Pinta (× 2). Figure 28. *A. consternans* Hayes, new species, paratype, female, Santa Cruz (× 2). Figure 29. *A. subterranea williamsi* (Schaus), male, Santiago (× 2). Figure 30. *A. subterranea williamsi* (Schaus), female, Santa Cruz (× 2). Figure 31. *A. ipsilon* (Hufnagel), male, Santa Cruz (× 2). Figure 32. *A. ipsilon* (Hufnagel), female, Santa Cruz (× 2).

Galápagos Islands: Baltra, April; Fernandina, February; Isabela, March, April, August; Pinta, May, October; Santa Cruz, January–July, October; Santiago, March, April, July, November. AMNH, BMNH, CAS, IRSNB, MCZ, USNM.

Biology. Larvae not found on the islands. Tietz (1972, p. 622) records the larvae of the nominate subspecies, the Granulate Cutworm, on a wide variety of plants.

Peridroma saucia (Hübner).

(Figure 40, Mexican specimen.)

Noctua saucia Hübner, [1808], Sammlung europäischer Schmetterlinge, vol. 4, fig. 378. Type material: Europe; not traced.

Peridroma margaritosa (Haworth) sensu Richards, 1941, Allan Hancock Pacific Expedition, vol. 5, p. 235. Misidentification.

I have only examined 3 very worn specimens from the Galápagos Islands. These specimens have been identified on genitalic characters.

Distribution. Europe, North Africa, Asia, North America, South America, Hawaii. *Galápagos Islands*: Floreana (Charles), 1300 ft., 1939, USC (2 ♂, 1 ♀).

Biology. Larvae not reared on the Galápagos Islands. Another general feeder, known as the Variegated Cutworm; Tietz (1972) lists a wide variety of foodplants including many crop species.

Psaphara conwayi (Richards), new combination.

(Figures 37 & 38.)

Peridroma conwayi Richards, 1941, Allan Hancock Pacific Expedition, vol. 5, p. 235. Holotype, male (photograph examined): Galápagos: Charles [Floreana]; USC.

This species is closely allied to *Psaphara interclusa* Walker. I am taking the genus out of synonymy to contain these two species which on genitalic evidence merit separation from *Peridroma*. Genitalia figured by Richards (1941).

Distribution. Endemic species. *Galápagos Islands*: Floreana, no month; Isabela, January; Pinta, October; Santa Cruz, April. BMNH, CAS, USC.

Biology. No data available.

Psaphara interclusa Walker, revived combination.

(Figures 35, 36, & 163.)

Psaphara interclusa Walker, 1857, List of the Specimens of Lepidopterous Insects in the Collection of the British Museum, vol. 11, p. 607. Holotype, male (examined): West Coast of America [Galápagos]; BMNH.

The type is labeled "W. Coast of America, Kellett and Wood, 1850–12." Naval records (Seemann, 1853) disclose that H.M.S. *Herald*, captained by Sir Henry Kellett C. B., and H.M.S. *Pandora*, captained by Lt. Wood, visited the Galápagos Islands 6–16 January 1846, anchoring at Floreana, San Cristóbal, and Santiago islands. The only additional material is a pair collected by Silberglied near 'El Junco' crater lake on San Cristóbal, the female of which


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is deposited in the BMNH. Both specimens match the type and this strongly suggests that the latter originated from the archipelago. Much historic material in the BMNH is labeled "W. Coast of America" and a proportion appears to have been taken on the Galápagos Islands.

Distribution. Endemic species. *Galápagos Islands*: San Cristóbal, April. BMNH, MCZ.

Biology. No data available.

Anicla oceanica (Schaus), new combination.

(Figures 33 & 34.)

Lycophotia oceanica Schaus, 1923, Zoologica, vol. 5, p. 32. Holotype, female (examined): Galápagos: South Seymour [Baltra]; USNM.

Lycophotia oceanica Schaus: Todd, 1973, Proc. Ent. Soc. Washington, vol. 75, p. 35 (Type specimen discussed).

A common insect on the Galápagos Islands. Sexes much alike but specimens show some variation in basic coloration from pinkish to grayish brown. Allied to *Anicla infecta* Ochsenheimer.

Distribution. Endemic species. *Galápagos Islands*: Baltra, April; Isabela, March, April, August; Pinta, October; Pinzón, April; Santa Cruz, January–April, June, August–October, December; Santiago, March, July. AMNH, BMNH, CAS, IRSNB, MCZ, RSM, USNM.

Biology. No data available.

Heliothinae

Heliothis cystiphora (Wallengren)

(Figures 41 & 42.)

Anthoecia cystiphora Wallengren, 1860, Wiener Entomologische Monatschrift, vol. 4, p. 172. Holotype, female: 'Panama'; NR.

Anthoecia inflata Wallengren, 1860, Wiener Entomologische Monatschrift, vol. 4, p. 172.

Anthoecia onca Wallengren, 1860, Wiener Entomologische Monatschrift, vol. 4, p. 172.

Sexually dimorphic, the male possessing two prominent sensory patches on the forewing. A common species, well represented in collections.

Distribution. Neotropical species. *Galápagos Islands*: Baltra, April; Española, May; Fernandina, February, April; Floreana, February–May; Gardner near Española, February; Genovesa, April; Isabela, February–April;

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Figure 33. *Anicla oceanica* (Schaus), male, Santa Cruz (× 2). Figure 34. *A. oceanica* (Schaus), female, Santa Cruz (× 2). Figure 35. *Psaphara interclusa* Walker, holotype, male, 'W. Coast of America' (Galápagos) (× 2 reversed). Figure 36. *P. interclusa* Walker, female, San Cristóbal (× 2). Figure 37. *P. conwayi* (Richards), male, Isabela (× 2). Figure 38. *P. conwayi* (Richards), female, Pinta (× 2). Figure 39. *Heliothis virescens* (Fabricius), female, Santa Cruz (× 2). Figure 40. *Peridroma saucia* (Hübner), male, Mexico (× 2).

San Cristóbal, February, March; Santa Cruz, January–June; Santiago, March, April. AMNH, BMNH, CAS, IRSNB, LACM, MCZ, USNM.

Biology. A fast-flying species, visiting flowers during day; common in March 1969 at plants of *Encelia hispida* in the inland parts of Santa Fé. *Foodplant. Sporobolus virginicus. Larva.* Head yellow with black spots. Body with central gray stripe bordered by yellow, reddish brown, and white; overlain with black spots; undersurface yellowish green.

Heliothis virescens (Fabricius).

(Figure 39.)

Noctua virescens Fabricius, 1781, Species Insectorum, vol. 2, p. 216. Type material: [Virgin Islands]: St. Crux [St. Croix]; not traced.

Some variation in the hindwing coloration is common in series of this moth.

Distribution. Widely distributed in the neotropics. *Galápagos Islands*: Floreana, July; Genovesa, April; Isabela, January–April, August; Pinta, May, October; San Cristóbal, February, April; Santa Cruz, January–April, June, July, October, December; Santiago, July. AMNH, BMNH, CAS, IRSNB, MCZ.

Biology. *Foodplants. Passiflora foetida, Scalesia affinis. Larva.* Head yellow. Body yellowish to brownish green merging into emerald below; some orange dorsally; black median and lateral lines; prominent black spots at bases of setae. Known as the Tobacco Budworm in the U.S.A. where it has been recorded on an extensive variety of plants.

HADENINAE

Mythimna solita (Walker).

(Figure 43.)

Leucania solita Walker, 1856, List of the Specimens of Lepidopterous Insects in the Collection of the British Museum, vol. 9, p. 99. Holotype, male (examined): BMNH.

The longitudinal streak on the forewing and the white hindwing are features of this species.

Distribution. Widespread neotropical species. *Galápagos Islands*: San Cristóbal, April; Santa Cruz, February, March, May, June, October–December. AMNH, BMNH, CAS, IRSNB, MCZ.

Biology. *Foodplant. Sporobolus virginicus. Larva.* Head gray with brown reticulation. Body reddish brown with darker markings and diffuse white lines.

Mythimna latiuscula (Herrich-Schäffer).

(Not figured.)

Leucania latiuscula Herrich-Schäffer, 1868, Korrespondez-Blatt des Zoologisch-Mineralogischen Vereines in Regensburg, vol. 22, p. 148. Type material: Cuba.

A specimen of this species was mailed to me after I had prepared the plates. It is figured by Draudt in Seitz, *Macrolepidoptera of the World*, vol. 7, pl. 24.

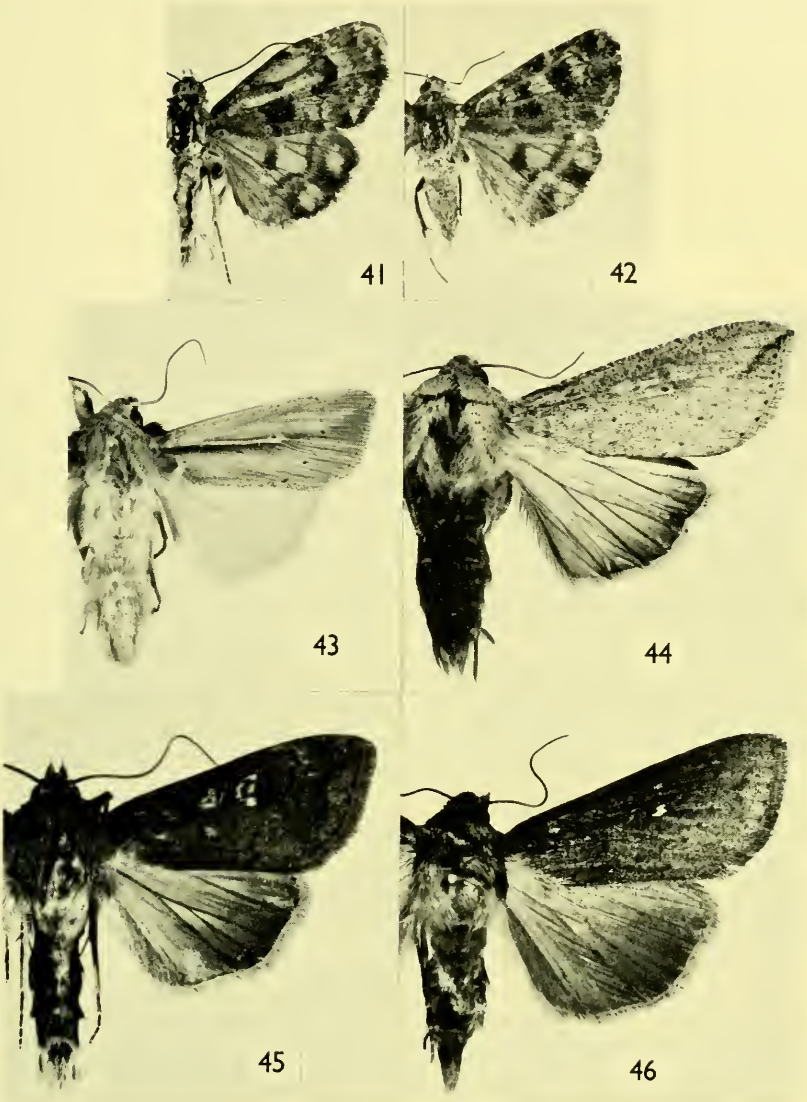

Figure 41. *Heliothis cystiphora* (Wallengren), male, Floreana (× 2). Figure 42. *H. cystiphora* (Wallengren), female, Isabela (× 2). Figure 43. *Mythimna solita* (Walker), male, Santa Cruz (× 2). Figure 44. *Pseudaletia sequax* Franclemont, male, Santa Cruz (× 2). Figure 45. *P. cooperi* (Schaus), male, Santa Cruz (× 2). Figure 46. *P. cooperi* (Schaus), female, Santa Cruz (× 2).

It is more drab than *M. solita* and lacks the longitudinal white streak on the forewing.

Distribution. Widely distributed in the neotropics. *Galápagos Islands*: San Cristóbal, 'El Junco' crater lake, 700 m., April. MCZ.

Biology. Not reared on the Galápagos Islands. Tietz (1972) lists graminaceous foodplants.

Pseudaletia sequax Franclemont.

(Figure 44.)

Pseudaletia sequax Franclemont, 1951, Proc. Ent. Soc. Washington, vol. 53, p. 70. Holotype, male (examined): Jalapa, Mexico; USNM.

Genitalia compared with Franclemont's figure and paratypes in the BMNH.

Distribution. Widespread neotropical species. Franclemont gives full coverage. *Galápagos Islands*: Isabela, February; San Cristóbal, April; Santa Cruz, January–April, June, August, October, December. AMNH, BMNH, CAS, IRSNB, LACM, MCZ, RSM.

Biology. No data available. Related species are general feeders.

Pseudaletia cooperi (Schaus).

(Figures 45 & 46.)

Cirphis cooperi Schaus, 1923, Zoologica, vol. 5, p. 33. Holotype, female (examined): Galápagos: Indefatigable [Santa Cruz]; USNM.

Pseudaletia cooperi Schaus: Franclemont, 1951, Proc. Ent. Soc. Washington, vol. 53, p. 64.

Both sexes figured.

Distribution. Endemic species. *Galápagos Islands*: Isabela, March, August; Pinta, October; San Cristóbal, April; Santa Cruz, January–June, September–November; Santiago, November. BMNH, CAS, IRSNB, MCZ, USNM.

Biology. No data known.

Acronictinae

Magusa erema Hayes, new species.

(Figures 53, 54, & 155.)

Magusa orbifera Walker sensu Schaus, 1923, Zoologica, vol. 5, p. 24 [Misidentification].

Description. Male 21.5 mm. Antenna simple. Palpus, head, thorax, and forewing dark brown. Prominent white apical mark on forewing. Abdomen and hindwing grayish brown. Genitalia as figured. Valve process short.

Female 20 mm. Similar to male but with broader forewing.

Although reddish brown coloration occurs on the forewing of some specimens, a series of this insect does not exhibit the extreme variation shown by its nearest relative *Magusa orbifera* Walker. The short valve process of the male genitalia also separates *M. erema.*

Distribution. Endemic species.

Holotype. Male. Santa Cruz, December 1968, R. Perry and Tj. de Vries. BMNH.

Paratypes. Isabela, April; San Cristóbal, April; Santa Cruz, January–May, July, August, October, December; Santa Fé, April. AMNH (1 specimen), BMNH (16 specimens), CAS (1,058 specimens), IRSNB (6 specimens), MCZ (143 specimens), RSM (3 specimens).

Biology. *Foodplant. Scutia pauciflora. Larva.* Green with paired, interrupted lines of gray-black and yellowish and creamy white stripes; some purple around legs and prolegs.

Trachea cavagnaroi Hayes, new species.

(Figures 49, 50, & 156.)

Description. Male 17 mm. Antenna strongly bipectinate. Palpus dark brown and buff. Forewing with dark and mid brown patterning. Burnished orbicular and reniform spots. Marginal band and discal spot of hindwing gray. Remainder of hindwing yellowish gold. Genitalia as figured.

Female 19–22 mm. Antenna simple. Broader winged but similar to male in maculation. Conspicuous buff pattern in apical area and bordering terminal line of forewing.

Only one male and two females of this species have been taken. Provisionally placed in the genus *Trachea.* Does not resemble any known species.

Distribution. Endemic species.

Holotype. Male. Santa Cruz, Horneman Farm, 220 m., 3 May 1964. D. Q. Cavagnaro. CAS.

Paratypes. Santa Cruz, Grasslands, 750 m., 10 April 1964. D. Q. Cavagnaro. CAS. (2 females.)

Biology. No data known.

Cropia infusa (Walker).

(Figures 47 & 48.)

Decelea infusa Walker, [1858] 1857, List of the Specimens of Lepidopterous Insects in the Collection of the British Museum, vol. 13, p. 1116. Holotype, female (examined): America but no data; BMNH.

Few specimens of this species have been collected on the Galápagos Islands. Although somewhat smaller than mainland examples, no striking genitalic differences separate Galápagos Islands specimens.

Distribution. Widespread neotropical species. *Galápagos Islands*: Española, May; Fernandina, February; Gardner near Española, April; Genovesa, Feb-


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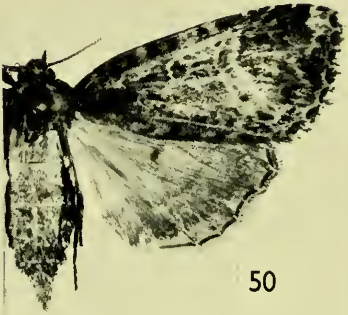
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ruary, March; Isabela, March; Santa Cruz, January, June; Santiago, July. AMNH, BMNH, CAS, MCZ.

Biology. No data known.

Callopistria floridensis (Guenée).

(Figure 51.)

Eriopus floridensis Guenée, 1852, in Boisduval & Guenée, Histoire Naturelle des Insectes. Lépidoptères, vol. 6, p. 292. Holotype, male (examined): [U.S.A.]: Florida; BMNH.

Identical with mainland specimens.

Distribution. Widespread neotropical species. *Galápagos Islands*: Isabela, January, August; Pinta, October; San Cristóbal, April; Santa Cruz, January–July. AMNH, BMNH, CAS, IRSNB, MCZ.

Biology. Not reared on the Galápagos Islands. Known as the Florida Fern caterpillar in the U.S.A.

Catabena seorsa Todd.

(Figure 52.)

Catabena seorsa Todd, 1972, Jour. Washington Acad. Sci., vol. 62, no. 1, p. 38. Holotype, male (examined): Galápagos: Santa Cruz; CAS. Todd (1972) gives full coverage. Schaus (1923, p. 25) referred to a specimen now located in AMNH as a *Catabena* species? too poor to identify.

Distribution. Endemic species. *Galápagos Islands*: Marchena, September, November; Española, September; Floreana, April, June, July; Genovesa, February–April; Isabela, January, March, August, October, November; Pinzón, April; San Cristóbal, February; Santa Cruz, January–May, October, December. AMNH, BMNH, CAS, IRSNB, MCZ, USNM, ZSBS.

Biology. Arid zones, generally. *Foodplant. Lantana peduncularis. Larva.* Head gray with black and orange markings. Body gray and black with fine lines of orange, yellow, and white. Pupation is within a parchmentlike cocoon.

Neogalea esula longfieldae Hayes, new subspecies.

(Figures 55 & 56.)

The extensive fuscous margin of the hindwing separates Galápagos specimens from the nominate subspecies.

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Figure 47. *Cropia infusa* (Walker), male, Española (× 2). Figure 48. *C. infusa* (Walker), female, Santiago (× 2). Figure 49. *Trachea cavagnaroi* Hayes, new species, holotype, male, Santa Cruz (× 2; CAS). Figure 50. *T. cavagnaroi* Hayes, new species, paratype, female, Santa Cruz (× 2; CAS). Figure 51. *Callopistria floridensis* (Guenée), male, Isabela (× 2). Figure 52. *Catabena seorsa* Todd, female, Santa Cruz (× 3). Figure 53. *Magusa erema* Hayes, new species, holotype, male, Santa Cruz (× 2). Figure 54. *M. erema* Hayes, new species, paratype, female, Santa Cruz (× 2).

DISTRIBUTION. Endemic subspecies. The widespread neotropical species has been introduced to Australia, Hawaii, and Norfolk Island in an endeavour to control *Lantana.*

HOLOTYPE. Male. 17 mm. Isabela (Albemarle), Tagus Cove, 150 ft., 3 August 1924, St. George Expedition, C. L. Collenette, BM. 1925–488, BMNH.

PARATYPES. Same data as holotype, 4 August 1924, 1 female, BMNH; same data as holotype, 7 August 1924, 1 female, BMNH: Isabela, Punta Albemarle, March 1970, R. Silberglied, BM. 1970—567, 1 female, BMNH; Isabela, Punta Albemarle, March 1970, R. Silberglied, 4 males, 1 female, MCZ.

BIOLOGY. Not reared on the Galápagos Islands. Tietz lists *Lantana* and *Verbena* as foodplants for the nominate subspecies.

Spodoptera eridania (Stoll).

(Figures 57 & 58.)

Phalaena (*Noctua*) *eridania* STOLL, 1781, in Cramer, Uitlandsche Kapellen, vol. 4, p. 133, pl. 358, figs. E & F. Type material: Surinam; not traced.

A variable insect that is a common pest on the mainland.

DISTRIBUTION. Widespread neotropical species. *Galápagos Islands*: Isabela, March; San Cristóbal, April; Santa Cruz, February–July. AMNH, BMNH, CAS, MCZ.

BIOLOGY. *Foodplants. Amaranthus viridis, Portulaca oleracea, Cryptocarpus pyriformis, Cissampelos pareira, Ipomoea pes-caprae. Larva.* Head reddish brown. Body gray, streaked green and reddish brown with black markings; lateral line black. Tietz lists a very wide range of foodplants. This species is known as the Southern Armyworm in the U.S.A.

Spodoptera latifascia (Walker).

(Figures 59 & 60.)

Prodenia latifascia WALKER, 1856, List of the Specimens of Lepidopterous Insects in the Collection of the British Museum, vol. 9, p. 195. Holotvpe, male (examined): Jamaica; UM.

Sexually dimorphic.

DISTRIBUTION. Widespread neotropical species. *Galápagos Islands*: Flore-

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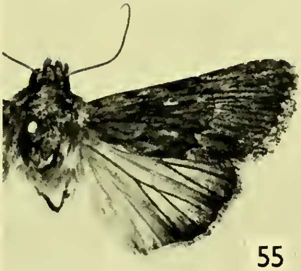
FIGURE 55. *Neogalea esula longfieldae* Hayes, new subspecies, holotype, male, Isabela (× 2 reversed). FIGURE 56. *N. esula longfieldae* Hayes, new subspecies, paratype, female, Isabela (× 2). FIGURE 57. *Spodoptera eridania* (Stoll), male, Santa Cruz (× 2). FIGURE 58. *S. eridania* (Stoll), female, Santa Cruz (× 2). FIGURE 59. *Spodoptera latifascia* (Walker), male, Santa Cruz (× 2). FIGURE 60. *S. latifascia* (Walker), female, Santa Cruz (× 2). FIGURE 61. *Spodoptera frugiperda* (Smith), male, Santa Cruz (× 2; CAS). FIGURE 62. *S. frugiperda* (Smith), female, Santa Cruz (× 2; AMNH).



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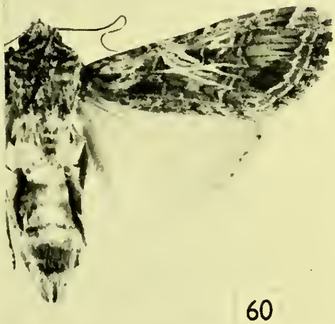

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ana, May; Isabela, April; San Cristóbal, February; Santa Cruz, March, April, October, December. BMNH, CAS, IRSNB.

BIOLOGY. Not reared on the Galápagos Islands. A pest of citrus on the mainland. Kimball and Tietz give foodplants.

Spodoptera dolichos (Fabricius).

(Figures 65 & 66.)

Noctua dolichos FABRICIUS, 1794, Entomologia Systematica, vol. 3, no. 2, p. 95. Type material: Americae meridionalis; not found by Zimsen, 1964, p. 570.

In common with some other members of the genus, this species is of economic importance on the mainland.

DISTRIBUTION. Widespread neotropical species. *Galápagos Islands*: Floreana, May; Santa Cruz, January–June, October, December. AMNH, BMNH, CAS, IRSNB.

BIOLOGY. Larvae reared on *Cryptocarpus pyriformis* have been referred to this species. Polyphagous.

Spodoptera frugiperda (Smith).

(Figures 61 & 62.)

Phalaena frugiperda J. E. SMITH, 1797, in Abbot & Smith, The Natural History of the Rarer Lepidopterous Insects of Georgia, vol. 2, p. 191, pl. 96. Type material: U.S.A., Georgia; not traced.

Another sexually dimorphic species of *Spodoptera*.

DISTRIBUTION. Widespread neotropical species. *Galápagos Islands*: Floreana, April; San Cristóbal, April; Santa Cruz, April, June; Santiago, March. AMNH, CAS, MCZ.

BIOLOGY. Not reared on the Galápagos Islands. A very general feeder.

Spodoptera roseae (Schaus).

(Figures 63 & 64.)

Trachea roseae SCHAUS, 1923, Zoologica, vol. 5, p. 33, pl. 1, fig. 4. (but proposed as '*Trachaea*' an incorrect spelling). Holotype, male (examined): Galápagos: Indefatigable [Santa Cruz]; USNM.

Laphygma roseae (Schaus): RICHARDS, 1941, Allan Hancock Pacific Expedition, vol. 5, p. 239.

Spodoptera roseae (Schaus): LINSLEY & USINGER, 1966, Proc. Calif. Acad. Sci., vol. 33, no. 7, p. 160.

Richards (1941) dealt with this species in detail.

DISTRIBUTION. Endemic species. *Galápagos Islands*: Floreana, April; Isabela, January, March; Pinta, October; San Cristóbal, April; Santa Cruz, January–July, October, December; Santiago, March. AMNH, BMNH, CAS, IRSNB, MCZ, USNM, ZSBS.

BIOLOGY. No data available.

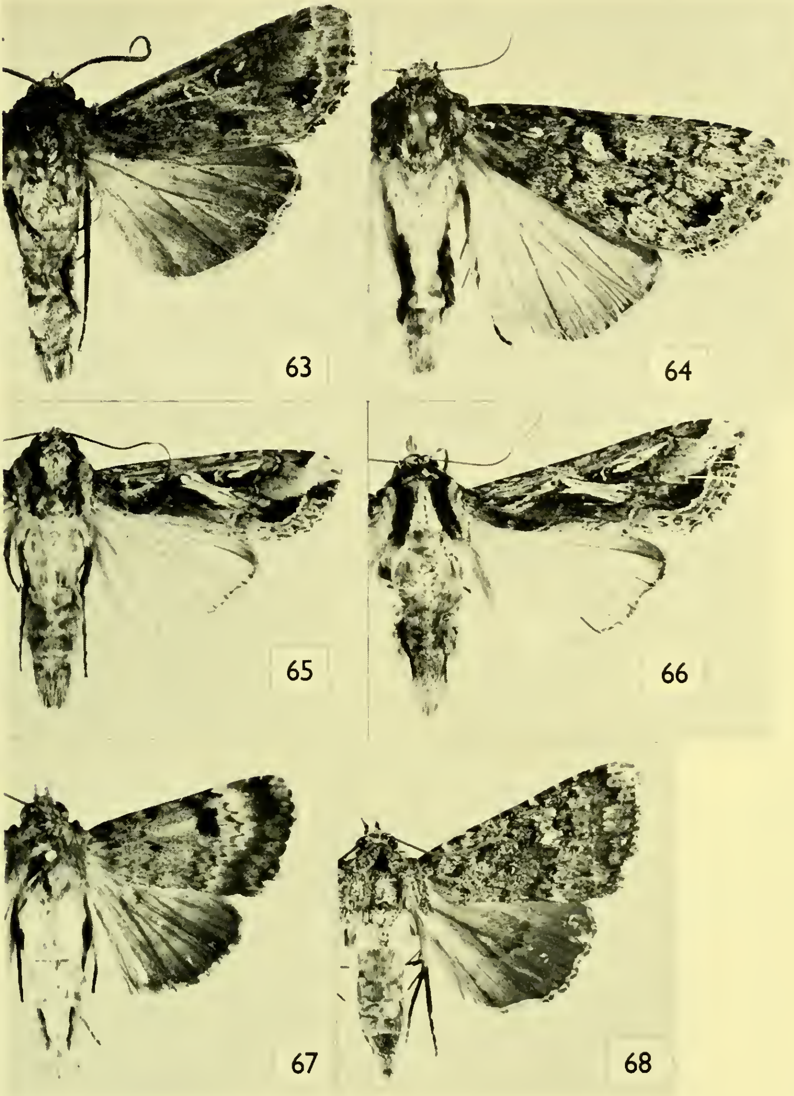

Figure 63. *Spodoptera roseae* (Schaus), male, Santa Cruz (× 2). Figure 64. *S. roseae* (Schaus), female, Santa Cruz (× 2). Figure 65. *Spodoptera dolichos* (Fabricius), male, Santa Cruz (× 2). Figure 66. *S. dolichos* (Fabricius), female, Santa Cruz (× 2). Figure 67. *Agrotisia williamsi* (Schaus), male, Santa Cruz (× 2). Figure 68. *Platysenta ruthae* (Schaus), male, Santa Cruz (× 2).

Elaphria encantada Hayes, new species.

(Figures 72, 73, 161, & 162.)

Elaphria dubiosa (Schaus) sensu Hayes, 1972, Pan-Pacific Entomologist, vol. 48, p. 104. Misidentification.

Description. Male 11 mm. Antenna simple. Palpus clothed with a mixture of dark brown and buff scales. Forewing with prominent orbicular and reniform spots. Claviform spot elongate. Variable in forewing color and patterning. Hindwing brown and buff. Genitalia as figured. Larger than average Pinta specimens cannot be separated structurally.

Female 10.5 mm. Similar to male. Variable.

Nearest relative is *Elaphria chalcedonia* Hübner. *Elaphria encantada* lacks the prominent apical spot of related species and can also be separated on genitalic structure.

Distribution. Endemic species.

Holotype. Male. Santa Cruz, December, 1968. R. Perry and Tj. de Vries. BMNH.

Paratypes. Española, February; Fernandina, February; Floreana, May; Isabela, January, March, August, September; Pinta, April, May, September, October; Pinzón, February, April, December; Santa Cruz, January–August, October–December; Santiago, March, April, July, August, November. AMNH (13 specimens), BMNH (331 specimens), CAS (853 specimens), IRSNB (46 specimens), MCZ (87 specimens), RSM (5 specimens), USC (1 specimen), ZSBS (1 specimen).

Biology. No data available.

Platysenta mobilis (Walker), revived species.

(Figure 71.)

Perigea mobilis Walker, [1857] 1856, List of the Specimens of Lepidopterous Insects in the Collection of the British Museum, vol. 10, p. 277. Holotype, male (examined): St. Domingo; BMNH.

Confusion has arisen in the literature and collections over this insect which has in the past been incorrectly determined as *Perigea apameoides* Guenée. Some specimens lack the white reniform spot.

Distribution. Widespread in the neotropical region. *Galápagos Islands*: Isabela, April; Santa Cruz, April–June; Santiago, April. AMNH, BMNH, CAS.

Biology. No data available.

Platysenta sutor (Guenée).

(Figures 69 & 70.)

Perigea sutor Guenée, 1852, in Boisduval & Guenée, Histoire naturelle des Insectes. Lépidoptères, vol. 5, p. 231. Holotype, male (examined): Brazil; BMNH.

Perigea apameoides Guenée, 1852, in Boisduval & Guenée, Historie naturelle des Insectes. Lépidoptères, vol. 5, p. 229. (Lectotype designated by Viette, 1951, Bulletin Mensuel de la Société Linnéenne de Lyon, vol. 20, p. 160.) MNHN. New synonym. Lectotype figured here—figure 70.

Perigea ebba Schaus, 1923, Zoologica, vol. 5, p. 36. New synonym.

Size and coloration of this species varies. The Guenée name *P. apameoides* has been incorrectly used in the literature and collections for *P. mobilis*. To avoid confusion, and acting as first reviser under the International Code of Zoological Nomenclature, Article 24, I am regarding '*apameoides*' as a synonym of *P. sutor* although *P. apameoides* has page priority. Subsequent to Viette's lectotype designation of *P. apameoides*, a paralectotype female from Coll. Guérin has been traced in the BMNH. It is conspecific with the lectotype and also bears the data "I. St. Thomas."

Distribution. Widespread in the neotropical region. *Galápagos Islands*: Baltra, April; Isabela, January, March; Pinzón, April; San Cristóbal, April; Santa Cruz, January–June, October, December; Santiago, March, April, November. AMNH, BMNH, CAS, IRSNB, MCZ, USNM.

Biology. No data available. Kimball lists *Wedelia* and *Tagetes* (Compositae) as foodplants in Florida.

Platysenta ruthae (Schaus).

(Figure 68.)

Perigea ruthae Schaus, 1923, Zoologica, vol. 5, p. 35. Lectotype, male (examined): Galápagos: Albemarle [Isabela]; USNM.

Platysenta ruthae (Schaus): Richards, 1941, Allan Hancock Pacific Expedition, vol. 5, p. 237.

Richards (1941) dealt with this species in detail. Widespread in the Islands.

Distribution. Endemic species. *Galápagos Islands*: Baltra, April; Floreana, April, July; Isabela, March, April, August; Pinta, October; Pinzón, April; Santa Cruz, January–June, August, October–December; Santiago, March, April, July. AMNH, BMNH, CAS, IRSNB, MCZ, USNM, ZSBS.

Biology. No data available.

Agrotisia williamsi (Schaus), new combination.

(Figure 67.)

Harrisonia williamsi Schaus, 1923, Zoologica, vol. 5. p. 36. Lectotype, male (examined): Galápagos: South Seymour [Baltra]; USNM.

Richards (1941) figured the genitalia of this species. I am indebted to Prof. J. G. Franclemont for pointing out that this species is congeneric with *A. subhyalina* Hampson, the type species of *Agrotisia* Hampson 1908. Widespread, seasonally abundant species.

Distribution. Endemic species. *Galápagos Islands*: Baltra, April; Es-


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FIGURE 69. *Platysenta sutor* (Guenée), male, Santa Cruz (× 2). FIGURE 70. *Perigea apameoides* (Guenée), lectotype, male, I. St. Thomas, Virgin Islands, synonym of *P. sutor* Guenée (× 2; MNHN). FIGURE 71. *Platysenta mobilis* Walker, male, Santa Cruz (× 2). FIGURE 72. *Elaphria encantada* Hayes, new species, holotype, male, Santa Cruz (× 2). FIGURE 73. *E. encantada* Hayes, new species, paratype, female, Santa Cruz (× 2).

pañola, February; Floreana, April; Gardner near Española, April; Isabela, March; Pinta, May; Santa Cruz, January–June, August–December; Santiago, July. AMNH, BMNH, CAS, IRSNB, MCZ, RSM, USNM, ZSBS.

Biology. No data available.

Acontiinae

Ozarba consternans Hayes, new species.

(Figures 75–78, & 158.)

Description. Male 8.5 mm. Antenna simple. Forewing blackish brown. Hindwing lighter shade of brown. Genitalia as figured. Unlike any known species.

Female 10 mm. Broader winged but similar to male.

Great variation in forewing maculation exists within this species (see figures). Provisionally placed in the genus *Ozarba*.

Distribution. Endemic species.

Holotype. Male. Santa Cruz, May 1970, R. Perry and Tj. de Vries.

Paratypes. Española, April; Floreana, April; Pinta, October; Santa Cruz, February, March, May, June; Santiago, March. BMNH (5 specimens), CAS (17 specimens), MCZ (17 specimens), ZSBS (5 specimens).

Biology. No data available.

Bagisara repanda (Fabricius), new combination.

(Figure 81.)

Bombyx repanda Fabricius, 1793, Entomologia Systematica, vol. 3, no. 1, p. 462. Lectotype (photograph examined): Americae meridionalis Insulis; UZM.

McDunnough (1938) and Kimball (1965) listed this species as *Atethmia subusta* Hübner. Draudt in Seitz used the combination *Bagisara subusta*.

Distribution. Widespread in the neotropical region. *Galápagos Islands*: Isabela (humid zone) Volcán Chico, June 1970, J. Gordillo; BMNH.

Biology. No data available. A specimen from Barbados in the BMNH was reared on *Sida glomerata*.

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Figure 74. *Eublemma recta* (Guenée), male, Santa Cruz (× 2). Figure 75. *Ozarba consternans* Hayes, new species, holotype, male, Santa Cruz (× 2). Figure 76. *O. consternans* Hayes, new species, paratype, female, Santa Cruz (× 2). Figure 77. *O. consternans* Hayes, new species, paratype, male, Santa Cruz (× 2; CAS). Figure 78. *O. consternans* Hayes, new species, paratype, female, Santa Cruz (× 2; CAS). Figure 79. *Amyna insularum* Schaus, male, Santa Cruz (× 2). Figure 80. *A. insularum* Schaus, male. Santa Cruz (× 2). Figure 81. *Bagisara repanda* (Fabricius), female, Isabela (× 2).

Eublemma recta (Guenée), new combination.

(Figure 74.)

Micra recta GUENÉE, 1852, in Boisduval & Guenée, Histoire naturelle des Insectes. Lépidoptères, vol. 6, p. 245. Holotype, male (examined): neotropical but stated to be "Sierra Leone?" by Guenée; USNM.

Somewhat variable in basic coloration.

DISTRIBUTION. Widespread in the neotropical region. *Galápagos Islands*: Genovesa, April; Santa Cruz, September. AMNH, BMNH.

BIOLOGY. *Foodplant. Ipomoea triloba. Larva.* Reddish brown. Pupation within silken cocoon. Forbes (1954) states the larvae feed on the buds and seeds of *Convolvulus* and sweet potato in the U.S.A. (Species listed as *Eublemma obliqualis* Fabricius).

Amyna insularum Schaus.

(Figures 79 & 80.)

Amyna insularum SCHAUS, 1923, Zoologica, vol. 5, p. 37. Lectotype, male (examined): Galápagos: Indefatigable [Santa Cruz]; USNM.

Two forms of this insect are recognized. One possesses a prominent white reniform spot. Both forms are figured. Well represented in collections.

DISTRIBUTION. Endemic species. *Galápagos Islands*: Baltra, April; Española, April; Fernandina, February; Floreana, January, April, July; Gardner near Española, April; Genovesa, no month; Isabela, January, March–June, August; Pinzón, April, June; Rábida, June; San Cristóbal, February–April; Santa Cruz, January–December; Santa Fé, April; Santiago, January, February–April. AMNH, BMNH, CAS, LACM, IRSNB, MCZ, RSM, ZSBS, USC.

BIOLOGY. Widespread, coastal regions; abundant; individuals at beginning of season may be smaller. At rest the wings are held flat and extended backwards, so that the insect assumes a characteristically triangular outline. *Foodplants. Alternanthera echinocephala, A. filifolia. Larva.* Pale green with darker lines.

Heliocontia margana (Fabricius).

(Figures 82 & 83.)

Pyralis margana FABRICIUS, 1794, Entomologia Systematica, vol. 3, no. 2, p. 257. Type material: Americae Insulis; UZM.

Sexually dimorphic.

DISTRIBUTION. Widely distributed in the neotropical region. *Galápagos Islands*: Baltra, April; Española, April; Floreana, April; Gardner near Española, April; Genovesa, February; Isabela, March; San Cristóbal, February, April; Santa Cruz, February, April, May, August; Santiago, February, March. AMNH, BMNH, CAS, MCZ, ZSBS, USC.

Biology. *Foodplants. Sida* species, *Abutilon depauperatum. Larva.* Variable, green with lighter and darker lines.

Spragueia creton Schaus.

(Figures 84–86.)

Spragueia creton Schaus, 1923, Zoologica, vol. 5, p. 38. Lectotype, male (examined): Galápagos: Genovesa (Tower); USNM.

Spragueia plumbeata Schaus, 1923, Zoologica, vol. 5, p. 38.

Spragueia creton Schaus: Todd, 1972, Jour. Washington Acad. Sci., vol. 62, no. 1, p. 36.

Todd has given full coverage of this sexually dimorphic species, placing *S. plumbeata* in synonymy.

Distribution. Endemic species. *Galápagos Islands*: Baltra, April; Española, February, April; Floreana, April; Gardner near Española, April; Genovesa, February, April; Isabela, March; San Cristóbal, April; Santa Cruz, March, May; Santiago, February, March. AMNH, BMNH, CAS, MCZ, USNM, ZSBS.

Biology. No data available.

Ponometia indubitans (Walker).

(Figures 92–94.)

Nonagria indubitans Walker, 1857, List of the Specimens of Lepidopterous Insects in the Collection of the British Museum, vol. 11, p. 712. Holotype, male (examined): [Brazil]: Para; BMNH.

Another sexually dimorphic, variable species. Further material of this species is needed.

Distribution. Widespread in the neotropical region. *Galápagos Islands*: Gardner near Hood, April; Genovesa, February; Isabela, March; San Cristóbal, February; Santa Cruz, May. BMNH, CAS, MCZ, USNM.

Biology. *Foodplant. Waltheria ovata. Larva.* Head greenish brown with black etchings. Body grayish green with black lines and markings. *Pupa.* Thin-walled, yellowish brown.

Euteliinae

Paectes arcigera (Guenée).

(Figures 89–91.)

Ingura arcigera Guenée, 1852, in Boisduval & Guenée, Histoire Naturelle des Insectes. Lépidoptères, vol. 6, p. 312. Holotype, female: [Virgin Islands]: Ile Saint-Thomas; not traced.

Paectes indefatigabilis Schaus, 1923, Zoologica, vol. 5, p. 38. New synonym.

Paectes isabel Schaus, 1923, Zoologica, vol. 5, p. 39. New synonym.

Sexually dimorphic, specimens exhibit considerable variation. The new synonymy has been established by genitalia preparations. Well represented in collections.

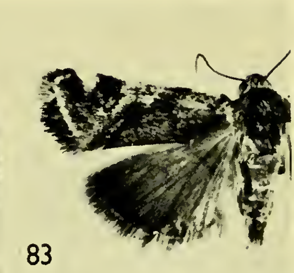

Figure 82. *Heliocontia margana* (Fabricius), male, Santa Cruz (× 4). Figure 83. *H. margana* (Fabricius), female, Santa Cruz (× 4). Figure 84. *Spragueia creton* Schaus, male, Santa Cruz (× 4). Figure 85. *S. creton* Schaus, female, Santa Cruz (× 4). Figure 86. *S. creton* Schaus, female, Santa Cruz (× 4). Figure 87. *Characoma nilotica* (Rogenhofer), female, Santa Cruz (× 2). Figure 88. *C. nilotica* (Rogenhofer), female, Santa Cruz

Distribution. Widespread neotropical species. *Galápagos Islands*: Baltra, April; Floreana, April, October; Gardner near Española, April; Genovesa, no month; Isabela, March–May, August; Pinta, May; Pinzón, April; San Cristóbal, April; Santa Fé, April; Santa Cruz, January–August, October, December; Santiago, March. AMNH, BMNH, CAS, IRSNB, MCZ, USNM.

Biology. On wing throughout the period December 1968 to May 1969, with a peak of abundance from mid March to early April; coastal areas, late afternoons, to be seen among foliage of *Cryptocarpus pyriformis*. *Foodplant. Bursera graveolens*. *Larva*. Green with pale lines; pale yellow on 1st segment and with 4 pigment spots at bases of setae.

SARROTHRIPINAE

Characoma nilotica (Rogenhofer).

(Figures 87 & 88.)

Sarrothripa nilotica Rogenhofer, 1882, Verhandlungen der Zoologisch-botanischen Gesellschaft in Wien, vol. 31, p. 26. Holotype (examined): Egypt; NM.

Variable species.

Distribution. Pantropical species. *Galápagos Islands*: Fernandina, January; San Cristóbal, April; Santa Cruz, January, February, June, September–November; Santiago, July. AMNH, BMNH, CAS, IRSNB.

Biology. Larval foodplant *Laguncularia racemosa*.

CATOCALINAE

Mocis incurvalis Schaus.

(Figures 95–97.)

Mocis incurvalis Schaus, 1923, Zoologica, vol. 5, p. 41. Lectotype, male (examined): Galápagos: Indefatigable [Santa Cruz]; USNM.

Sexually dimorphic. Some variation in female specimens.

Distribution. Endemic species. *Galápagos Islands*: Baltra, April; Fernandina, April; Isabela, March, April, August; Pinta, May, October; San Cristóbal, April; Santa Cruz, March–July, September, October. AMNH, BMNH, CAS, IRSNB, MCZ, RSM, USNM, ZSBS.

Biology. No data available. Gramineae are listed as important among foodplants of related species.

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(× 2; IRSNB). Figure 89. *Paectes arcigera* (Guenée), male, Santa Cruz (× 2). Figure 90. *P. arcigera* (Guenée), male, Santa Cruz (× 2). Figure 91. *P. arcigera* (Guenée), female, Santa Cruz (× 2). Figure 92. *Ponometia indubitans* (Walker), male, Isabela (× 2; CAS). Figure 93. *P. indubitans* (Walker), male, Floreana (× 2). Figure 94. *P. indubitans* (Walker), female, Santiago (× 2).

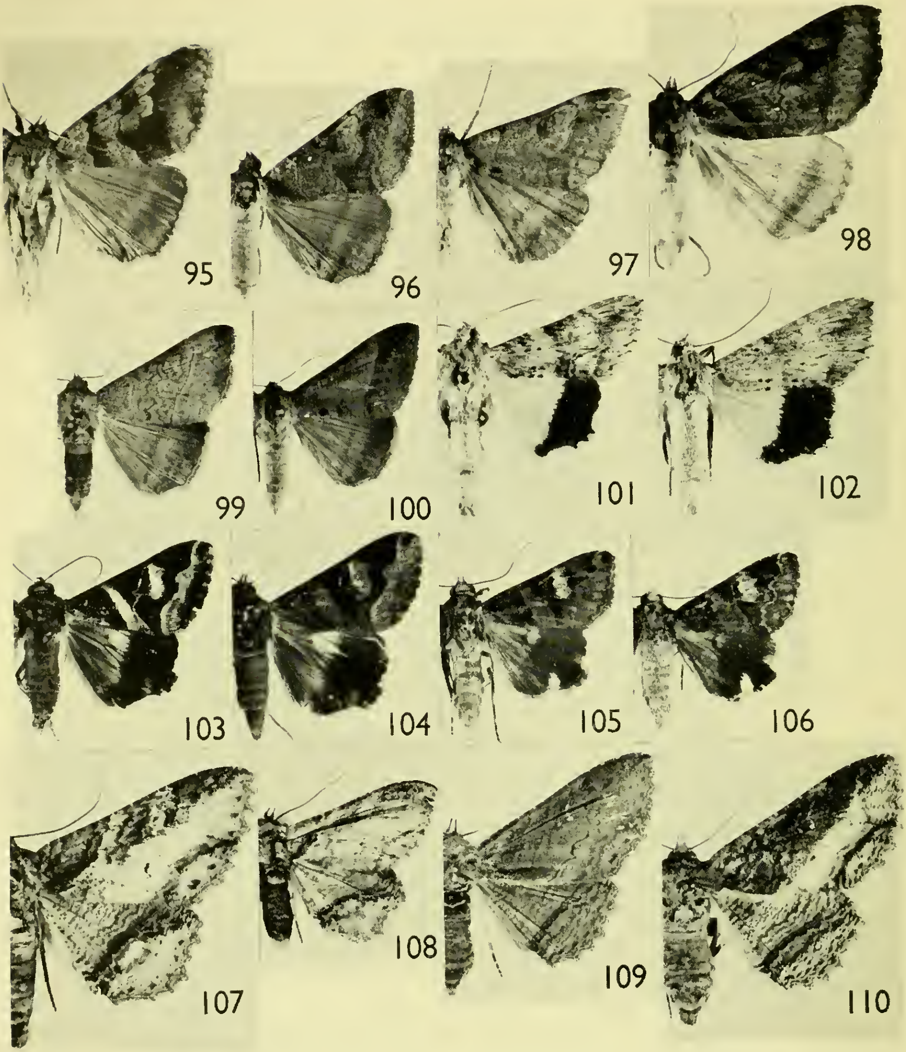

FIGURE 95. *Mocis incurvalis* Schaus, male, Santa Cruz (× 1). FIGURE 96. *M. incurvalis* Schaus, female, Santa Cruz (× 1). FIGURE 97. *M. incurvalis* Schaus, female, Santa Cruz (× 1). FIGURE 98. *Celiptera remigioides* (Guenée), female, Santa Cruz (× 1). FIGURE 99. *Mocis latipes* (Guenée), female, Santa Cruz (× 1). FIGURE 100. *M. latipes* (Guenée), female, Santa Cruz (× 1). FIGURE 101. *Melipotis acontioides producta* Hayes, new subspecies, holotype, male, Santa Cruz (× 1). FIGURE 102. *M. acontioides producta* Hayes, new subspecies, paratype, female, Santa Cruz (× 1). FIGURE 103. *M. indomita* (Walker), male, Santa Cruz (× 1). FIGURE 104. *M. indomita* (Walker), female, Santa Cruz (× 1). FIGURE 105. *M. harrisoni* Schaus, male, Santa Cruz (× 1). FIGURE 106. *M. harrisoni* Schaus, female, Santa Cruz (× 1). FIGURE 107. *Zale obsita* (Guenée), male, Santa Cruz (× 1). FIGURE 108. *Z. obsita* (Guenée), male, Santa Cruz (× 1; CAS). FIGURE 109. *Z. obsita* (Guenée), female, Santa Cruz (× 1). FIGURE 110. *Z. obsita* (Guenée), female, Santiago (× 1).

Mocis latipes (Guenée).

(Figures 99 & 100.)

Remigia latipes Guenée, in Boisduval & Guenée, 1852, Histoire Naturelle des Insectes. Lépidoptères, vol. 7, p. 314. Lectotype, male (examined): Guadeloupe; BMNH.

Variable species.

Distribution. Widespread in the neotropical region. *Galápagos Islands*: Baltra, April; Floreana, May; San Cristóbal, April; Santa Cruz, April–June. AMNH, BMNH, CAS, MCZ, USC.

Biology. Larvae not yet found on the Galápagos Islands. In the U.S.A. this species feeds on grasses and other crops.

Celiptera remigioides (Guenée).

(Figure 98.)

Ophiodes remigioides Guenée, 1852, in Boisduval & Guenée, Histoire Naturelle des Insectes. Lépidoptères, vol. 7, p. 230, pl. 21, fig. 5. Syntype male (examined): neotropical but stated to be Central India; BMNH.

The hindwing of this species varies from yellow to fuscous.

Distribution. Widespread in the neotropical region. *Galápagos Islands*: Genovesa, March; Santa Cruz, February–April, July, October, December. AMNH, BMNH, CAS.

Biology. No data available.

Zale obsita (Guenée), revived species.

(Figures 107–110.)

Homoptera obsita Guenée, 1852, in Boisduval & Guenée, Histoire Naturelle des Insectes. Lépidoptères, vol. 7, p. 12. Holotype, female (examined): Brazil; BMNH.

Zale species, *viridans* group Richards, 1941, Allan Hancock Pacific Expedition, vol. 5, p. 243.

Richards figured the male genitalia of this variable species which was previously synonymized with *Z. viridans*. I am indebted to Dr. E. L. Todd for help with this identification.

Distribution. A neotropical species. *Galápagos Islands*: Santa Cruz, February–April, June, October, November; Santiago, November. AMNH, BMNH, CAS, IRSNB, MCZ.

Biology. No data available.

PLUSIINAE

Autoplusia egena galapagensis (Schaus).

(Figure 111.)

Syngrapha egena galapagensis Schaus, 1923, Zoologica, vol. 5, p. 41. Holotype, female (examined): Galápagos: James [Santiago]; USNM.

This is the dullest colored of the three species of this subfamily known from the Galápagos Islands.

DISTRIBUTION. Endemic subspecies of the neotropical species. *Galápagos Islands*: Baltra, April; Isabela, May, September; Pinzón, June; San Cristóbal, April, June; Santa Cruz, February, May, June; Santiago, April. AMNH, BMNH, CAS, USNM.

BIOLOGY. No data available. In the U.S.A. the nominate subspecies feeds on *Phaseolus* (Leguminosae).

Argyrogramma verruca (Fabricius).

(Figure 112.)

Noctua verruca FABRICIUS, 1794, Entomologia Systematica, vol. 3, pt 2, p. 81. Type material: Americae meridionalis Insulis; UZM.

This is the smallest species of this subfamily found on the Galápagos Islands.

DISTRIBUTION. Widespread in the neotropics, extending to Canada. *Galápagos Islands*: Floreana, January; Isabela, January; Santa Cruz, February, April. AMNH, BMNH, CAS.

BIOLOGY. No data available. Foodplants in the U.S.A. include *Sagittaria* and *Calendula*.

Pseudoplusia includens (Walker).

(Figure 113.)

Plusia includens WALKER, [1858] 1857, List of the Specimens of Lepidopterous Insects in the Collection of the British Museum, vol. 12, p. 914. Type female (examined): St. Domingo; BMNH.

Previously treated as *Phalaena oo* (Stoll) by some workers, but this is a junior primary homonym.

DISTRIBUTION. Widespread in the neotropical region. *Galápagos Islands*:

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FIGURE 111. *Autoplusia egena galapagensis* (Schaus), male, Santa Cruz (× 1). FIGURE 112. *Argyrogramma verruca* (Fabricius), male, Isabela (× 1). FIGURE 113. *Pseudoplusia includens* (Walker), female, Santa Cruz (× 1). FIGURE 114. *Ascalapha odorata* (Linnaeus), male, Santa Cruz (× ¾; CAS). FIGURE 115. *A. odorata* (Linnaeus), female, Santa Cruz (× ¾). FIGURE 116. *Letis mycerina* (Cramer), male, Panama (× ¾). FIGURE 117. *L. mycerina* (Cramer), female, Santa Cruz (× ¾). FIGURE 118. *Epidromia zetophora* Guenée, male, Isabela (× 1). FIGURE 119. *Psorya hadesia* Schaus, male, Santa Cruz (× 1). FIGURE 120. *P. hadesia* Schaus, female, Santa Cruz (× 1). FIGURE 121. *P. hadesia* Schaus, female, Punta Suarez, Española (× 1). FIGURE 122. *Epidromia zephyritis* Schaus, male, Santa Cruz (× 1). FIGURE 123. *E. zephyritis* Schaus, female, Santa Cruz (× 1). FIGURE 124. *Anticarsia prona* (Möschler), male, Isabela (× 1). FIGURE 125. *A. prona* (Möschler), female, Isabela (× 1). FIGURE 126. *A. gemmatalis* Hübner, male, Santa Cruz (× 1). FIGURE 127. *A. gemmatalis* Hübner, male, Santa Cruz (× 1). FIGURE 128. *A. gemmatalis* Hübner, female, Santa Cruz (× 1).


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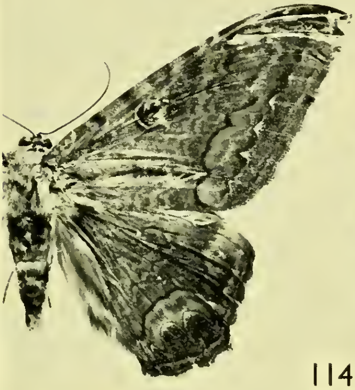
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Baltra, April, June; Isabela, March, May; Floreana, no month; San Cristóbal, February, April; Santa Cruz, February–April; Santiago, April. AMNH, BMNH, CAS, MCZ, USNM, USC.

BIOLOGY. Abundant some years, particularly from February to May. Diurnal, coming especially to flowers of *Clerodendrum molle* and *Cordia* species. *Foodplants. Cordia leucophlyctis, Tournefortia psilostachya, Heliotropium angiospermum, Lantana peduncularis, Mentzelia aspera. Larva.* Smooth; pale green with thin white lines. *Pupa.* Greenish, thin-walled in flimsy cocoon in coiled underside of leaf of host plant.

OPHIDERINAE

Melipotis acontioides producta Hayes, new subspecies.

(Figures 101 & 102.)

Galápagos specimens can be separated by the extended marginal band on the posterior margin of the hindwing.

DISTRIBUTION. Endemic subspecies of the widespread neotropical species.

HOLOTYPE. Male. 26 mm., Santa Cruz, February 1970, R. Perry and Tj. de Vries, BM 1970–170.

PARATYPES. Española, April; Floreana, April; Isabela, March; Santa Cruz, January–March, August–November. AMNH (31 specimens), BMNH (27 specimens), CAS (63 specimens), IRSNB (7 specimens), MCZ (25 specimens), RSM (2 specimens).

BIOLOGY. *Foodplant. Parkinsonia aculeata. Larva.* A pattern of gray-black markings outlined with white; some reddish brown on side. The larvae have the habit of lying pressed to the central part of the leaf.

Melipotis indomita (Walker).

(Figures 103 & 104.)

Bolina indomita WALKER, [1858] 1857, List of the Specimens of Lepidopterous Insects in the Collection of the British Museum, vol. 13, p. 1161. Holotype, female (examined): Brazil; BMNH.

Sexually dimorphic. This insect has recently reached Hawaii.

DISTRIBUTION. Widespread in the neotropical region. *Galápagos Islands*: Baltra, April; Española, April; Floreana, January, February–July, October; Genovesa, April; Isabela, March, April, August; Pinta, October; Pinzón, April, June; San Cristóbal, February, April, July; Santa Cruz, January–June, August, October, December; Santa Fé, April, July; Santiago, March, July. AMNH, BMNH, CAS, IRSNB, MCZ, USNM, ZSBS, USC.

BIOLOGY. A common species, found in all months except at prolonged dry periods; adults come to flowers at dusk in the rainy season. *Foodplant. Prosopis jubiflora. Larva.* Head shiny brown. Body greenish white with red and gray-brown markings; more reddish laterally; underside pale, unmarked. Larvae are found during the day in litter or under rocks at the base of the plants. *Pupa.* Pupation takes place in a loose cocoon of particles of soil and litter.

Melipotis harrisoni Schaus.

(Figures 105 & 106.)

Melipotis harrisoni Schaus, 1923, Zoologica, vol. 5, p. 42. Lectotype, male (examined): Galápagos: South Seymour [Baltra]; USNM.

Sexually dimorphic. The prominent white spots on the hindwing separate this species from *M. indomita.*

Distribution. Endemic species. *Galápagos Islands*: Baltra, January, February, April, November; Floreana, April; Isabela, January–April, August; Pinzón, April, December; Rábida, June; San Cristóbal, February; Santa Cruz, January–October, December; Santiago, January, July. AMNH, BMNH, CAS, IRSNB, LACM, MCZ, RSM, USNM, ZSBS, USC.

Biology. *Foodplants. Acacia macracantha, Acacia rorudiana. Larva.* Head gray bordered with black. Body pale greenish gray with darker markings; some purplish suffusion.

Ascalapha odorata (Linnaeus).

(Figures 114 & 115.)

Phalaena (*Bombyx*) *odorata* Linnaeus, 1758, Systema Naturae (10th Ed.), vol. 1, p. 505. Type material (examined): America; LS.

Sexually dimorphic. Has been seen on some of the smaller and drier islands such as Genovesa and Pinzón. Generally seen at dusk. I believe this to be the species mentioned by Nelson (1968) as a saturniid. Galápagos specimens are usually smaller than those from the mainland.

Distribution. Widespread in the neotropical region. *Galápagos Islands*: Floreana, April, May; San Cristóbal, April; Santa Cruz, March–June, October. AMNH, BMNH, CAS, MCZ, USC.

Biology. No data available. Tietz lists *Acacia* and *Cassia* among its foodplants in the U.S.A.

Letis mycerina (Cramer).

(Figures 116 & 117.)

Phalaena (*Attacus*) *mycerina* Cramer, 1777, Uitlandsche Kapellen, vol. 2, p. 115, pl. 172, fig. B. Holotype, female: Surinam; not traced.

A fairly large, sexually dimorphic noctuid which may have been dismissed as *A. odorata* previously. I have illustrated a male from Panama since this species is only represented from the Islands in the BMNH by a female.

Distribution. Neotropical species. *Galápagos Islands*: Santa Cruz, April, June. AMNH, BMNH.

Biology. No data available.

Rivula asteria (Druce), new combination.

(Figure 144.)

Thalpochares asteria DRUCE, 1898, Biologia Centrali-Americana, Heterocera, vol. 2, p. 497, pl. 95, fig. 25. Holotype, female (examined): Teapa, Mexico; BMNH.

Rivula ? dubiosa SCHAUS, 1923, Zoologica, vol. 5, p. 44. New synonym. Lectotype, female (examined): Galápagos, Indefatigable [Santa Cruz]; USNM.

I have illustrated a male of this species which is rare in collections. Galápagos material I have examined has been in poor condition. The genus *Rivula* is used provisionally until revisionary work is undertaken.

DISTRIBUTION. Mexico, Bolivia, Galápagos archipelago. *Galápagos Islands*: Santa Cruz, March, April, June. AMNH, BMNH, CAS.

BIOLOGY. No data available.

Glympis toddi Hayes, new species.

(Figures 140 & 141.)

DESCRIPTION. MALE 12 mm. Antenna simple. Palpus gray brown. Slight concavity in costal margin of forewing. Forewing narrow, fuscous, and darker brown. Antemedial band angled. Postmedial band well-defined. Undersurface orange, yellow, and fuscous. Postmedial line of hindwing prominent orange. Abdominal tufts reduced.

Female 14 mm. Broader winged but similar to male.

Both sexes highly variable in forewing maculation. Differs from the nearest species *Glympis incusalis* Grote by the differing forewing maculation and more fuscous hindwing.

DISTRIBUTION. Endemic species.

HOLOTYPE. Male. Floreana, Asilo de la Paz, 360 m., January 1971.

PARATYPES. Floreana, April; Isabela, March, September; Pinta, May, September; Santa Cruz, January–March, May–June, August–September. AMNH (4 specimens), BMNH (133 specimens), CAS (86 specimens), IRSNB (11 specimens), MCZ (7 specimens), RSM (5 specimens), ZSBS (8 specimens).

BIOLOGY. No data available.

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FIGURE 129. *Anomis editrix* (Guenée), male, Floreana (× 2). FIGURE 130. *A. illita* (Guenée), male, Santa Cruz (× 2). FIGURE 131. *A. luridula professorum* Schaus, male, Isabela (× 2). FIGURE 132. *A. erosa* Hübner, male, Floreana (× 2). FIGURE 133. *Bendis formularis* Geyer, male, Mexico (× 2). FIGURE 134. *B. formularis* Geyer, female, Santa Cruz (× 2). FIGURE 135. *Gonodonta fulvangula* Geyer, female, Santa Cruz (× 2; AMNH). FIGURE 136. *G. biarmata evadens* Walker, male, Santa Cruz (× 2). FIGURE 137. *G. biarmata evadens* Walker, female, Santa Cruz (× 2).


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Anomis editrix (Guenée).

(Figure 129.)

Gonitis editrix Guenée, 1852, in Boisduval & Guenée, Histoire Naturelle des Insectes. Lépidoptères, vol. 6, p. 404. Type material (examined): Haiti; BMNH.

One of four species in this genus found on the Galápagos Islands. Lacks yellow coloration but possesses an angled margin to the forewing. Variable species.

Distribution. Widespread in the neotropical region. *Galápagos Islands*: Floreana, January; Santa Cruz, June. AMNH, BMNH.

Biology. No data available.

Anomis illita Guenée.

(Figure 130.)

Anomis illita Guenée, 1852, in Boisduval & Guenée, Histoire Naturelle des Insectes. Lépidoptères, vol. 6, p. 400. Lectotype, female: Brazil; MNHN.

Possesses the straightest forewing margin of the four species of *Anomis* found on the Galápagos Islands.

Distribution. Widespread neotropical species. *Galápagos Islands*: Santa Cruz, March–July. AMNH, BMNH, CAS.

Biology. *Foodplant. Hibiscus tiliaceus. Larva.* Head green, spotted black. Body pale, purplish brown; anal plate green. The single larva found was feeding on the flower of the above hostplant.

Anomis luridula professorum Schaus, new status.

(Figure 131.)

Anomis professorum Schaus, 1923, Zoologica, vol. 5, p. 42. Lectotype, male (examined): Galápagos: Chatham [San Cristóbal]; USNM.

Variable species. I am reducing '*professorum*' to subspecific status. Genitalia match those of mainland specimens but Galápagos specimens are smaller and less strongly marked.

Distribution. Endemic subspecies of the widespread neotropical species. *Galápagos Islands*: Baltra, April; Floreana, March, August; Genovesa, April; Isabela, February–April, August; Rábida, June; San Cristóbal, February, April; Santa Cruz, February, April–July; Santiago, April. AMNH, BMNH, CAS, LACM, USNM, ZSBS.

Biology. No data available.

Anomis erosa Hübner.

(Figure 132.)

Anomis erosa Hübner, 1823, Zuträge zur Sammlung Exotischer Schmetterlinge, vol. 2, p. 19, figs. 287–288. Type female: [U.S.A.] Savannah; not traced.

Forewing yellow and gray with angled margin.

DISTRIBUTION. Widespread neotropical species. *Galápagos Islands*: Floreana, January; Santa Cruz, March, June. AMNH, BMNH, CAS, MCZ, USC.

BIOLOGY. No data available. Foodplants in the U.S.A. are members of Malvaceae.

Plusiodonta clavifera (Walker).

(Figures 138 & 139.)

Tafalla clavifera WALKER, 1869, Characters of undescribed Lepidoptera Heterocera, p. 43. Type material (examined): [Honduras] Limas; BMNH.

Sexually dimorphic.

DISTRIBUTION. Widespread neotropical species. *Galápagos Islands*: Santa Cruz, February–May, September–November. BMNH, CAS, ZSBS.

BIOLOGY. No data available.

Gonodonta biarmata evadens Walker, new status.

(Figures 136 & 137.)

Gonodonta evadens WALKER, [1858] 1857, List of the Specimens of Lepidopterous Insects in the Collection of the British Museum, vol. 12, p. 955. Lectotype, female (examined): [Galápagos] 'W. Coast of America'; BMNH.

Gonodonta biarmata galapagensis TODD, 1959, Tech. Bull. Agric. Res. Serv. U.S. Dept. Agric., no. 1201, p. 20, new synonym. Holotype, male (examined): Galápagos, Indefatigable [Santa Cruz]; AMNH.

Facts relating to the origin of the two female specimens studied by Walker, labelled "W. Coast of America," (already mentioned under *Psaphara interclusa*,) strongly suggested they were taken on the Galápagos Islands. This is confirmed as they match Galápagos specimens.

DISTRIBUTION. Endemic subspecies of the widespread neotropical species. *Galápagos Islands*: Fernandina, February; Floreana, no month; Isabela, March; Pinta, October; San Cristóbal, January, April, June; Santa Cruz, January–July, November, December. AMNH, BMNH, CAS, MCZ, MRAC, USNM, USC.

BIOLOGY. The adults of some species of *Gonodonta* have caused injury to citrus crops by piercing the fruit. Todd (1959, p. 19) gives foodplants of nominate subspecies.

Gonodonta fulvangula Geyer.

(Figure 135.)

Gonodonta fulvangula GEYER, 1832, in Hübner, Zuträge zur Sammlung Exotischer Schmetterlinge, vol. 4, p. 32, figs. 737, 738. Type material: Monte Video; not traced.

Only one specimen has so far been taken.

DISTRIBUTION. Widespread neotropical species. *Galápagos Islands*: Santa Cruz, Horneman Farm, 200 m., 27 June 1965, Mrs. J. DeRoy, 1 female, AMNH.

Biology. No data available. Todd's revision of this genus quotes an 1882 reference to Araticú as the foodplant. This name refers to species of *Annona* and possibly to *A. montana*.

Metallata absumens contiguata Hayes, new subspecies.

(Figures 145 & 146.)

I am separating the Galápagos population of this extremely variable insect as a distinct subspecies. In each specimen examined the reniform spot on the forewing is fused or in very close proximity to the postmedial fascia. This is in direct contrast to mainland specimens where the two markings are always separated by at least 1 mm.

Distribution. Endemic subspecies of the species widespread in the neotropical region.

Holotype. Male. 14.5 mm. Floreana, Asilo de la Paz, 360 m., January 1971. BMNH.

Paratypes. Floreana, April; Isabela, August; Marchena, November; San Cristóbal, April; Santa Cruz, February–July, September, October. AMNH (16 specimens), BMNH (15 specimens), CAS (31 specimens), IRSNB (1 specimen), MCZ (1 specimen), ZSBS (14 specimens).

Biology. No data available.

Bendis formularis Geyer.

(Figures 133 & 134.)

Bendis formularis Geyer, 1837, in Hübner, Zuträge zur Sammlung Exotischer Schmetterlinge, vol. 5, p. 26, figs. 903–904. Type female: Brazil; not traced.

I have seen only three specimens from the Galápagos Islands.

Distribution. Widespread neotropical species. *Galápagos Islands*: Floreana, no month; Santa Cruz, June, September. AMNH, BMNH, USC.

Biology. No data available.

Anticarsia gemmatalis Hübner.

(Figures 126–128.)

Anticarsia gemmatalis Hübner, 1818, Zuträge zur Sammlung Exotischer Schmetterlinge, vol. 1, p. 26, figs. 153–154. Type material: Surinam; not traced.

An extremely variable, common species.

Distribution. Widespread neotropical species. *Galápagos Islands*: Baltra, March, April; Fernandina, April; Floreana, February; Genovesa, March, April; Isabela, March–May; Pinta, October; San Cristóbal, February, April; Santa Cruz, January–July, October. AMNH, BMNH, CAS, IRSNB, MCZ, USNM, ZSBS.

Biology. Found in the arid and humid zones of the main islands; abundant at times; diurnal to an extent. *Foodplants. Cryptocarpus pyriformis, Piscidia carthagenensis, Rhynchosia minima. Larva.* Green, paler lines edged with black. In the U.S.A. this species is known as the Velvetbean Caterpillar. It feeds on a wide range of plants.

Anticarsia prona (Möschler).

(Figures 124 & 125.)

Thermesia prona Möschler, 1880, Verhandlungen der Zoologisch-botanischen Gesellschaft in Wien, vol. 30 (Abh.), p. 443. Type material: [Panama] Chiriqui; [Venezuela] Puerto Cabello; Surinam, Paramaribo; not traced.

Sexually dimorphic.

Distribution. Widespread neotropical species. *Galápagos Islands*: Isabela, January, August; Santa Cruz, February–July. AMNH, BMNH, CAS, ZSBS.

Biology. No data available.

Psorya hadesia Schaus.

(Figures 119–121.)

Psorya hadesia Schaus, 1923, Zoologica, vol. 5, p. 44. Lectotype, female (examined): Galápagos: South Seymour [Baltra]; USNM.

A single female in the BMNH from Punta Suarez, Española (fig. 121) differs in its lighter brown and white coloration. Introduced goats are destroying the recorded foodplant on Española and this interesting form may well be endangered.

Distribution. Endemic species. *Galápagos Islands*: Baltra, April, September; Española, May; Floreana, April, May, July; Isabela, March, April, August; Pinzón, December; Santa Cruz, January–December; Santiago, July. AMNH, BMNH, CAS, IRSNB, MCZ, RSM, USNM, ZSBS.

Biology. *Foodplant. Maytenus octogona. Larva.* Head and body uniform green.

Epidromia zetophora Guenée.

(Figure 118.)

Epidromia zetophora Guenée, 1852, in Boisduval & Guenée, Histoire Naturelle des Insectes. Lépidoptères, vol. 7, p. 326, pl. 23, fig. 5. Holotype, male: Brazil; not traced.

Variable species. Only one male of this species has been taken on the Islands. It was collected in 1932 by M. Willows, Jr. of the Templeton-Crocker Expedition.

Distribution. Widespread neotropical species. *Galápagos Islands*: Isabela, May. CAS.

Biology. No data available.

Epidromia zephyritis Schaus.

(Figures 122 & 123.)

Epidromia zephyritis SCHAUS, 1923, Zoologica, vol. 5, p. 43. Holotype, female (examined): Galápagos: Indefatigable [Santa Cruz]; USNM.

Another variable species.

DISTRIBUTION. Endemic species. *Galápagos Islands*: Baltra, no month; Floreana, April, July; Isabela, January, March, July–September; Pinzón, April; San Cristóbal, April, October; Santa Cruz, January–December; Santiago, March, July. AMNH, BMNH, CAS, IRSNB, MCZ, RSM, USNM, ZSBS.

BIOLOGY. Arid and coastal areas where its foodplant occurs. *Foodplant. Scutia pauciflora.* Larvae collected on the mangrove *Laguncularia racemosa,* at Punta Espinosa, Fernandina in September 1970, although not reared, have been referred to this species. *Larva.* Whitish with extensive gray and brown markings.

HYPENINAE

Sorygaza variata Hayes, new species.

(Figures 142, 143, 164, & 165.)

DESCRIPTION. Male 10 mm. Antenna simple. Palpus prominent, clothed with buff and dark brown scales. Forewing cream, orange-brown, and darker brown. Postmedial band and antemedial band crenulate. Darker scaling of subterminal line forming cresent at apex. Prominent dark spotting forming adterminal line. Genitalia figured.

Female 9.5 mm. Broader winged but similar to male.

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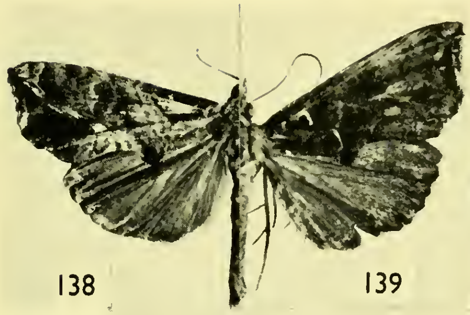
FIGURE 138. *Plusiodonta clavifera* (Walker), male, Santa Cruz (× 2; CAS). FIGURE 139. *P. clavifera* (Walker), female, Santa Cruz (× 2). FIGURE 140. *Glympis toddi* Hayes, new species, holotype, male, Floreana (× 2). FIGURE 141. *G. toddi* Hayes, new species, paratype, female, Floreana (× 2). FIGURE 142. *Sorygaza variata* Hayes, new species, holotype, male, Santa Cruz (× 2; CAS). FIGURE 143. *S. variata* Hayes, new species, paratype, female, Isabela (× 2). FIGURE 144. *Rivula asteria* (Druce), male, Santa Cruz (× 2; CAS). FIGURE 145. *Metallata absumens contiguata* Hayes, new subspecies, holotype, male, Floreana (× 2). FIGURE 146. *M. absumens contiguata* Hayes, new subspecies, paratype, male (× 2). FIGURE 147. *Hypena microfuliginea* Hayes, new species, holotype, male, Isabela (× 2). FIGURE 148. *H. microfuliginea* Hayes, new species, paratype, female, Floreana (× 2). FIGURE 149. *Peliala fuliginea* Hayes, new species, holotype, male, Pinta (× 2). FIGURE 150. *P. fuliginea* Hayes, new species, paratype, female, Pinta (× 2). FIGURE 151. *Hypena vetustalis* (Guenée), female, Floreana (× 2). FIGURE 152. *Ophiuche lividalis* (Hübner), male, Floreana (× 2; CAS). FIGURE 153. *O. minualis constans* Hayes, new subspecies, holotype, male, Santa Cruz (× 2; CAS). FIGURE 154. *O. minualis constans* Hayes, new subspecies, paratype, female, Pinta (× 2).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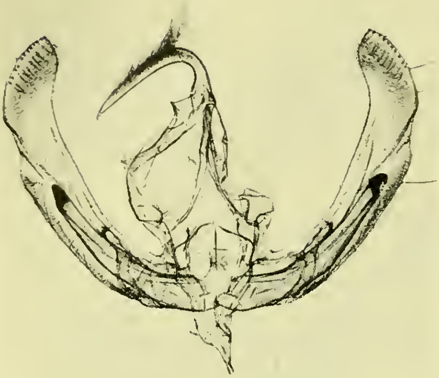

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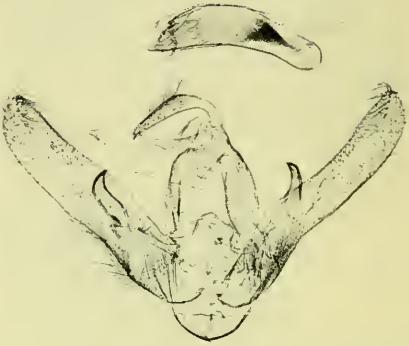

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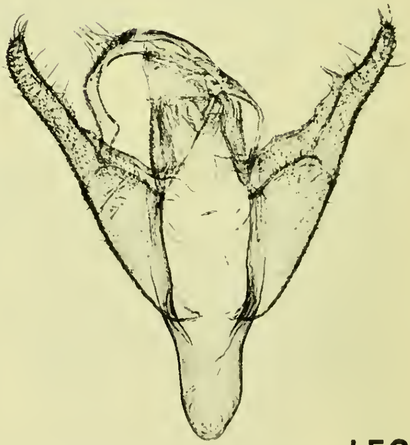

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FIGURE 155. *Magusa erema* Hayes, new species, paratype, male, genitalia. FIGURE 156. *Trachea cavagnaroi* Hayes, new species, holotype, male, genitalia (CAS). FIGURE 157. *Hypena microfuliginea* Hayes, new species, paratype, male, genitalia. FIGURE 158. *Ozarba consternans* Hayes, new species, paratype, male, genitalia (CAS).

Variable species.

Nearest species is *Sorygaza didymata* Walker. The forewing of *S. variata* has a more evenly rounded postmedial band and is a more strongly colored species. The diagnostic dorsal process of the male genitalia (see figure) also separates *S. variata*.

Distribution. Endemic species.

Holotype. Male. Santa Cruz, Horneman Farm, 220 m., 5 April 1964, D. Q. Cavagnaro. CAS.

Paratypes. Isabela, January, August; Santa Cruz, April, May. BMNH (7 specimens), CAS (15 specimens).

Biology. No data available.

Hypena vetustalis (Guenée).

(Figure 151.)

Bomolocha vetustalis Guenée, 1854, in Boisduval & Guenée, Histoire Naturelle des Insectes. Lépidoptères, vol. 8, p. 35. Holotype, female (examined): Haiti; BMNH.

Known only from female specimens. Further material may prove a species-complex is involved.

Distribution. Widespread neotropical species. *Galápagos Islands*: Floreana, January; Isabela, August; Santa Cruz, May, June, July. AMNH, BMNH.

Biology. No data available.

Hypena microfuliginea Hayes, new species.

(Figures 147, 148, & 157.)

Description. Male 13.5 mm. Antenna simple. Palpus prominent, heavily scaled. Midbrown forewing with prominent orbicular spot. Postmedial fascia with two rounded extensions terminad. Hindwing drab brown.

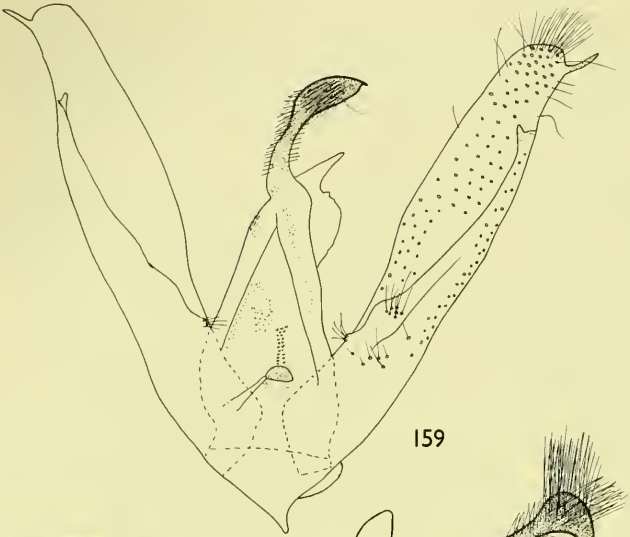
Female 14 mm. Broader winged but similar to male.

Nearest species is *Hypena vetustalis* Guenée but *H. microfuliginea* can also be confused with the larger *Peliala fuliginea*. However, *H. vetustalis* has a straight median line. Palpus structure and male genitalia also separate *H. microfuliginea* from *P. fuliginea*.

→

Figures 159 and 160. *Rivula asteria* (Druce) male genitalia (CAS). Figures 161 and 162. *Elaphria encantada* Hayes, new species, paratype, male, genitalia. Figure 163. *Psaphara interclusa* Walker, holotype, male, genitalia.

Figures 164 and 165. *Sorygaza variata* Hayes, new species, holotype, male, genitalia (CAS). Figures 166 and 167. *Peliala fuliginea* Hayes, new species, paratype, male, genitalia. Figures 168 and 169. *Epiplema becki* Hayes, new species, holotype, male, genitalia (CAS). Figure 170. *E. becki* Hayes, new species, paratype, female, genitalia.



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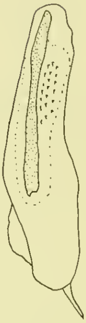

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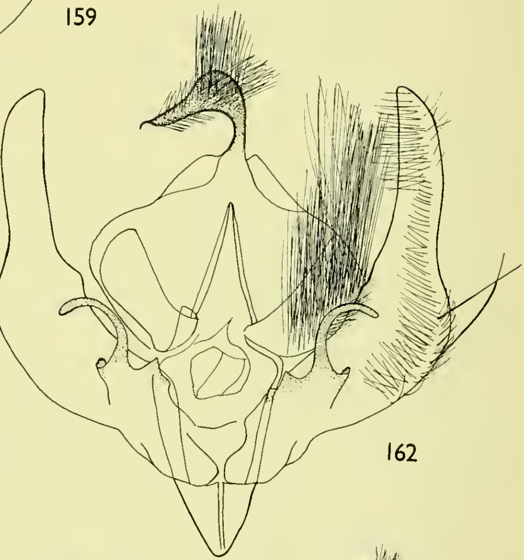

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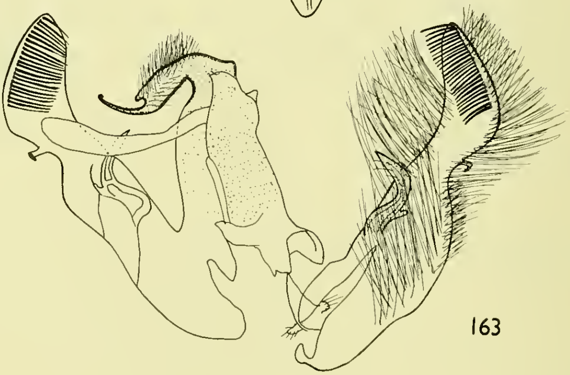

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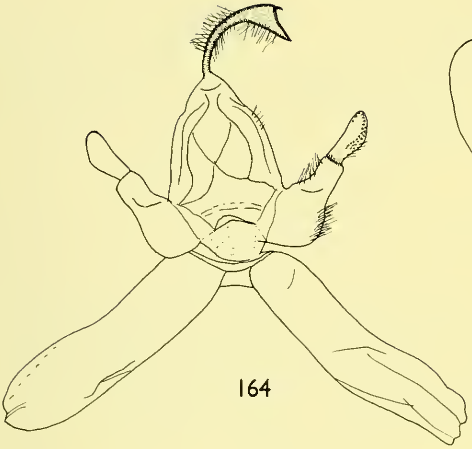

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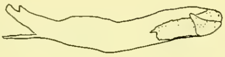

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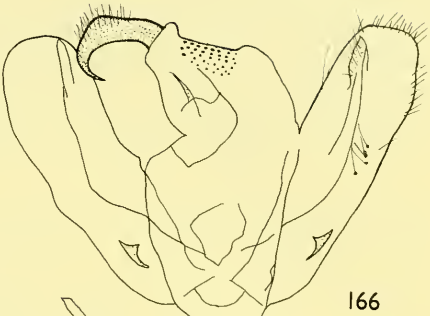

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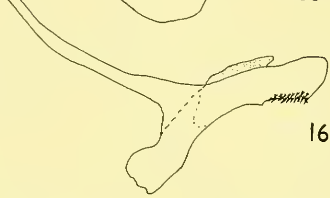

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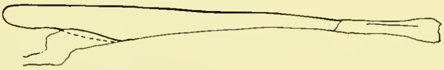

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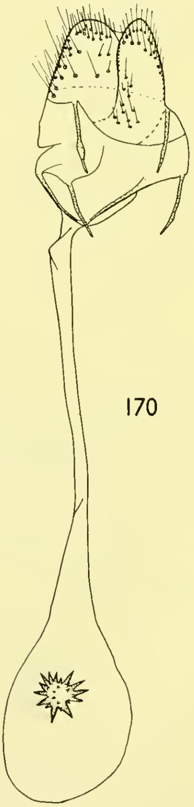

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Distribution. Endemic species.

Holotype. Male. Isabela (Albemarle) 200 ft., 7 August 1924, St. George Expedition, C. L. Collenette. BMNH.

Paratypes. Floreana, January, April; Isabela, August; Santiago, July. BMNH (3 specimens), ZSBS (1 specimen).

Biology. No data available.

Peliala fuliginea Hayes, new species.

(Figures 149, 150, 166, & 167.)

Description. Male 16 mm. Antenna simple. Palpus prominent, thinly scaled. Tornus of forewing less strongly angulate, rounded. Postmedial fascia with two rounded extensions terminad. Dark brown coloration throughout with prominent orbicular spot. Hindwing midbrown. Genitalia figured.

Female 15 mm. Broader winged but similar to male. Somewhat variable in maculation.

Peliala fuliginea has rounded extensions on the postmedial fascia of the forewing which separates it from *Hypena vetustalis.* Palpus structure and genitalia also separate *P. fuliginea* from *H. microfuliginea.*

Distribution. Endemic species.

Holotype. Male. Pinta, 630 m., November 1970, R. Perry & Tj. de Vries. BMNH.

Paratypes. Floreana, January; Isabela, April, August, September; James, July; Pinta, October, November; Santa Cruz, February–August, December. AMNH (49 specimens), BMNH (28 specimens), CAS (73 specimens), ZSBS (4 specimens).

Biology. No data available.

Ophiuche lividalis (Hübner).

(Figure 152.)

Pyralis lividalis Hübner, 1790, Beiträge zur Geschichte der Schmetterlinge, vol. 2, no. 4, pp. 86–87, pl. (4) 1, fig. E. Holotype: Italy, Florence; not traced.

Based on a specimen in the CAS and a worn example in the ZSBS.

Distribution. Almost cosmopolitan. *Galápagos Islands*: Floreana, April. CAS, ZSBS.

Biology. No data available.

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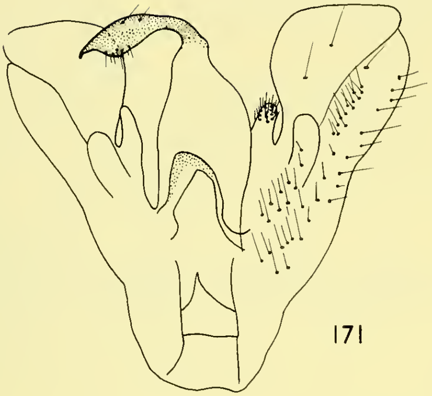
Figures 171 and 172. *Utetheisa perryi* Hayes, new species, paratype, male, genitalia. Figures 173 and 174. *Agrotis consternans* Hayes, new species, holotype, male, genitalia. Figures 175 and 176. *Utetheisa devriesi* Hayes, new species, paratype, male, genitalia.



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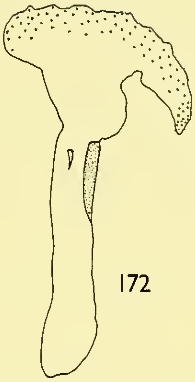

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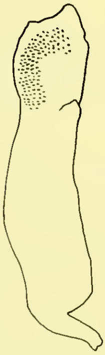

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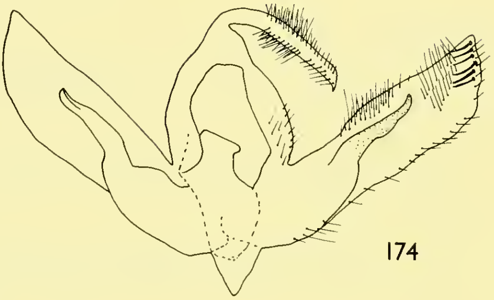

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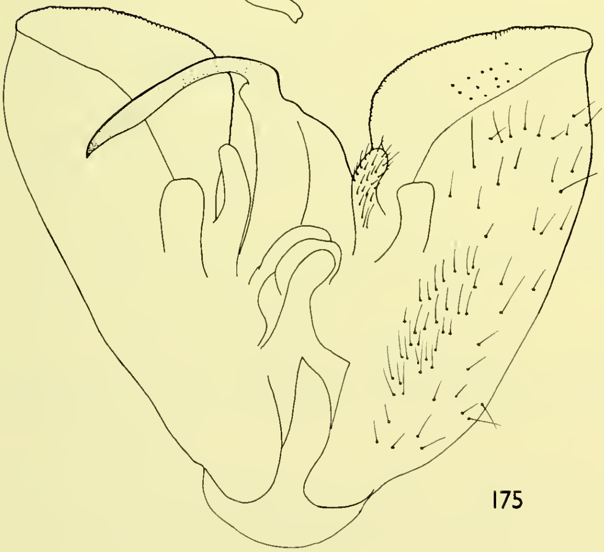

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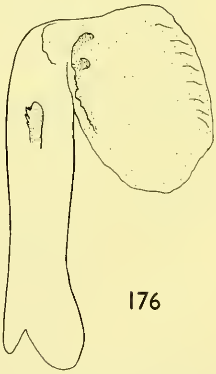

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Ophiuche minualis constans Hayes, new subspecies.

(Figures 153 & 154.)

The median line on the forewing of Galápagos specimens is always straighter than that of mainland specimens.

DISTRIBUTION. Endemic subspecies of the neotropical species.

HOLOTYPE. Male. 8 mm. Santa Cruz, Horneman Farm, 220 m., 5 March 1964, D. Q. Cavagnaro. CAS.

PARATYPES. Floreana, January, April; Isabela, September; Pinta, October, November; Santa Cruz, February–June, October. AMNH (6 specimens), BMNH (49 specimens), CAS (32 specimens), MCZ (1 specimen), MRAC (1 specimen), ZSBS (1 specimen).

BIOLOGY. No data available.

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NEW SPECIES AND NEW COMBINATIONS OF FERNS FROM CHIAPAS, MEXICO

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In preparation for a pteridophyte flora of the state of Chiapas, Mexico, I find it necessary to describe the following new species and make several new combinations. Most of the new species were discovered after intensive field investigations by Dr. Dennis Breedlove and myself; these explorations have resulted in approximately 4000 new collections of pteridophytes, many from previously uncollected or poorly collected areas of Chiapas. In circumscribing the new species I have relied most heavily on herbarium holdings of Mexican and Central American ferns in Dudley Herbarium, Stanford University (DS), University of California Herbarium (UC), United States National Museum (US), New York Botanical Garden (NY), Philadelphia Academy of Science (PH), Field Museum of Natural History (F), and Universidad Nacional de México (MEXU). I thank curators of these herbaria for making their collections available for study. Isotypes and duplicates of Breedlove collections will be distributed to MEXU, NY, and US. I also thank Charlotte Mentges for preparing the illustrations.

Asplenium breedlovei A. Reid Smith, sp. nov.
(Figure 1, A–B.)

Plantae terrestres; rhizomata breve repentia, ca. 4 mm. diametro, frondibus paucis (1–3) praedita; stipites atropurpurei vel atrobrunnei, impoliti, glabri, ca. 2 mm. diametro, laminas fere aequantes; rhachides leviter flexuosae, basi fuscatae, apicem versus viridescentes; frondes basi fere quadripinnatae, usque 35 cm. longae, 15 cm. latae, deltoideae, apicem versus gradatim reductae, non


A
B
C
D
E
F
G
c.m.
c.m.
c.m.
5 cm
B, G, E
1 cm
D
1 cm
A, F
0.5 cm
C

proliferae; pinnae usque ca. 10-jugae, atrovirides, non articulatae, alternae, ascendentes, usque 10 cm. longae, 3 cm. latae, axibus virellis; segmenta penultima cuneiformia, maximam partem 2–5-loba; segmenta ultima usque 1.5 mm. lata, apice acuta vel subacuta; sori secus venas segmentorum ultimorum usque ca. 3 mm. longi; indusia integra vel leviter erosa, ca. 0.6 mm. lata, fulva.

Holotype. Mexico. Chiapas: municipio Villa Corzo, east base of Cerro Tres Picos near Cerro Bola, SW. of Colonia Agronimos Mexicanos, 1500–1800 m., *Breedlove 30041* (DS).

Remarks. Superficially, this species resembles more dissected members of the *A. radicans* complex, but the stipe and rachis are dull, the lamina is deltoid, and the pinnae ascend at an angle of about 60° from a slightly flexuose, non-proliferous, non-flagelliform rachis. The relationship to *A. cristatum* Lamarck is perhaps closer, but the general architecture of the fronds and the creeping rhizomes of *A. breedlovei* adequately distinguish it from that species.

Asplenium munchii A. Reid Smith, sp. nov.

(Figure 7, A–B.)

Plantae terrestres; rhizomata suberecta, basibus stipitum abscondita, caudices usque 1.3 cm. diametro; frondes numerosae, caespitosae, stipites 4–9 cm. longi, ca. 1 mm. diametro, brunnei vel plumbei, non lustrati, glabri; laminae tripinnatifidae, (17)25–30 cm. longae, (3.5)5–7 cm. latae, apicem versus attenuatae et proliferae; pinnae usque ca. 25-jugae, plerumque alternae, sessiles, maximae in medio, 4 cm. longae, 1.5 cm. latae, gradatim reductae sursum et deorsum (infimae deflexae), inaequilaterae, pinnulis grandioribus acroscopicis; pinnulae ad angulum 45–60° costis, maximae profunde 5-lobae; segmenta ultima ca. 1 mm. lata, apice rotundata vel acutiuscula; laminae membranaceae, glabrae; sori secus venas segmentorum ultimorum positi, usque 3 mm. longi, indusiis 0.6 mm. latis, integris, fulvis.

Holotype. Mexico. Chiapas: San Pablo, *Münch 114* (DS).

Paratypes. Mexico. Chiapas: municipio Tenejapa, sumidero of Yochib, paraje Koltol Te', *Breedlove 6222* (DS); 4 mi. N. of Jitotol, *Thorne & Lathrop 41783* (DS); municipio La Independencia, Las Margaritas to Campo Alegré, *Breedlove 33648* (DS).

Remarks. Allied to *A. sessilifolium* Desvaux, but much more dissected than that species and occurring at lower elevations (1300–2300 m.). The

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Figure 1. A–B. *Asplenium breedlovei*, *Breedlove 30041*, DS: A, ultimate segment; B, plant. C–E. *Asplenium soleirolioides*, *Breedlove & Smith 31820*, DS: C, pinnae; D, frond apex; E, plant. F–G. *Asplenium olivaceum*, *Hatch & Wilson 149*, US: F, plant; G, pinnae.

blades of *A. munchii* are similar in dissection to large fronds of *A. myriophyllum* (Swartz) Presl, which always lacks buds and has less oblique pinnules.

Asplenium olivaceum A. Reid Smith, sp. nov.

(Figure 1, F–G.)

Rhizomata compacta, frondibus numerosis erectis vel arcuatis praedita; stipites nigrescentes, glabri, nitidi, ca. 0.6 mm. diametro, laminis 0.2–0.6 plo breviores; frondes usque 15 cm. longae, 1.5 cm. latae, non proliferae, segmento ovali terminali; pinnae usque 15-jugae, olivaceae, articulatae, oppositae, oblongae, usque 8 mm. longae, 5 mm. latae, secus marginem superiorem integrae vel leviter undulatae, apice rotundatae; sori 1–2 per pinnam, 2–3 mm. longi, soro primario parallelo margini inferiori, interdum soro secundario secus venam acropetam; indusia plus minusve integra, usque 0.9 mm. lata, albida vel cinerascentia.

Holotype. Guatemala. Alta Verapaz: Senahu, summit of Cerro Sillab, limestone cliffs, 6000 ft. [1800 m.], *Hatch & Wilson 149* (US).

Paratype. Mexico. Chiapas: municipio La Trinitaria, Lagos de Monte Bello, along Comitan River at its sumidero, limestone rocks, 1300 m., *Breedlove & Smith 22379* in part (DS).

Remarks. Perhaps most closely related to *A. heterochroum* Kunze, which was collected with the paratype cited. It can be distinguished easily from that species by the peculiar olivaceous color of the fronds, number and placement of the sori, and the oblong, entire (or nearly so) pinnae.

Asplenium soleirolioides A. Reid Smith, sp. nov.

(Figure 1, C–E.)

Rhizomata minuta, radicibus paleisque abscondita, frondibus numerosis arcuatis vel decumbentibus praedita; stipites rhachidesque castaneae, glabrae, nitidae, ca. 0.3 mm. diametro; frondes usque 9 cm. longae, 5 mm. latae, apicem versus proliferae et radicantes; pinnae infra gemmam usque 15-jugae, subvirides, articulatae, plerumque alternae, rotundatae vel irregulariter ovales, usque 2.5 mm. longae, 2 mm. latae, venis 2–3-jugis; sori 1–2 per pinnam, grandissimi secus venam inferioram in quoquo segmenta; indusia integra, usque 0.6 mm. lata, fulva.

Holotype. Mexico. Chiapas: municipio La Grandeza, 10 km. E. of El Porvenir along road from Huixtla to Siltepec, 2800 m., *Breedlove & Smith 31820* (DS).

Remarks. Named after the monotypic genus *Soleirolia* (Urticaceae), which it resembles in habit and general shape of the segments.

I am unable to suggest close relatives for this peculiar species, but it is certainly a member of *A. trichomanes* group. The pinnae of *A. soleirolioides* are much thinner in texture than in most other species of this alliance.

Ctenitis bullata A. Reid Smith, sp. nov.

(Figure 2, E–H.)

Rhizomata suberecta, basibus stipitum et paleis abscondita, caudices ca. 2.5 cm. diametro; stipites usque ca. 40 cm. longi, 4 mm. diametro, brunneoli, basin versus paleis usque 1 cm. longis patentibus vel reflexis subulatis atrobrunneis nitentibus; rhachides paleis similaribus sed brevioribus; laminae atrovirides, usque ca. 45 cm. longae, 25 cm. latae, basi bipinnatae vel tripinnatifidae, sursum profunde bipinnatifidae; pinnae usque ca. 20-jugae, alternae vel suboppositae, basi latissimae, aequilaterae, usque ca. 13 cm. longae, 3.3 cm. latae, usque 6 mm. petiolulatae, pinnae distales sessiles; pinnulae usque 1 mm. petiolulatae, serratae, pinnulae pinnarum distaliorum sessiles serratae vel integrae; venae usque 10-jugae, simplices vel furcatae, margine terminatae; costae subtus paleis numerosis bullatis castaneis, pilis paucis longis (usque 0.7 mm.) articulatis, et pilis numerosis brevibus glandiferis (ca. 0.1 mm. longis); pagina laminarum super glandiferae, pilis articulatis costis venisque; pagina laminarum infra glabra; sori inframediales, ca. 1 mm. diametro; indusia persistentia, rotundato-reniformia, ca. 0.6–0.8 mm. diametro, glandifera, fulva, margine erosa vel glanduloso-ciliata.

Holotype. Mexico. Chiapas: municipio La Trinitaria, Lagos de Monte Bello, 1400 m., *Breedlove 25339* (DS).

Paratypes. Same locality, 1600 m., *Breedlove 14968* (DS); same locality, 1300 m., *Breedlove & Smith 22331* (DS); same locality, *Breedlove 38909* (DS).

Remarks. Most closely related to *C. strigilosa* (Davenport) Copeland, known from Veracruz (type) and Guatemala, but differing in its much larger fronds, eglandular tissue below, presence of long, articulate hairs on costae and costules below, larger indusia, and costal scales decidedly more bullate (scarcely bullate in *C. strigilosa*).

Ctenitis baulensis A. Reid Smith, sp. nov.

(Figure 2, I–K.)

Rhizomata suberecta, basibus numerosis stipitum veterum abscondita, caudices 2–3 cm. diametro; frondes caespitosae, stipites usque 20 cm. longi, ca. 2 mm. diametro, basi fuscati, sursum straminei vel viridi-straminei, dense squamosi, paleis usque 3 mm. longis, 1.5 mm. latis, complanatis usque subbullatis, fulvis (apicem versus fuscatis); laminae pinnato-pinnatifidae, usque 20 cm. longae, 13 cm. latae; pinnae usque ca. 10-jugae, sessiles, maximae 7 cm. longae, 2.5 cm. latae, fere ad costas profunde incisae; segmenta obliqua, maxima 12 mm. longa, 4.5 mm. lata, apicem obtusum vel acutiusculum versus integra usque denticulata, approximata vel etiam imbricata; paria basalia segmentorum leviter reducta pinnis infimis; venae usque 9-jugae, marginem supra sinum attingentes; costae infra parce glandiferae, dense squamosae, paleis basi fulvis

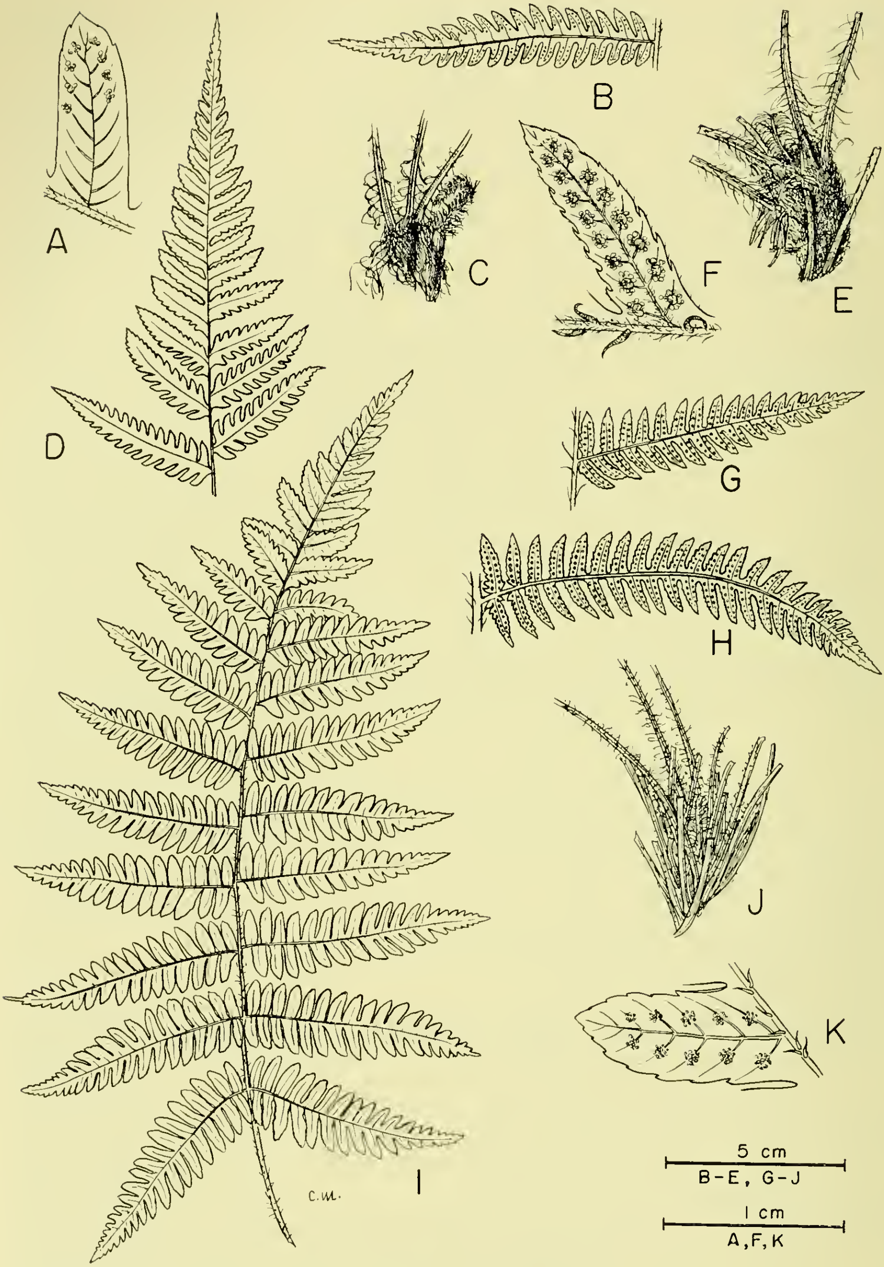

FIGURE 2. A–D. *Ctenitis thelypteroides*: A, segment, *Breedlove 33280*, DS: B, lower pinna, *Lundell 18115*, US; C, rhizome and stipe bases, *Breedlove 33280,* DS; D, frond apex, *Lundell 18115*, US. E–H. *Ctenitis bullata*: E, rhizome, *Breedlove & Smith 22331*, DS; F,

et manifeste bullatis, apice fuscatis et attenuatis, costae supra pilis densis *Ctenitidis* ca. 0.5 mm. longis; paginae laminarum utrinque glabrae vel infra pilis paucis appressis glandulosis; sori inframediales, exindusiati, usque 1 mm. diametro.

Holotype. Mexico. Chiapas: municipio Cintalapa, 16 km. NW. of Rizo de Oro, SE. of Cerro Baul, 1600 m., *Breedlove & Smith 21812* (DS).

Paratype. Same locality, *Breedlove & Smith 31328* (DS).

Remarks. Most closely related to *Dryopteris tonduzii* (Christ) C. Christensen, from Guatemala and Cost Rica, differing from that in the exindusiate, inframedial sori, approximate segments, and smaller, more decidedly bullate-scaly fronds. Also related to *C. nigrovenia* (Christ) Copeland, but differing in the more or less glabrous blade surfaces, inframedial sori, and approximate segments.

Ctenitis thelypteroides A. Reid Smith, sp. nov.

(Figure 2, A–D.)

Rhizomata breve repentia vel oblique erecta, basibus stipitum maximam partem abscondita, usque 4 mm. diametro; stipites usque 28 cm. longi, 2 mm. diametro, basi paleis patentibus lanceolatis castaneis usque 5 mm. longis; rhachides paleis paucis similaribus; laminae pinnato-pinnatifidae, usque ca. 30 cm. longae, 16 cm. latae; pinnae usque 15-jugae, petiolulatae usque 2 mm., usque 9 cm. longae, 2 cm. latae, profunde incisae fere costis; segmenta obliqua ca. 3 mm. lata, apice acuta vel obtusa, serrulata, segmentis basilaribus quam segmentis distalibus leviter reductis et congestioribus; venae usque 8-jugae, infimae marginem 1–2.5 mm. supra sinum attingentes; costae infra glanduliferae, paleis dispersis lineari-lanceolatis castaneis non bullatis integris usque 1.5 mm. longis, supra pilis densis *Ctenitidis* usque 0.5 mm. longis; pagina laminarum infra glabra vel glandulis inconspicuis dispersis appressis tubularibus luteolis; sori usque 6-jugi, plerumque ad apices segmentorum limitati, 0.5–1.0 mm. diametro; indusia ca. 0.3 mm. diametro, fulva, persistentia.

Holotype. Mexico. Chiapas: municipio Las Margaritas, eastern side of Laguna Miramar E. of San Quintín, 366 m., *Breedlove 33280* (DS).

Paratypes. Mexico. Chiapas: jct. of Río Perlas and Río Jataté at San Quintin, 200 m., *Sohns 1696* (US). Guatemala. Peten: ca. 4.5 mi. NEE. of Pucté on La Libertad trail, *Lundell 18115* (US).

Remarks. Closely related to *C. nigrovenia* (Christ) Copeland, but distin-

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segment, *Breedlove 14968*, DS; G, upper pinna, *Breedlove 14968*, DS; H, lowermost pinna, *Breedlove 14968*, DS. I–K. *Ctenitis baulensis*: I, lamina, *Breedlove & Smith 21812*, DS; J, rhizome and stipe bases, *Breedlove & Smith 31328*, DS; K, segment, *Breedlove & Smith 21812*, DS.

guished by the smaller sori localized at the tips of the segments, the reduced basal pinna segments that are more crowded, and the habit of the rhizome.

Ctenitis ursina A. Reid Smith, sp. nov.
(Figure 3, C–E.)

Rhizomata ignota (probabiliter suberecta, ampla); stipites 50 cm. vel plures longi, usque ca. 1 cm. diametro, paleis patentibus lanceolatis integris vel parce denticulatis lustratis brunneis usque ca. 1 cm. longis, 1 mm. latis perdense vestiti; rhachides, costae costulaeque similes stipitibus, sed paleis parvioribus et minor densis et coloratis pallidioribus, denique paleis bullatis costis costulisque; laminae quadripinnatifidae, usque 75 cm. longae, 70 cm. latae, deltoideae; pinnae ca. 10–12-jugae, usque ca. 37 cm. longae, 13 cm. latae, aequilaterae; pinnulae usque ca. 20-jugae per pinnam, usque 7 cm. longae, 1.5 cm. latae, apicem versus pinnarum adnatae decurrentes, basin versus leviter reductae; segmenta profunde serrata vel integra; venae prae margine terminatae; axes supra pilis densis *Ctenitidis* ca. 0.5 mm. longis; paginae utrinque laminarum glabrae; sori ca. 1 mm. diametro; indusia persistentia rotundato-reniformia fulva, in centro leviter fuscata, ad marginem erosa vel glanduloso-ciliata.

Holotype. Mexico. Chiapas: municipio La Trinitaria, E. of Laguna Tzikaw, Monte Bello National Park, 1300 m., *Breedlove & Smith 32274* (DS —2 sheets).

Paratype. Same locality, *Breedlove 35261* (DS).

Remarks. Most closely related to *C. melanosticta* (Kunze) Copeland, differing by the densely scaly, even shaggy, stipes and by the indusia not so distinctly bicolorous.

Dryopteris futura A. Reid Smith, sp. nov.
(Figure 3, F–I.)

Rhizomata non visa (probabiliter erecta, crassa); stipites usque 45 cm. longi, 5 mm. lati, basin versus dense paleacei, paleis ovato-lanceolatis, usque 2.5 cm. longis, 5 mm. latis, integris, brunneis (sursum fulvis), concoloribus sublustratis; rhachides stramineae, glabrae vel parce stipitato-glandulosae; laminae infra tripinnato-pinnatifidae usque 4-pinnatae, usque ca. 40 cm. longae, 30 cm. latae, deltoideae; pinnae oppositae usque subopposita, ca. 12-jugae, ad

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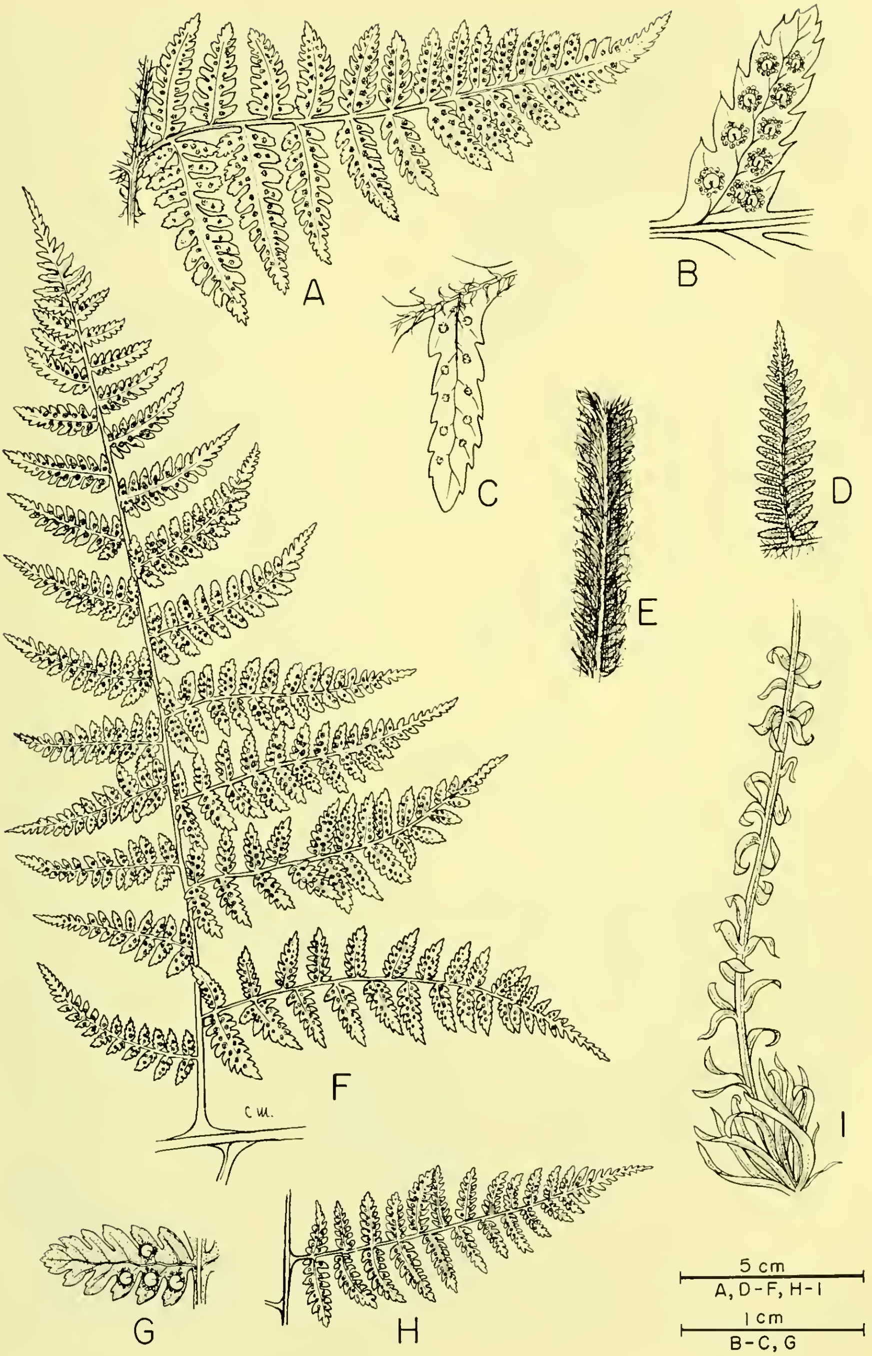
Figure 3. A–B. *Dryopteris munchii, Münch 116*, DS: A, lowermost pinna; B, ultimate segment. C–E. *Ctenitis ursina, Breedlove & Smith 33274*, DS: C, ultimate segment; D. pinnule; E, stipe base. F–I. *Dryopteris futura, Breedlove & Smith 32058*, DS: F, lowermost pinna; G, ultimate segment; H, fourth pinna from base; I, stipe base.


A
B
C
D
E
F
C.W.
I
G
H
5 cm
A, D-F, H-I
1 cm
B-C, G

angulum 45–60° ascendentes, infimae deltoideae, usque 25 cm. longae, 15 cm. latae, petiolulatae usque 1.5 cm., basiscopicae, anadromae, ceterae catadromae sublanceolatae; pinnae secundariae suboppositae usque alternae, lanceolatae, leviter basiscopicae usque fere aequilaterae, infimae petiolulatae usque 5 mm.; pinnulae usque 12-jugae, pinnatae usque profunde pinnatifidae, segmentis ultimis denticulatis; laminae membranaceae, sine paleis, utrinque glabrae vel subtus stipitato-glandulosae (praesertim axibus); indusia orbiculari-reniformia, ca. 1 mm. diametro, persistentia, fulva, ad marginem stipitato-glandulosa; $n = 41$.

HOLOTYPE. Mexico. Chiapas: municipio El Porvenir, 3–4 km. W. of El Porvenir along road from Huixtla to Siltepec, 2800 m., *Breedlove & Smith 31772* (DS).

PARATYPE. Mexico. Chiapas: municipio San Cristóbal Las Casas, Cerro Huitepec (Muk'ta vits), 2700 m., *Breedlove & Smith 32058* (DS).

REMARKS. This species can be compared only to *D. nubigena* Maxon & Morton, from which it differs by the more densely scaly stipe bases, strongly ascending pinnae, the larger, more persistent indusia, and the less glandular, thinner-textured blades.

The paratype cited showed $2n = 41$ II at meiotic metaphase.

Dryopteris munchii A. Reid Smith, sp. nov.

(Figure 3, A–B.)

Rhizomata ignota (probabiliter erecta); stipites usque 35 cm. longi, 5 mm. diametro, brunneoli, basin versus squamati, paleis anguste lanceolatis, usque ca. 10 mm. longis, 1(2) mm. latis, saepe bicoloribus, apice fulvis integris, basin versus denigratis dentatis, non lustratis; rhachides fulvae, eglandulosae, epilosae, paleis dispersis; laminae infra subtripinnatae, sursum bipinnato-pinnatifidae, ca. 45 cm. longae, 27 cm. latae; pinnae basi suboppositae, sursum alternae, ca. 16-jugae, ad angulum 60–80° ascendentes, infimae deltoideae, usque 15 cm. longae, 8.5 cm. latae, petiolulatae usque 6 mm., basiscopicae, anadromae, ceterae gradatim aequilaterae; pinnae secondariae oppositae usque alternae, patentes (ca. 90°), lanceolatae, fere aequilaterae, sessiles usque petiolulatae ca. 1 mm.; pinnulae usque ca. 10-jugae, apicem versus spinulosae; laminae chartaceae, in costis costulisque infra paleis minutis fulvis ovatis usque linearibus praeditae, alibi glabrae, eglandulosae; indusia orbiculari-reniformia, ca. 0.8 mm. diametro, persistentia, porphyrea, glabra.

HOLOTYPE. Mexico. Chiapas: Baduitz, *Münch 116* (DS).

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FIGURE 4. A. *Elaphoglossum albomarginatum*, plant, *Breedlove & Smith 31629*, DS. B–D. *Elaphoglossum chiapense*, *Breedlove & Smith 32649*, DS: B, plant; C, stipe base scale; D, laminar scale.


10 cm
A, B
1 mm
C, D
C
D
CM.
A
B

PARATYPE. Mexico. Chiapas: municipio Tenejapa, paraje Banabil, 2800 m., *Breedlove & Smith 22027* (DS).

REMARKS. Related to *Dryopteris rossii* C. Christensen from western Mexico (later treated by Christensen as a variety of *D. patula*), from which it differs by its larger, narrower, eglandular blades. From *D. patula* (Swartz) Underwood it differs in the smaller, bicolorous stipe scales, spreading, nearly equilateral secondary pinnae, and eglandular blades.

Elaphoglossum albomarginatum A. Reid Smith, sp. nov.

(Figure 4, A.)

Rhizomata breve repentia, crassa, caudices ca. 1 cm. diametro, dense paleacei; stipites ca. 25 cm. longi, 2.5 mm. diametro, straminei, non nisi basi squamati, paleis lanceolatis, usque 2.5 cm. longis, 2 mm. latis, integris, fulvis, glabris, ascendentibus et flexilibus; laminae steriles ovato-lanceolatae, ca. 30 cm. longae, 7 cm. latae, basi rotundatae, apice acutae usque acuminatae, margine scarioso, albido, 0.8 mm. lato, chartaceae, utrinque glabrae; venae 1–2-furcatae plerumque liberae, prope apicem saepe bifurcatae, secus rhachim 3–4 mm. inter se distantes, prope marginem 1.3 mm. inter se distantes; laminae fertiles 13 cm. longae, 3.5 cm. latae, ambitu laminis sterilibus similes, margine albido-hyalino ca. 1.5 mm. lato.

HOLOTYPE. Mexico. Chiapas: municipio Unión Juárez, SE. side of Vol. Tacaná, above Talquian, 2100 m., *Breedlove & Smith 31629* (DS).

REMARKS. Related to *E. latifolium* (Swartz) J. Smith, but with a very broad scarious margin, wider-spaced veins, totally glabrous laminae, and very long, twisted stipe base and rhizome scales.

Elaphoglossum chiapense A. Reid Smith, sp. nov.

(Figure 4, B–D.)

Rhizomata longe repentia (ca. 1 cm. inter bases stipitum), 2–3 mm. diametro, dense squamosa, paleis lanceolatis, 3–4 mm. longis, brunneis, lustratis, denticulatis, plerumque patentibus; stipites usque 15 cm. longi, 2 mm. diametro, straminei usque basin versus fuscati, paleis ca. 2 mm. longis, brunneis, patentibus; laminae steriles usque ca. 20 cm. longae, 3.5 cm. latae, apice acutae, basi cuneatae, chartaceae, utrinque in laminis, venis, rhachidibusque paleis appressis, lanceolatis, 0.7–1.5 mm. longis e basi circulari, minute denticulatis, fulvis; laminae fertiles 3.5 cm. longae, 1.2 cm. latae, oblongae, margine revolutae; venae simplices vel prope basin 1-furcatae, 1.5–2.0 mm. inter se distantes, hydathodis ca. 1 mm. intra marginem terminantes.

HOLOTYPE. Mexico. Chiapas: municipio Rayón, 10 km. above Rayón Mezcalapa along road to Jitotal, 1700 m., *Breedlove & Smith 32649* (DS).

PARATYPE. Same locality, *Breedlove & Smith 32429* (DS).

REMARKS. A very distinct species, seemingly related to the smaller *E. mathewsii* (Fée) Moore, of high elevations; also related to *E. alfredii* Rosen-stock (type from Costa Rica), but differing from that species in the longer, narrower, darker, and more prominently toothed rhizome scales, the longer stipes of the sterile fronds, and the more persistently scaly blade surface and stipes.

Grammitis margaritata A. Reid Smith, sp. nov.
(Figure 5, D–E.)

Rhizomata breve repentia, crassa (caudices ca. 0.7 cm. diametro), squamata, paleis numerosis rigidis castaneis opacis anguste lanceolatis, usque 5 mm. longis, basi ca. 0.5 mm. latis, margine evidenter ciliatis, ciliis 0.3 mm. longis, albidis, patentibus; stipites usque 14 cm. longi, 1 mm. diametro, brunnei, teretes, non alati, dense setosi, setis patentibus rigidis usque 3.5 mm. longis brunneis et pilis articulatis brevioribus; rhachides fuscae, setosae supra et infra; laminae subcoriaceae lanceolatae, basi pinnatisectae, ca. 11 cm. longae, 2.5 cm. latae; segmenta ca. 20-juga, usque 1.5 cm. longa, 4.5 mm. lata, margine leviter revoluta setosa, apice rotundata vel vix acuta, basi adnata, supra atroviridia, infra pallide viridia, utrinque glabra, supra sine hydathodis calcareis; venae ca. 7-jugae, simplices; sori uniseriati mediales usque submarginales rotundi, glandulis stipitatis numerosis sphaericis albis mixti; $n = 37$.

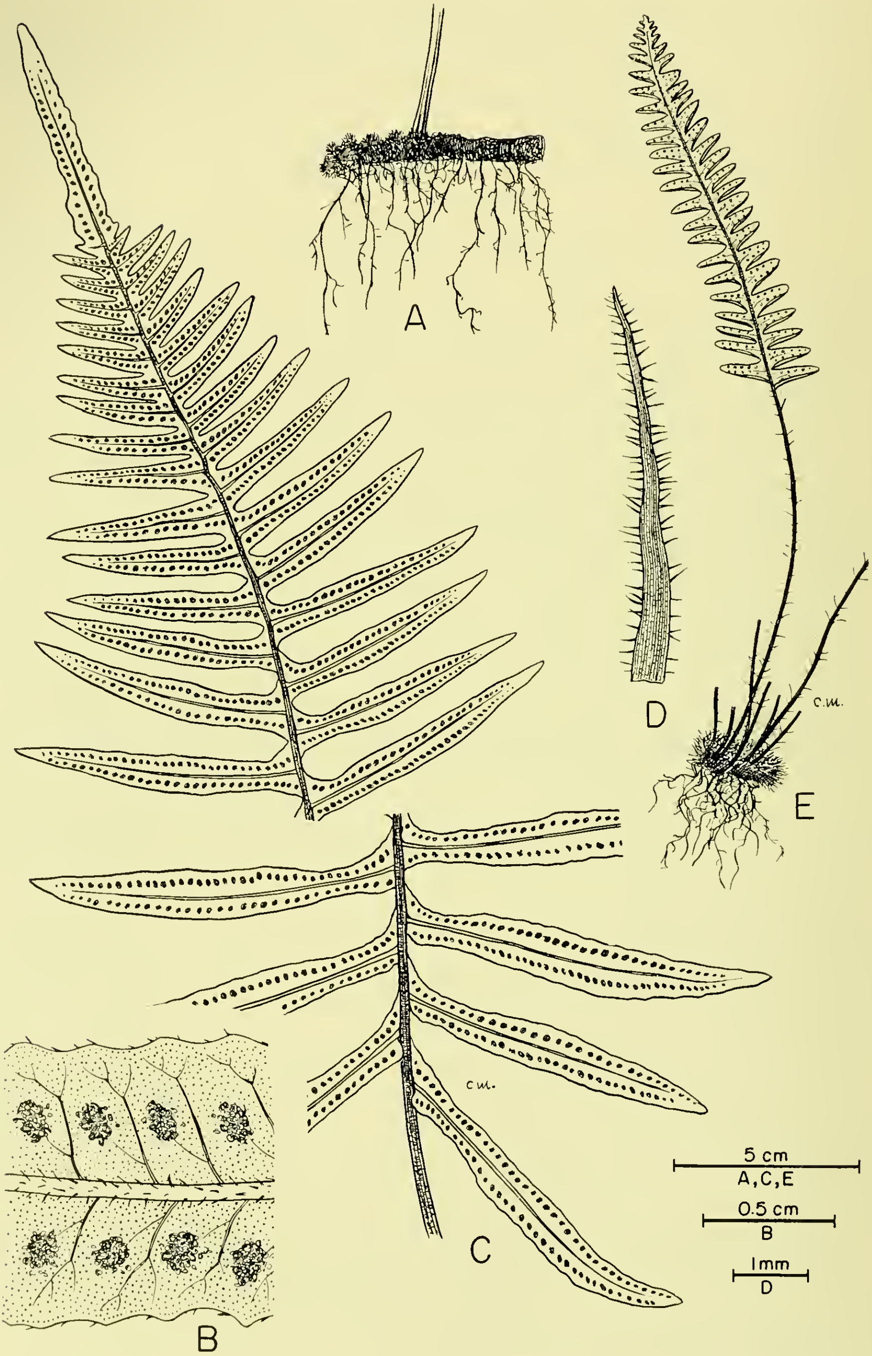
Holotype. Mexico. Chiapas: municipio El Porvenir, 3–4 km. W. of El Porvenir along road from Huixtla to Siltepec, 2800 m., *Breedlove & Smith* 31801 (DS).

Remarks. Known only from a single collection, growing on rocky ledge, in evergreen cloud forest (with *Quercus, Drimys, Clethra, Symplocos*). Most closely related to *Polypodium* (*Grammitis*) *meridensis* Klotzsch, but differing in the narrower, less deltoid laminae, the rounded (rather than acute) segments, and the darker, more rigid and stiffly ciliate rhizome scales. The holotype showed $2n = 37$ II at meiotic metaphase.

The specific epithet recalls the pearly glands that adorn and nearly obscure the young sori.

Hypolepis melanochlaena A. Reid Smith, sp. nov.
(Figure 7, D–E.)

Rhizomata et stipites ignoti; rhachides infra fulvae usque brunneolae, supra secus sulcum pubescentes, pilis rufis pluricellularibus, minute et perparce aculeatae, aculeis 0.2 (0.5) mm. longis; laminae 3-pinnatopinnatifidae, plus quam 60 cm. longae (specimina incompleta), dissectae similes *H. repenti* (Linnaeus) Presl; pinnae alternae, maximae plus quam 35 cm. longae, 10 cm. diametro; segmenta ultima oblonga, apice rotundata, integra usque lobata ca. 0.5; laminae chartaceae, infra omnino glabrae in statu sicco viridi-brunneae, supra secus sulcos costarum costularumque pubescentes, in statu sicco nigrescentes; sori 1(2)-jugi per segmentum, indusiis ca. 1 mm. × 0.5 mm. semicircularibus integris denigratis instructi.


A
D
C.M.
E
C.M.
C
B
5 cm
A, C, E
0.5 cm
B
1mm
D

HOLOTYPE. Mexico. Chiapas: without further locality, *Münch 35* (DS); probable isotype: *Münch s.n.* (DS).

REMARKS. This species differs from all other species of *Hypolepis* known to me by the glabrous, blackish indusia; additionally it differs from all other Mexican species of *Hypolepis* by the glabrous laminae below.

Polypodium surcurrens A. Reid Smith, sp. nov.

(Figure 5, A–C.)

Rhizomata repentia, usque 6 mm. diametro, ca. 7 mm. inter bases stipitum, paleis appressis castaneis lustratis comosis vestita; stipites usque 30 cm. longi, 3 mm. diametro, laminis ca. 0.7 plo breviores, fulvi vel brunneoli; laminae usque 45 cm. longae, 25 cm. latae, basi pinnatisectae, apicem versus pinnatipartitae, denique segmento terminali usque 7 cm. longo, 1 cm. lato; pinnae usque 27-jugae, usque 14 cm. longae, 1.4 cm. latae, saepe arcuatae, apice acutae, medio latissimae, valde sursumcurrentes, infra pinnis infimis excisis, deflexis, marginibus undulatis pinnarum; venae discretae, 3–4-furcatae, venis primariis ca. 8 per 3 cm.; costae infra pilis ca. 0.2 mm. longis (pilis similaribus secus margines pinnarum), supra pilis densioribus *Ctenitidis*; paginae glabrae utrinque laminarum; sori mediales, elliptici, usque 2 mm. longi, 1.3 mm. latae, venula prima acroscopica venarum lateralium locati; sporangia glabra.

HOLOTYPE. Mexico. Chiapas: municipio Cintalapa, 16 km. NW. of Rizo de Oro, SE. of Cerro Baul on border with State of Oaxaca, 1600 m., *Breedlove & Smith 31311* (DS).

PARATYPES. Mexico. Chiapas: Cerro del Ocote, 1500 m., *Breedlove 28918* (DS); between Bochil and Simojovel, 1400 m., *Breedlove & Smith 32493* (DS); Ocotal Grande, 750 m., *Breedlove 33118* (DS); Cerro Baul, 1600 m., *Breedlove & Smith 21795* (DS). Veracruz: Mirador, *Galeotti 6414* (BR, photo US); Jalapa, *C. L. Smith 2207* (UC).

REMARKS. Apparently a relatively common species at middle elevations in Chiapas. *Polypodium surcurrens* is closely related to *P. longepinnulatum* Fournier, from which it differs in the strongly surcurrent pinnae.

Polystichum bicolor A. Reid Smith, sp. nov.

(Figure 6, E–G.)

Rhizomata erecta, caudices ca. 2 cm. diametro; stipites ca. 25 cm. longi, 5(8) mm. diametro, dense squamosi, paleis ascendentibus, anguste lanceolatis,

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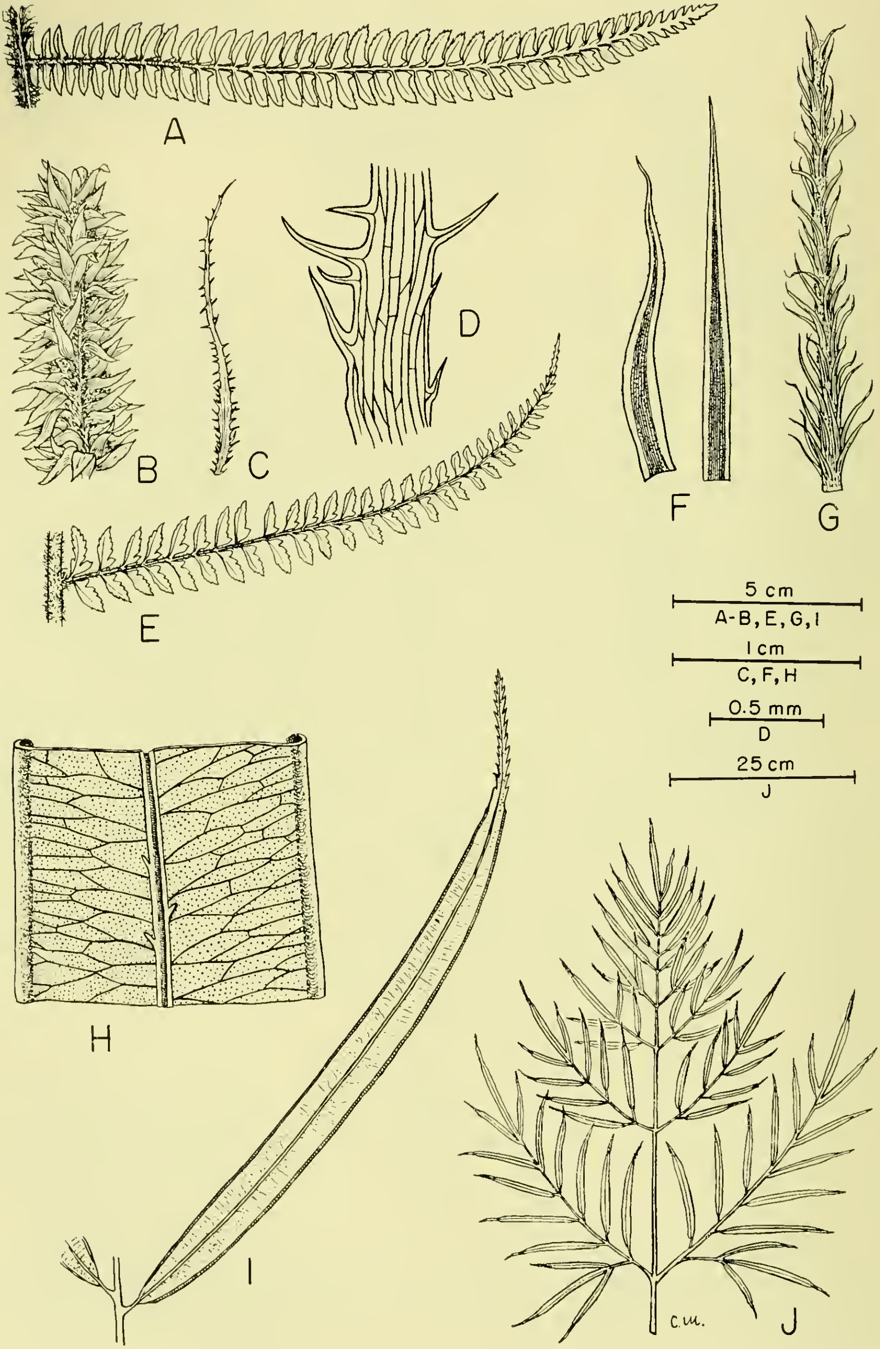
FIGURE 5. A–C. *Polypodium surcurrens*: A, rhizome and stipe base, *Breedlove 33118*, DS; B, portion of pinna, *Breedlove & Smith 31311*, DS; C, lamina, *Breedlove & Smith 31311*, DS. D–E. *Grammitis margaritata*, *Breedlove & Smith 31801*, DS: D, rhizome scale; E, plant.


A
B
C
D
E
F
G
5 cm
A-B, E, G, I
1 cm
C, F, H
0.5 mm
D
25 cm
J
H
I
C.M.
J

ca. 1.5 cm. longis, 1–2 mm. latis, integris, distincte bicoloribus, margine stramineis, in centro brunneis; rhachides non proliferae, minute squamosae, paleis plerumque 1–3 mm. longis, stramineis, integris sed basi dilatatis et minute fimbriatis; laminae chartaceae, bipinnato-pinnatifidae, usque 90 cm. longae, 28 cm. latae; pinnae usque 36-jugae, leviter inaequilaterae, non imbricatae, lanceolatae, usque 15 cm. longae, 2.4 cm. latae, inferiores 5–8-jugae gradatim reductae (infimae × 0.3–0.6); pinnulae usque ca. 25-jugae, non congestae, maximae (basales) usque 1.5 cm. longae, 6 mm. latae, in latere acroscopico profunde lobatae usque crenatae, apice spinulosae; costae infra paleis dispersis stramineis similibus illis rhachidum vestitae, costulae venaeque glabrae: sori indusiis peltatis 0.5–0.8 mm. diametro, fulvis, brunnescentibus, margine irregularibus.

Holotype. Mexico. Chiapas: municipio Tenejapa, Colonia 'Ach'lum, *Ton 1987* (DS).

Paratypes. Mexico. Chiapas: municipio Tenejapa, Colonia 'Ach'lum, *Ton 890* (DS); Vol. Tacana, 2100 m., *Matuda 2971* (NY); municipio San Andres Larrainzar, summit of Chuchil Ton, NE. of Bochil, *Breedlove 34686* (DS).

Remarks. Distinguished from *P. ordinatum* (Kunze) Liebmann and *P. drepanoides* Fournier by the narrowly lanceolate, adpressed, distinctly bicolorous scales on the stipe bases, and by the reduced basal pinnae.

Polystichum erythrosorum A. Reid Smith, sp. nov.

Rhizomata ignota, probabiliter erecta, crassa; stipites usque 60 cm. longi, 0.8 cm. diametro, dense paleacei, aliquot paleis ovato-lanceolatis, usque 2 cm. longis, 0.8 cm. latis, nigricantibus et lustratis, vel paleis bicoloribus margine angusto fulvo, sursum paleis concoloribus, fulvis, parvioribus; rhachides non proliferae, moderate squamosae, paleis plerumque lineari-lanceolatis, usque 0.7 cm. longis, 0.1 cm. latis, fulvis, parce denticulatis vel basin versus fimbriatis; laminae subcoriaceae, bipinnatae, usque 70 cm. longae, 40 cm. latae; pinnae usque 26-jugae, non imbricatae, lineari-lanceolatae, usque 26 cm. longae, 3.2 cm. latae, infimae deflexae vix reductae; pinnulae usque 30-jugae per pinnam, non congestae, maximae 1.6 cm. longae, 0.7 cm. latae, lobo parvo acroscopico praeditae, aliter integrae vel crenatae, apice spinulosae, margine basiscopico arcuato; costae costulae venaeque infra paleis numerosis tortis fulvis capillaceis vestitae; sori indusiis peltatis 0.6–0.8 mm. diametro rubiginosis planis margine irregularibus.

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Figure 6. A–D. *Polystichum furfuraceum*: A, lower pinna, *Münch 113,* DS; B, stipe base, *Breedlove & Smith 31807,* DS; C–D, stipe scales, *Breedlove & Smith 31807,* DS. E–G. *Polystichum bicolor, Breedlove 34686,* DS: E, lower pinna; F, stipe base scales; G, stipe base. H–J. *Pteris chiapensis, Breedlove & Smith 22492,* DS: H, portion of ultimate segment; I, ultimate segment; J, lamina.

HOLOTYPE. Mexico. Chiapas: municipio Motozintla de Mendoza, road from Huixtla to El Porvenir and Siltepec, 3000 m., *Breedlove & Smith 22709* (DS).

PARATYPES. Mexico. Chiapas: Zontehuitz, *Münch 113* (US); Zontehuitz, *Mickel 1250* (US); Zontehuitz, 2800 m., *Breedlove & Smith 22047* (DS); municipio El Porvenir, 3–4 km. W. of El Porvenir along road from Huixtla to Siltepec, 2800 m., *Breedlove & Smith 31769* (DS).

REMARKS. Similar to *P. furfuraceum* A. Reid Smith in size and dissection and growing in similar habitats, but with numerous black stipe base scales, pinnae and pinnules less crowded, never imbricate, scales not setiform along the margin, and reddish indusia.

Polystichum furfuraceum A. Reid Smith, sp. nov.

(Figure 6, A–D.)

Rhizomata ignota, probabiliter crassa, erecta; stipites ca. 30 cm. longi, 0.7 cm. diametro, perdense paleacei, aliquot paleis ovatis, usque 1.8 cm. longis, 0.9 cm. latis, ceteris anguste lanceolatis, ca. 0.3 cm. longis, paleis omnibus ferrugineis usque brunneis, concoloribus vel basin versus leviter fuscatis, margine manifeste setiformis, dentibus usque 0.4 mm. longis; rhachides non proliferae, perdense paleaceae, paleis lanceolatis usque ca. 1 cm. longis, 0.2 cm. latis, similibus illis stipitum; laminae subcoriaceae, bipinnatae, ca. 60 cm. longae, 24–38 cm. latae; pinnae usque 45-jugae, approximatae vel etiam imbricatae, lineari-lanceolatae, usque 20 cm. longae, 2 cm. latae, infimae deflexae et aliquantum abbreviatae (× 0.7); pinnulae usque 40-jugae per pinnam, approximatae vel imbricatae, maximae 1 cm. longae, 0.4 cm. latae, indivisae sed lobo parvo acroscopico praeditae, apice spinulosae, margine basiscopico arcuatae integrae vel apicem versus parce spinulosae; costae costulae venaeque infra paleis numerosis fulvis tortis capillaceis praeditae; sori indusiis peltatis 0.4–0.7 mm. diametro fulvis in centro depressis praediti.

HOLOTYPE. Mexico. Chiapas: Zonehuitz [Zontehuitz], *Münch 113* (DS 267622); isotype: DS 267621.

PARATYPE. Mexico. Chiapas: municipio El Porvenir, 3–4 km. W. of El Porvenir, 2800 m., *Breedlove & Smith 31807* (DS).

REMARKS. Distinguished from all Mexican and Central American species by the very densely scaly stipe and rachis, the approximate or imbricate entire pinnules, and by the scales' being prominently setiform. Perhaps most closely related to *P. erythrosorum* A. Reid Smith.

Pteris chiapensis A. Reid Smith, sp. nov.

(Figure 6, H–J.)

Rhizomata erecta, caudices ca. 3 mm. diametro; stipites plus quam 30 cm. longi, ca. 8 mm. diametro, straminei, glabri; laminae chartaceae, ca. 60 cm. longae, basi bipinnatae usque tripinnatae, sursum bipinnatae, ultimo pinnatae; pinnae infimae maximae, ca. 50 cm. longae, 35 cm. latae; segmenta ultima et pinnae distales usque 25 cm. longae, 1.5 cm. latae, basi anguste cuneatae et petiolatae usque 3 cm., integrae, apice sterili acute serratae; venatio areolata, areolis 2–3-seriatis, areolis costalis 2.0–2.5 mm. latis, brevissimis, margine areolis ca. 1 mm. latis; sori marginales continui (apice excepto).

Holotype. Mexico. Chiapas: municipio Ocozocoautla de Espinosa, 26–28 km. N. of Ocozocoautla, 700 ft. [213 m.], *Breedlove & Smith 22492* (DS—2 sheets).

Remarks. Most closely allied to *P. mexicana* (Fée) Fournier, but differing from that species in the sharply serrate apices of pinnae and pinnules, the narrower and more elongate pinnae and pinnules, fewer rows of areoles, and marginal areoles mostly 1 mm. or more broad (rather than ca. 0.5 mm. broad).

Thelypteris blepharis A. Reid Smith, sp. nov.

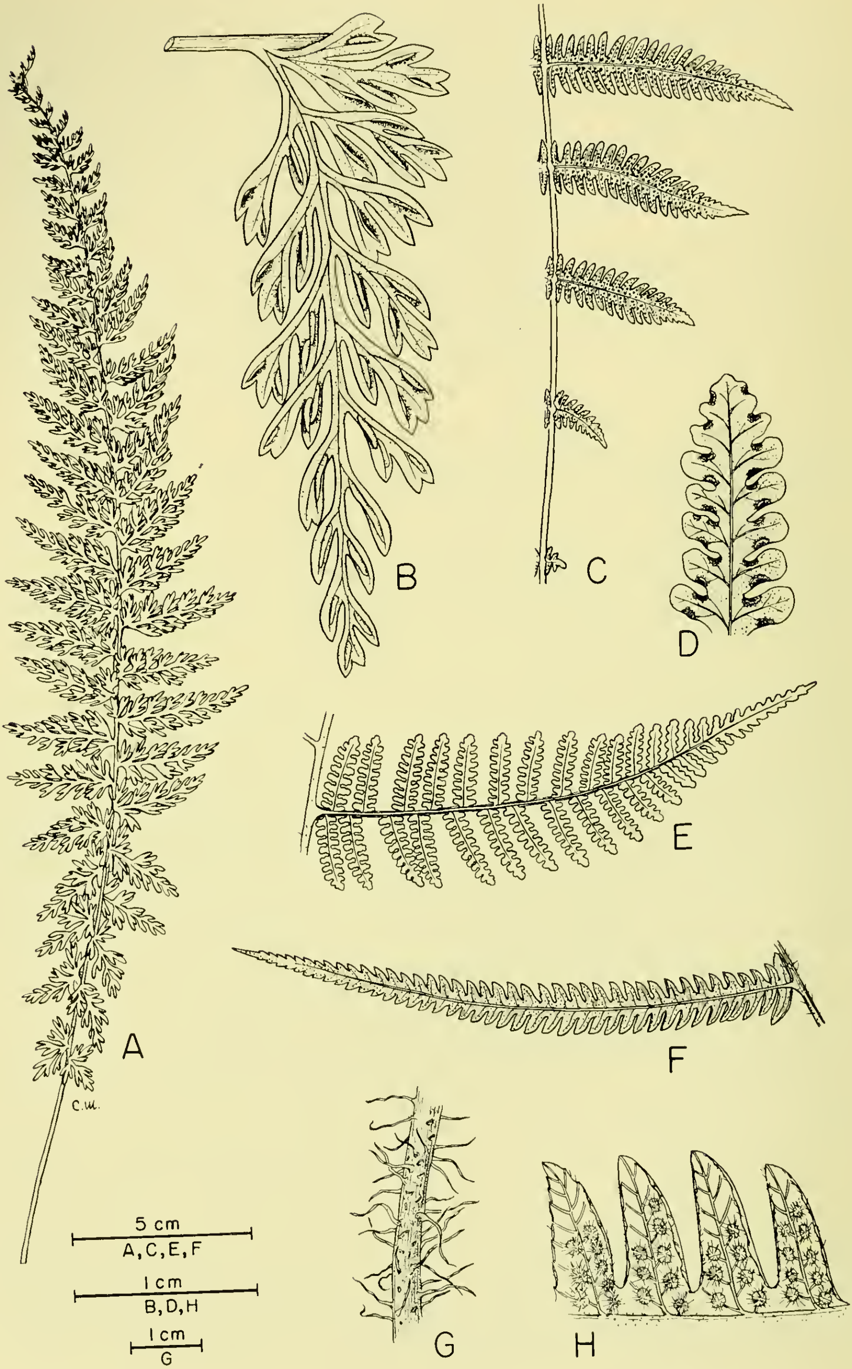
(Figure 7, F–H.)

Rhizomata repentia, 0.8 mm. diametro; stipites 20–40 cm. longi, 4–6 mm. diametro, brunneoli vel dilute purpurei, paleis numerosis patentibus lineari-lanceolatis usque 8 mm. longis, 1 mm. latis praediti, his glabris vel margine minute glandulosis, atrocastaneis, lustratis; rhachides fulvae, paleis paucis similaribus; laminae chartaceae usque subcoriaceae, atrovirides, 50–70 cm. longae, 30–36 cm. latae, apice gradatim decrescentes; pinnae 20–35 jugae, usque 19 cm. longae, 2.1 cm. latae, basi suboppositae, sursum alternae, fere costis incisae; segmenta obliqua, subfalcata, apice acuta vel obtusa, segmentis basalibus pinnarum infimarum leviter amplificatis, auriformibus; venae prominentes, usque 13-jugae, infimae marginem supra sinum attingentes; rhachides costae venaeque infra epilosae vel sparsim pubescentes, glandulibus minutis dispersis stipitatis luteolis, supra pilis usque ca. 0.5 mm. longis; paginae laminarum utrinque glabrae; sori mediales; indusia porphyrea, glandulifera, dense pilosa, pilis usque ca. 1 mm. longis.

Holotype. Mexico. Chiapas: municipio La Independencia, road from Las Margaritas to Campo Alegre, 2300 m., *Breedlove 33605* (DS).

Paratype. Guatemala. Huehuetenango: slope above San Juan Ixcoy, Sierra de los Cuchumantanes, travertine limestone, 2400 m., *Steyermark 49997* (F, GH).

Remarks. This is one of the most distinct species in section *Cyclosorus*, differing from its relatives [*T. puberula* (Baker) Morton, *T. ovata* R. St. John, *T. tuerckheimii* (Donnell-Smith) Reed] by the narrow, dark, bristlelike scales on the stipes and by the densely long-hairy indusia but otherwise glabrous laminae. Its discovery reinforces my belief that southern Mexico-Guatemala is the center of evolution of section *Cyclosorus* in the New World (Univ. Calif. Publ. Bot. Vol. 59, pp. 1–136, 1971).


A
B
C
D
E
F
G
H
C.W.
5 cm
A, C, E, F
1 cm
B, D, H
1 cm
G

Thelypteris nubigena A. Reid Smith, sp. nov.

(Figure 7, C.)

Rhizomata suberecta; stipites usque 15 cm. longi, 3 mm. lati, puberuli, basi fuscati et parce squamulosi, paleis ovatis, fulvis, margine sparsim ciliatis; frondes usque 65 cm. longae, rhachidibus stramineis; pinnae ca. 25-jugae, infimae deinceps 1 mm., 1.5 cm., 4.0 cm., 7.0 cm. longae; pinnae maximae lanceolatae, ca. 7 cm. longae, 1.8 cm. latae, basi latissimae, ca. 0.9 costam versus lobatae; segmenta obliqua, subfalcata, usque 10 mm. longa, 2 mm. lata, apice subacuta; venae usque 10-jugae, marginem supra sinum attingentes; aerophora usque 1 mm. longa basi pinnarum inferiorum; rhachides costae costulaeque utrinque sine paleis, pilis dispersis interdum subfasciculatis ca. 0.2 mm. longis; glandes infra in venis costulis laminisque numerosa, aurantiaca, sessiles, glutinosa; sori mediales; indusia minuta, glandibus aurantiacis abscondita.

Holotype. Mexico. Chiapas: municipio San Cristóbal Las Casas, E. side of Zontehuitz near summit, 2800 m., *Breedlove & Smith 22057* (DS).

Paratypes. Mexico. Oaxaca: Distrito Ixtlán, 19 km. N. of Ixtlán on Rte. 175, 2600 m., *Mickel 5533* (NY). Guatemala. Quezaltenango: Vol. Santo Tomás, *Steyermark 34709* (F).

Remarks. This species can be compared only to *T. thomsonii* (Jenman) Proctor, but the hairs of *T. nubigena* are less obviously fasciculate, and the fronds are much smaller, the segments narrower and more acute. It occurs at perhaps a higher elevation than any other *Thelypteris* in Mexico.

Ctenitis chiapasensis (Christ) A. Reid Smith, comb. nov.

Aspidium chiapasense Christ, Bull. Herb. Boissier II, 5:727. 1905. Type: Mexico, Chiapas, Baduitz, *Münch 117* (isotype DS!).

Ctenitis lanceolata (Baker) A. Reid Smith, comb. nov.

Nephrodium lanceolatum Baker, Syn. Fil, second edition. 498. 1874. Type: Guatemala [Alta Verapaz], Cobán, *Salvin & Godman s.n.*

Ctenitis lindenii (Kuhn) A. Reid Smith, comb. nov.

Aspidium lindenii Kuhn, Linnaea 36:116. 1869. Type: Mexico, Tabasco, Teapa, *Linden 1489.*

Grammitis blepharodes (Maxon) A. Reid Smith, comb. nov.

Polypodium blepharodes Maxon, Contr. U.S. Natl. Herb. 17:407. 1914. Type: Costa Rica, La Palma, *Maxon 406.*

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Figure 7. A–B. *Asplenium munchii, Münch 114,* DS: A, frond; B, pinna. C, *Thelypteris nubigena,* lowermost five pinnae, *Breedlove & Smith 22057,* DS. D–E. *Hypolepis melanochlaena, Münch 35*: D, ultimate segment; E, pinna. F–H. *Thelypteris blepharis, Breedlove 33605,* DS: F, lower pinna; G, stipe base; H, portion of pinna.

Grammitis harrisii (Jenman) A. Reid Smith, comb. nov.

Polypodium harrisii Jenman, Gard. Chron. III, 27:241. 1900. Type: Jamaica, *Harris.*

Grammitis leptostoma (Fée) A. Reid Smith, comb. nov.

Polypodium leptostomum Fée, Mem. Foug. 7:58. 1857. Type: Mexico [Veracruz], near Orizaba, *Schaffner 210.*

Microgramma nitida (J. Smith) A. Reid Smith, comb. nov.

Phlebodium nitidum J. Smith, Bot. Mag. 72. Comp. 13. 1846. Type: cultivated specimen, originally from Honduras, introduced to Kew in 1844.

Maxon (Proc. Biol. Soc. Wash. Vol. 51, p. 38, 1938) discussed the identity of J. Smith's species. A synonym is *Polypodium palmeri* Maxon (Contr. U.S. Natl. Herb. Vol. 17, p. 600, 1917).

Microgramma reptans (Cavanilles) A. Reid Smith, comb. nov.

Acrostichum reptans Cavanilles, Anales Hist. Nat. 1:104. 1799. Type: Ecuador, Guayaquil, *Née s.n.* The type was seen and commented upon by Christensen [Dansk. Bot. Ark. vol. 9, no. 3, p. 9, 1937].

Polypodium ciliatum Willdenow [= *Microgramma ciliata* (Willdenow) Alston], the earliest name for this species in *Polypodium,* becomes a taxonomic synonym when *Microgramma* is recognized.

Pleopeltis munchii (Christ) A. Reid Smith, comb. nov.

Polypodium munchii Christ, Bull. Herb. Boissier II, 3:147. 1903. Type: Mexico, Chiapas, San Cristóbal Las Casas, *Münch 90* (isotype DS!).

Pleopeltis revoluta (Sprengel ex Willdenow) A. Reid Smith, comb. nov.

Grammitis revoluta Sprengel ex Willdenow, Sp. Pl. 5:139. 1810. Type: locality not stated.

This species has gone under a great many names, most notably *Polypodium astrolepis* Liebmann, which is the earliest name for this species in *Polypodium* (see Weatherby, Contr. Gray Herb. No. 65, pp. 3–14, 1922, for additional synonymy). However, the epithet *revoluta* is prior and available in *Pleopeltis.*

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A NEW GENUS AND SPECIES OF EUCERINE BEE FROM NORTH AMERICA (HYMENOPTERA: ANTHOPHORIDAE)

By

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Abstract: A new genus and species of eucerine bee, *Simanthedon linsleyi*, from the southwestern United States and northern Mexico is described and figured. In southeastern Arizona, this aestival bee is primarily a matinal forager on the flowers of *Menodora scabra* Gray (Oleaceae).

Shortly after daybreak on a morning in late August 1972, I collected a few eucerine bees that appeared to be *Martinapis luteicornis* (Cockerell). They were taken from a plant with yellow, star-shaped flowers found growing near the town of Bisbee in southeastern Arizona. Subsequent examination of the bees disclosed that they were not *M. luteicornis*, but were instead an undescribed species that is sufficiently distinct from all other New World eucerines to be placed into a new genus. Subsequent examination of the plant showed that it was *Menodora scabra* Gray (Oleaceae). During the summers of 1973 and 1974, I returned to southeastern Arizona in order to study the pollination of *M. scabra* and collected more of the unusual eucerine bees on it. This new genus and species of bee is described in the present paper.

The generic description includes the characters that have been used to define the numerous New World genera of Eucerini by Moure and Michener (1955) and LaBerge (1957), and numerous additional characters that I believe are also of generic value. Characteristics common to both sexes are included in the generic and specific descriptions of the male.

The abbreviations used in the list of specimens examined and the museums they represent are: AMNH, American Museum of Natural History; ASU, Arizona State University; CAS, California Academy of Sciences; UCB, California Insect Survey Collection, University of California at Berkeley; UCR, P. H. Timberlake Collection, University of California at Riverside.

Simanthedon Zavortink, new genus

Male. *Head*: Face narrow, minimum distance between eyes 0.70–0.75 length of eye. Inner margins of eyes parallel to slightly convergent ventrally. Vertex weakly elevated behind ocelli, median ocellus separated from apex of head by 0.35–0.45 of its width in frontal view. Ocelli slightly enlarged, distance from median ocellus to lateral ocellus 0.29–0.44 diameter of median ocellus. Distance between lateral ocelli 1.6–2.1 times distance from lateral ocellus to eye. Lower paraocular carina absent. Minimum oculoclypeal distance 0.3–0.7 minimum width of first flagellar segment. Clypeus approximate to eye for distance subequal to basal width of mandible; strongly protuberant, in lateral view extended beyond anterior margin of eye by 0.70–0.85 width of eye; moderately produced, in facial view extended beyond lower end of eye by 0.7–1.1 width of median ocellus; lateral part not reflexed mesad of lateroclypeal carina; upper part narrow, width at level of anterior tentorial pit 0.85–0.95 width of labrum; 'pug-nosed', with surface concave in upper 0.65–0.75 medially, strongly reflexed and flat in lower 0.25–0.35. Malar area short, 0.10–0.13 as long as wide. Anterior mandibular articulation slightly farther from eye than posterior one. *Antenna*: Long, extended to pterostigma in repose. Scape thick, short, slightly thicker than width of median ocellus, as long as to longer than interantennal distance. Flagellum slender, greatest diameter less than width of median ocellus, slightly flattened, tapered distally; segment 1 long, 1.20–1.35 length of scape, 0.75–0.85 length of segment 2; segments 3–10 progressively shorter; segment 11 long, as long as segments 5, 6, or 7, curved, tapered to a blunt point. *Mouthparts*: Labrum 0.60–0.65 as long as wide; distal margin convex with shallow median emargination. Mandible short, 0.50–0.60 length of eye; with weak subapical tooth on inner margin. Proboscis moderately long, distal part of galea 1.0–1.2 length of eye. Maxillary palpus 5-segmented; 0.32–0.37 length of distal part of galea; lengths of segments in ratio of 1.00:0.94:0.82:0.53:0.41. Segment 1 of labial palpus 1.8–2.3 length of segment 2.

Mesosoma: Scutellum 0.22–0.28 length of scutum; strongly convex; with moderately long, median, longitudinal, impunctate ridge or line anteriorly. Metanotum strongly convex. Propodeum with basal part steeply declivous; posterior surface without vertical carina laterally. Without spatuloplumose hairs. Tegula oval. *Wings*: Forewing with prestigma short. Pterostigma shorter than prestigma, with inner margin barely extended distad of base of vein r. Marginal cell subequal in length to distance from its apex to apex of wing or slightly longer; 3.7–4.3 times as long as wide; basal part subequal in length to

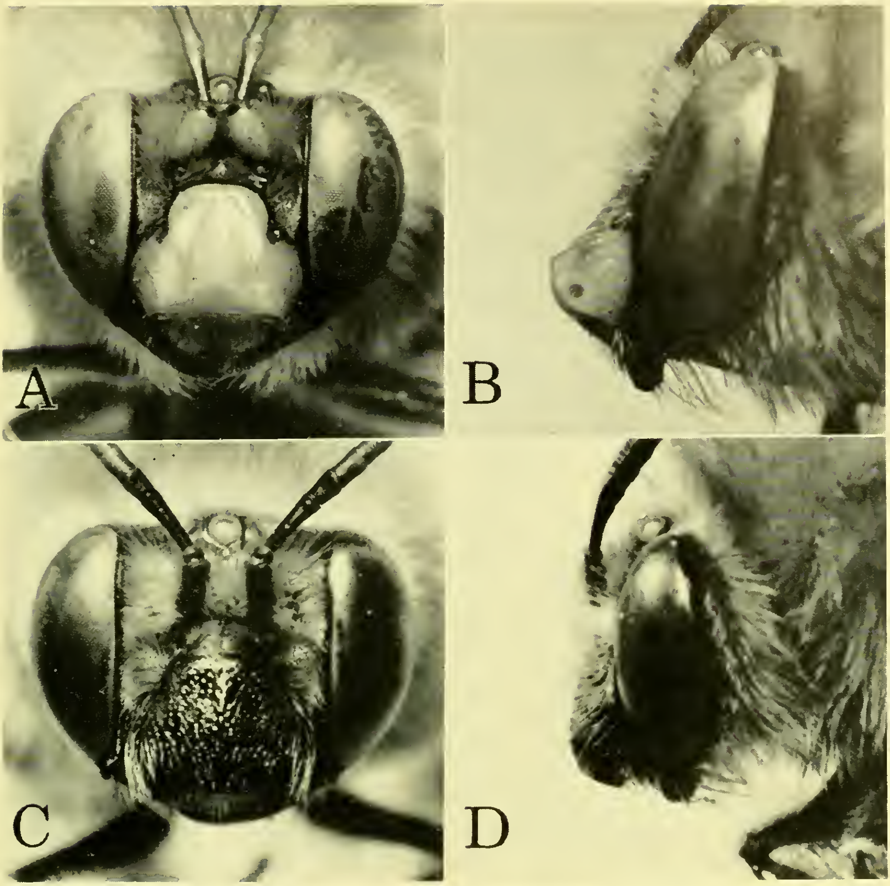

Figure 1. *Simanthedon linsleyi*, new species, head. A, facial view of male; B, lateral view of male; C, facial view of female; D, lateral view of female.

free part. Three submarginal cells; first 1.4–1.7 length of second, 1.0–1.2 length of third; second strongly rhomboid. Cell 1M petiolate, 0.84–0.94 length of marginal cell. Vein C not strongly expanded at base. Vein 2nd r-m sharply angled, usually appendiculate. Vein 1st m-cu ending 0.70–0.82 distance from base of second submarginal cell. Vein 2nd m-cu joined to Cu_1 in nearly even curve. Hindwing with 13–18 hamuli. Vein cu-v 0.53–0.67 length of 2nd abscissa of vein M + Cu. Jugal lobe 0.87–0.95 length of cell Cu. *Legs*: Femora slender; femur I 1.0–1.1 length of femur II, flattened dorsoventrally, broadest near base; femur III unusually slim, 4.3–4.8 times longer than maximum width. Tibiae slender; tibia III long, 1.5–1.7 length of tibia II. Tibia I spur long, longer than spurs of tibiae II and III, 0.6–0.7 length of basitarsus I, with postvelar portion of malus long, sinuous; spur II moderately long, 0.43–0.49 distance from its base to anterior tibiofemoral articulation, curved at apex; outer spur III short, inner spur III moderately long, subequal in length to spur II, both gently curved toward each other, so their distal portions are subparallel. Tarsi short; tarsus I 1.0–1.1 length of tibia I; tarsus II 1.5–1.6 of tibia II; tarsus III subequal in length to tarsus II and tibia III. Basitarsus I 0.6–0.7 length of tarsus I; basitarsus II 0.9–1.0 length of tibia II, 0.6 length of tarsus II; basitarsus III 0.6–0.7 length of tarsus III, 5.3–5.6 times longer than wide, with outer surface sparsely pubescent, flattened or concave apically. Claws small, symmetrical on all legs. Arolia present.

Metasoma: Anterior face of tergum I subequal in length to dorsal face; concave. Terga VI, VII without gradular teeth. Pygidial plate wider than long, not narrowed basally, truncate, with notched lateral margin; marginal carina progressively strengthened posteriorly basad of notch, weak distad of notch; surface sparsely pubescent. Sternum I without conspicuous eminence. Sterna II–IV not emarginate. Terga II–IV with basal and narrower apical bands of pale pubescence; without spatuloplumose hairs. *Distal sterna and genitalia*: Sternum V weakly trilobed, with mesal edge of lateral lobe bearing clump of posteriorly directed, strong, long, curved, terete, barbed setae. Sternum VI with oblique lateral carina progressively weakened distad, curved laterally proximad; with median longitudinal sulcus bordered by setae; with pair of lateral subquadrate areas delimited by weak carinae on dorsal surface of disk. Sternum VII with lateral plate large, strongly sclerotized, strongly pigmented, with very deep, narrow lateral emargination; clear membranous area long, narrow, not produced; median plate long, without basal tubercle, with distal portion narrow, straplike, reflexed basally, directed laterad, glabrate; without unpaired median projection; basal apodeme broad, curved, pointed. Sternum VIII narrowed distad of apodeme, with rounded, slightly emarginate apex bearing a few short setae; tubercles far basad of apex; dorsal tubercle moderately broad, with rounded apex; ventral tubercle narrow, elevated distad. Gonocoxite with strong, moderately long dorsoapical process; with moderately long ventral process extended over base of penis valve; without ventroapical process; either without or with very few ventroapical setae. Gonostylus with base broad, sparsely pubescent with simple and inconspicuously plumose hairs; distal 0.6 very slender, gently curved inward. Spatha 1.7–1.8 times wider than long; basolateral angle slightly produced; distal margin with pair of deep, oblique emarginations that receive dorsobasal edges of penis valves, and shallow median emargination; without median longitudinal apodeme. Penis valve with dorsobasal edge strongly oblique, set into emargination of spatha basally, barely extended beyond dorsolateral tooth distally; dorsolateral tooth short, not extended to dorsoapical process of gonocoxite; ventromesal margin not ex-

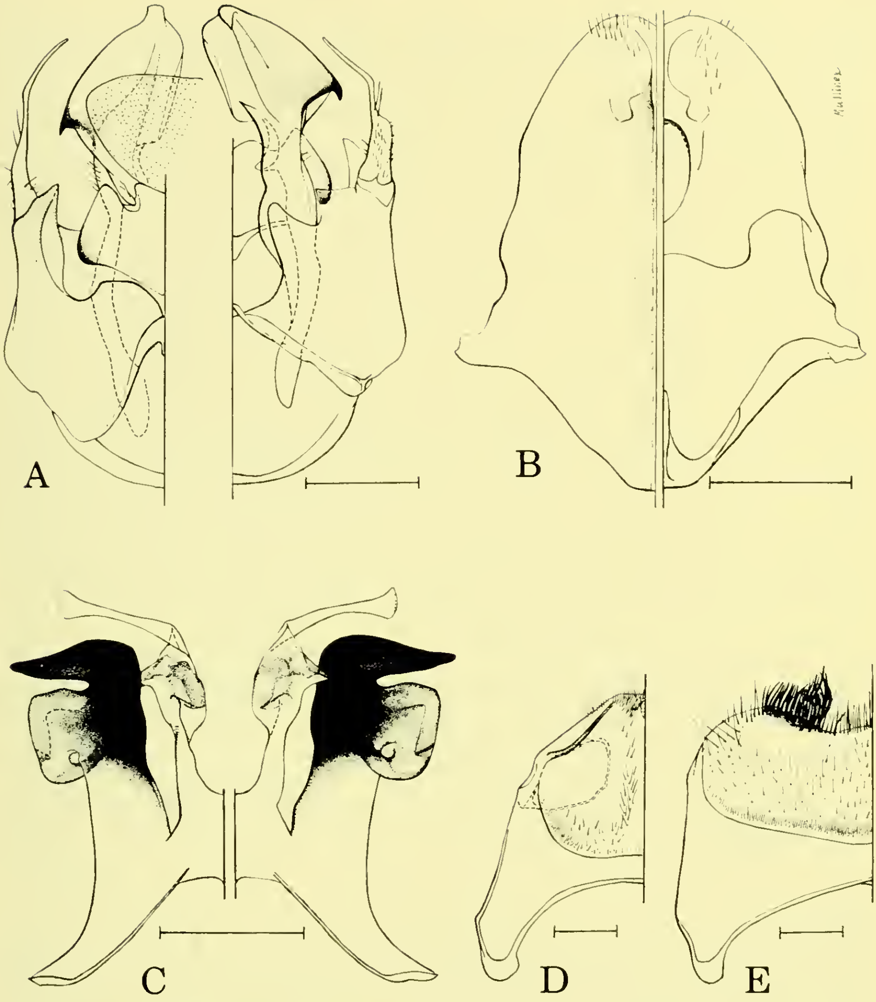

Figure 2. *Simanthedon linsleyi*, new species, distal sterna and genitalia of male. A, genitalia, dorsal surface on left; B, sternum VIII, ventral surface on left; C, sternum VII, ventral surface on left; D, sternum VI, left half of ventral surface; E, sternum V, left half of ventral surface. The scale lines represent 1.0 mm.

panded, nearly straight; with broad apodeme extended distad to base of apical process. Penis broad, extended far beyond spatha.

Female. *Head:* Minimum distance between eyes 0.84–0.91 length of eye. Inner margins of eyes parallel. Median ocellus separated from apex of head by 0.27–0.40 of its width. Distance between lateral ocelli 1.3–1.5 distance from lateral ocellus to eye. Minimum oculoclypeal distance 0.5–0.8 minimum width of first flagellar segment. Clypeus moderately protuberant, extended beyond anterior margin of eye by 0.55–0.65 width of eye; width at level of anterior tentorial pit 0.95–1.00 width of labrum; surface normal, convex throughout; disk without median longitudinal impunctate ridge or line. *Antenna*: Scape slender, obconic, longer than interantennal distance. Flagellum slender, greatest diameter less than width of median ocellus; segment 1 0.85–0.95 length of scape, 2.1–2.5 length of segment 2; segment 2 obconic, 0.75–0.95 length of segment 3; segments 3–9 much longer than wide; segment 10 1.8–2.2 times longer than wide. *Mouthparts*: Labrum 0.55–0.65 as long as wide; with small tuft of dense pubescence around apical emargination. Mandible 0.54–0.66 length of eye; simple; outer lower carina less salient than inferolateral carina. Stipes without hooked hairs.

Legs: Anterior coxa with short apical spine. Femora and tibiae not unusually slender or long. Basitibial plate hidden or defined posteriorly. Scopal hair dense, simple. Tibia I spur short, shorter than spurs of tibiae II and III, 0.45–0.55 length of basitarsus I; spur II long, 0.56–0.66 distance from its base to anterior tibiofemoral articulation, curved at apex; inner and outer spurs III subequal in length, longer than spur II. Tarsi not unusually short. Basitarsus III with inner surface densely hairy. Claws small, symmetrical on all legs.

Metasoma: Gradulus of tergum VI without lateral parts. Pygidial plate more or less V- or Y- shaped, narrow and pointed apically, with distal lateral margin concave; length 1.2 times basal width. Gradulus of sternum II moderately strongly biconvex. Sternum VI emarginate at apex.

Type species. *Simanthedon linsleyi* Zavortink, new species.

Etymology. *Simanthedon* (feminine) from the Greek *simos*, pugnosed, and *anthedon*, bee.

Simanthedon linsleyi Zavortink, new species.

(Figures 1, 2.)

Male. *Measurements*: Length, exclusive of antenna, 12.0–15.0 mm. Length of forewing 9.0–10.1 mm. Width of head 3.7–4.1 mm. *Color*: Integument nonmetallic. Dark, black or black suffused with red, with clypeus yellow; scape and labrum cream-colored to yellow; flagellum largely yellowish in life but usually more reddish or brownish when dried; mandible yellow basally, dark amber medially, red apically; tegula amber, darker anteriorly; wing membrane weakly infuscated; veins and pterostigma brown and black; legs reddish brown to brown distad; tibial spurs testaceous; apical margin of terga amber; pygidial plate largely red. *Vestiture*: Face, vertex, posterior surface of head, entire mesosoma, and tergum 1 with long, dense whitish to ochraceous, light fulvous, or light ferruginous pubescence, this densest and darkest on pronotum and scutum; legs with pubescence largely ochraceous to fulvous, but white or whitish on posterior surface of trochanter II, femur II, and tibiae II and III; hind femur and tibia sparsely pubescent; tergum I with long pubescence extended nearly to apical margin, without an apical band of appressed pale pubescence, with an apicolateral patch of short black pubescence; pubescence of other terga black or brownish black, with basal and/or apical pale bands as follows: basal white pubescent band moderately broad to broad laterally and narrow medially on tergum II, uniformly broad on tergum III, uniformly broad and fused with apical pale band laterally on tergum IV; apical pubescent band very narrow and whitish on terga II and III, moderately broad and white on tergum IV, moderately broad and white or dingy white laterally and strongly tinged with black or blackish brown medially on tergum V; terga III–VI with scattered, long, erect, black and ochraceous to fulvous hair. Sterna with pubescence short medially on II–V, white to fulvous; strong specialized setae of sternum V orange-brown to brown. *Sculpture*: Clypeus smooth, shiny, very finely and sparsely punctate medially, tessellate and more coarsely punctate laterally; face roughened, moderately coarsely and moderately closely punctate below, smoother and more finely and closely punctate above; thorax shiny, moderately coarsely and closely to very closely punctate, the punctures more widely separated on posterior center of scutum, anterior part of scutellum, and pleuron; anterior and lower parts of hypoepimeral area impunctate; sides of propodeum roughened, moderately coarsely and closely punctate above, smoother and more sparsely punctate below; basal part of propodeum indistinctly to distinctly tessellate, coarsely and moderately closely punctate; lower part of propodeal triangle smooth, impunctate; dorsal face of tergum I roughened basally, tessellate apically, moderately coarsely and closely to moderately closely punctate; interband zones of terga II–IV tessellate, finely and closely to moderately closely punctate.

Female. *Measurements*: Length, exclusive of antenna, 13.0–15.0 mm. Length of forewing 9.0–10.3 mm. Width of head 4.0–4.5 mm. *Color*: Without light integumental areas; apical part of clypeus, underside of flagellum, labrum, and base or middle of mandible usually reddish or reddish brown; pygidial plate black. *Vestiture*: Legs with some pubescence whitish or white on coxae, trochanters, femora, and posterior surface of tibia II; scopal hair stramineous to ochraceous on outer surface of hind tibia and basitarsus, orange to ferruginous on inner surface of basitarsus; basal white pubescent band moderately broad laterally and narrow medially on tergum II, uniformly moderately broad to broad or narrowed medially on tergum III, uniformly moderately broad to broad on tergum IV; apical white pubescent band narrow on tergum II, narrow to moderately broad on tergum III, moderately broad on tergum IV; tergum V with some white hair apicolaterally; terga V, VI with apical hair ferruginous; terga III, IV with scattered, long, erect, black and ochraceous to fulvous hair.

Pubescence of sterna white and orange to orange-brown. *Sculpture*: Clypeus tessellate, often diagonally wrinkled, coarsely and moderately closely punctate; interband zones of terga II, III tessellate, finely and closely to moderately closely punctate.

Type material. *Holotype*: male, 6.0 mi. SW. Bisbee, Cochise Co., Arizona, United States, 4800 ft. elevation, 26 July 1973, on *Menodora scabra*, 0615–0630 Mountain Standard Time (MST), T. J. Zavortink [CAS type No. 12254]. *Allotype*: female, same data as holotype except collected 0530–0545 MST [CAS]. *Paratypes* (21 males, 88 females): United States. Arizona. *Cochise Co.*: Bisbee (6.0 mi. SW.), 4800 ft., 26 Aug. 1972, on *Menodora scabra*, 0545–0615 MST, 1 ♂, 3 ♀, 0615–0645 MST, 1 ♀; 26 July 1973, on *Menodora scabra*, 0530–0545 MST, 1 ♀, 0545–0600 MST, 1 ♂, 1 ♀, 0600–0615 MST, 1 ♀; 27 July 1973, on *Menodora scabra*, 0545–0600 MST, 1 ♀, 0600–0615 MST, 2 ♀, 0615–0630 MST, 2 ♀, 0700–0715 MST, 1 ♀, 0715–0730 MST, 1 ♂; 28 July 1973, on *Menodora scabra*, 0530–0545 MST, 1 ♀, 0600–0615 MST, 1 ♀, 0615–0630 MST, 1 ♂, 1 ♀, 0630–0645 MST, 1 ♀; 29 July 1973, on *Menodora scabra*, 0600–0615 MST, 1 ♀, 0615–0630 MST, 2 ♀, 0630–0645 MST, 2 ♀, on *Polygala racemosa*, 0545–0600 MST, 1 ♀; 30 July 1973, on *Menodora scabra*, 0545–0600 MST, 1 ♀, 0600–0615 MST, 1 ♂, 1 ♀; 16 Aug. 1974, on *Menodora scabra*, 0515–0530 MST, 1 ♀, 0530–0545 MST, 1 ♀, 0545–0600 MST, 2 ♀, 0600–0615 MST, 4 ♀, 0615–0630 MST, 4 ♀, 0630–0645 MST, 2 ♀, 0645–0700 MST, 1 ♀, 0700–0715 MST, 1 ♀, 0715–0730 MST, 2 ♀; 26 Aug. 1974, on *Menodora scabra*, 0515–0530 MST, 3 ♀, 0530–0545 MST, 6 ♀, 0545–0600 MST, 1 ♂, 2 ♀, 0600–0615 MST, 2 ♂, 0615–0630 MST, 1 ♂, 0630–0645 MST, 1 ♀, 0645–0700 MST, 1 ♀, 0700–0715 MST, 1 ♀, on *Ipomoea hirsutula*, 0700–0715 MST, 1 ♀, T. J. Zavortink [CAS]. Douglas (1.0 mi. E.), 14 July 1962, on *Conyza* species, 1 ♂, M. A. Cazier [ASU]; 26 July 1962, on *Mentzelia pumila*, 1800–1900 hours, 1 ♂, M. A. Cazier [UCB]. Douglas (4.1 mi. E.), 4400 ft., 27 Aug. 1974, on *Menodora scabra*, 0530–0545 MST, 2 ♂, 8 ♀, 0545–0600 MST, 6 ♀, 0600–0615 MST, 3 ♀, 0615–0630 MST, 1 ♂, 3 ♀, 0630–0645 MST, 1 ♂, 1 ♀, on *Desmanthus cooleyi*, 0545–0600 MST, 1 ♀, on *Salvia reflexa*, 0700–0715 MST, 1 ♂, T. J. Zavortink [CAS]. Portal (1.0 mi. S.), 3 Aug. 1969, on *Hoffmannseggia densiflora*, 0550–0559 MST, 3 ♀ [UCB], 1 ♀ [UCR], flying around *Solanum elaeagnifolium*, 0530–0544 MST, 1 ♀ [UCB], E. G. Linsley. Portal (2.0 mi. NW.), 5100 ft., 21 Aug. 1973, on *Menodora scabra*, 0600–0615 MST, 1 ♀, 0615–0630 MST, 1 ♀; 31 Aug. 1974, on *Menodora scabra*, 0515–0530 MST, 1 ♂, 0545–0600 MST, 1 ♂, 0600–0615 MST, 1 ♂, 0630–0645 MST, 1 ♀, T. J. Zavortink [CAS]. New Mexico. *Eddy Co.*: Whites City, 8 July 1954, 1 ♂, M. A. Cazier and W. J. Gertsch [AMNH]. Mexico. Durango. La Zarca (26 mi. S.), 16 July 1964, on *Cevallia sinuata*, 1 ♂, J. A. Chemsak [UCB].

Etymology. This species is dedicated to E. Gorton Linsley in recognition of his contributions to knowledge of the systematics and biology of bees.

Discussion

The monotypic genus *Simanthedon* may be distinguished from all other North American genera of Eucerini as follows: The male by (1) the strongly protuberant, 'pug-nosed' clypeus; (2) the long, slender, lightly pigmented antenna, with flagellar segment 1 long and segment 11 long, curved, and tapered to a blunt point (the antenna is similar to that of *Martinapis luteicornis*, but longer); (3) the combination of the slender femora I and III, the long and slender tibia III, the short tarsal segments 2–5 on I and III, and the sparsely pubescent and apically flattened or concave outer surface of basitarsus III; (4) the combination of the long spur on tibia I and the unequally shortened spurs on tibia III; (5) the paired patches of posteriorly directed, strong, long, curved, terete, barbed setae on sternum V; (6) the strongly sclerotized, strongly pigmented, and deeply laterally emarginate lateral plate and the long, narrow, reflexed, glabrate median plate of sternum VII; and (7) the pair of deep, oblique emarginations in the distal margin of the spatha. The female is distinguished by the combination of (1) the parallel inner margins of the eyes; (2) the moderately protuberant clypeus; (3) the short malar area; (4) the 5-segmented maxillary palpus; (5) the absence of spatuloplumose hairs on the mesosoma or metasoma; (6) the simple scopal hair; (7) the small, symmetrical claws on all legs; (8) the narrow, pointed, V- or Y- shaped pygidial plate; and (9) the absence of lateral parts on the gradulus of tergum VI.

Both sexes of *Simanthedon linsleyi* bear a strong but only superficial resemblance to *Martinapis luteicornis*. *Simanthedon linsleyi* may be distinguished from *M. luteicornis* by all the features of the male and features 1, 6, 7, and 8 of the female mentioned in the preceding paragraph, and by the following additional significant characters: (1) the absence of a median longitudinal, impunctate ridge or line on the clypeus of the female; (2) the simple, apically narrowed mandible of the female; (3) the oval tegula (the lateral margin of the tegula of *M. luteicornis* is stated to be convex in the anterior half by LaBerge (1957), but it is actually distinctly concave); (4) the short pterostigma (the pterostigma of *M. luteicornis* is unusual in being longer than the prestigma and extended far beyond the base of vein r); (5) the absence of a strong expansion at the base of the costal vein; (6) the absence of a gradular tooth on tergum VI of the male; (7) the more weakly biconvex gradulus of sternum II of the female; (8) the presence of a ventral process on the gonocoxite of the male; and (9) the simple, sparsely pubescent gonostylus of the male.

In LaBerge's (1957) key to the North and Central American genera of Eucerini, males of *Simanthedon linsleyi* run to *Martinapis* and females run to the couplet separating *Synhalonia* (as *Tetralonia*) and *Xenoglossodes*. The numerous characteristics that distinguish *Simanthedon* from the North American *Martinapis* (*M.*) *luteicornis* have been enumerated above; females of *Simanthedon* may be separated from those of *Synhalonia* by the five segmented maxillary palpus and the narrow, pointed, V- or Y- shaped pygidial plate, and from those of *Xenoglossodes* by the moderately protuberant clypeus and the longer galea. In Moure and Michener's (1955) key to the South American genera of Eucerini, both sexes of *S. linsleyi* run to *Martinapis* if the reflexed median plate of sternum VII of the male and the simple apex of the mandible of the female are ignored. Unfortunately, specimens of the Argentine *Martinapis* (*Svastropsis*) *bipunctata* (Friese) have not been available for study and I cannot give a detailed list of the differences between *S. linsleyi* and that species. However, on the basis of the descriptions and illustrations in Moure and Michener (1955), males of *S. linsleyi* probably differ from those of *M. bipunctata* (female unknown to Moure and Michener) by all seven of the distinguishing features given in the first paragraph of this section.

The affinities of *Simanthedon* are unknown; it does not appear to be closely related to any North or South American genus of Eucerini. It does belong, however, in the "central group" of eucerine genera, as defined by Moure and Michener (1955). Sternum VII of the male of *S. linsleyi* is remarkably similar to that of the Chilean *Svastrides melanura* (Spinola), but beyond that, there is little resemblance between these species.

I have not observed any significant variation in the specimens of *S. linsleyi* available for study; even the males from New Mexico and Durango, Mexico appear to be indistinguishable from those from Arizona.

The majority of the known specimens of *Simanthedon linsleyi* have been collected from the flowers of *Menodora scabra*. The species is apparently not oligolectic on this plant however, as many females, including some collected on *Menodora*, bear a heavy load of pollen from other flowers in their scopae. The non-oleaceous pollen that has been collected in significant amounts appears to be of six different kinds, three of which I have been able to determine as *Agave palmeri* Engelmann, *Datura meteloides* A. P. de Candolle, and *Polygala racemosa* Blake. This identification was done by comparing, in temporary glycerol mounts, pollen removed from the scopae of females with that removed from anthers of herbarium specimens of plants that were common at the type locality of *S. linsleyi* in 1973. Numerous other females of *S. linsleyi* collected on *Menodora* bear what I consider to be insignificant amounts of non-oleaceous pollen in their general vestiture; this pollen was undoubtedly obtained incidentally while these individuals were foraging for nectar only, and I have made no attempt to identify it. A complete list of flower records, along with an indication of the type of pollen borne in significant amounts by the females, for 21 males and 89 females is: *Cevallia sinuata* Lagasca y Segura, 1♂; *Conyza* species, 1♂; *Desmanthus cooleyi* (Eaton) Trelease, 1♀ (with *Menodora* pollen); *Hoffmannseggia densiflora* Benthan ex Gray, 4♀ (none with *Hoffmannseggia* pollen, 1 with *Datura* pollen, 1 with *Agave* and an unknown large spherical pollen, 2 with the unknown large spherical pollen); *Ipomoea hirsutula* J.

Jacquin, 1♀ (with *Ipomoea* and *Menodora* pollen); *Menodora scabra*, 17♂, 81♀ (45♀ with pure or nearly pure *Menodora* pollen, 1♀ with *Menodora* and *Datura* pollen, 1♀ with *Menodora, Datura,* and *Polygala* pollen, 1♀ with *Menodora* and *Agave* pollen, 1♀ with *Menodora* and *Ipomoea* pollen, 1♀ with *Menodora* and an unknown small spherical pollen, 5♀ with *Datura* pollen, 1♀ with an unknown moderately large oval pollen, 25♀ without pollen); *Mentzelia pumila* (Nuttall) Torrey & Gray, 1♂; *Salvia reflexa* Hornemann, 1♂; *Polygala racemosa* Blake, 1♀ (with *Datura* pollen); flying around *Solanum elaeagnifolium* Cavanilles, 1♀ (without *Solanum* pollen, but with *Agave* and an unknown large spherical pollen).

All but one of the 19 males and 89 females of *S. linsleyi* for which the time of collection has been recorded were taken in the early morning, between 0515 and 0730 MST. The single exception is a male taken in the evening, between 1800 and 1900 hours, on *Mentzelia pumila* near Douglas, Arizona. On the basis of my collections on *Menodora scabra*, the main flight period, during which 75 percent of the specimens were taken, of *S. linsleyi* extends from 0.50 hour before sunrise to 0.75 hour after sunrise, the females usually arriving at the flowers slightly earlier than males. However, since the flowers of *Menodora scabra* are closed at daybreak and do not start opening until 0.50–0.25 hour before sunrise, bees active at dawn cannot forage on this plant, and the daily flight period of *S. linsleyi* may start earlier than my data show. This hypothesis is supported by the fact that most of the females of *S. linsleyi* which bore non-oleaceous pollen and were collected on *Menodora scabra* were among the first bees to arrive at the flowers of this plant each morning.

The seasonal flight period of *S. linsleyi* is during the summer rainy season typical of the region it inhabits. The earliest and latest recorded dates are 8 July and 31 August.

S. linsleyi is presently known from three areas near the edge of the Chihuahuan Desert: southeastern Arizona and southeastern New Mexico, United States, and northeastern Durango, Mexico. All the specimens collected by me in Arizona have been taken in areas of calcareous soil, where *Menodora scabra* is particularly abundant. The single specimens from New Mexico and Durango are also from regions characterized by abundant limestone and, incidentally, within or near the known range of *Menodora scabra* (Steyermark, 1932). All of the specimens of *S. linsleyi* examined for this study (22 males, 89 females) are part of the type series, cited above.

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THE TAXONOMIC STRUCTURE OF SIX GOLDEN TROUT (*SALMO AGUABONITA*) POPULATIONS FROM THE SIERRA NEVADA, CALIFORNIA (PISCES: SALMONIDAE)

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Abstract: Two hundred and eighty-eight specimens representing six populations of the golden trout (*Salmo aguabonita* Jordan) from the Sierra Nevada, California, were examined for similarities in 11 meristic characters. On the basis of mean similarity and phenetic relationships estimated from Euclidian distances, the six populations were divided into three distinct taxonomic groups. Two populations sampled from the eastern Kern River basin, and one from the Owens River drainage, were identified as the subspecies *S. a. aguabonita*. Two populations, sampled from the Little Kern River basin, displayed characteristics which tended toward those reported for *S. gairdneri* Richardson, and were suspected of having a relatively recent hybrid origin. The final population, sampled from the headwaters of a stream tributary to the Little Kern River, was tentatively classified as the threatened Little Kern golden trout, *S. a. whitei* Evermann. The latter classification is in contrast to an earlier one that held the Little Kern golden trout to be synonymous with the Kern River rainbow trout, *S. g. gilberti* Jordan.

Introduction

The historic distribution and zoogeographic relationships among many salmonine fishes are confounded both by the 'coffee pot' transfers of fish by the early settlers of the late 1800's and by the introduction of nonnative, hatchery-reared trout for recreational purposes. Moreover, the absence of complete biological isolating mechanisms among salmonine species, resulting in numerous instances of interspecific hybridization, has further confounded attempts to discern the historic distributions of individual species.

The systematic status and distribution of the golden trout of the Sierra Nevada has been in dispute since the first taxonomic descriptions (Evermann, 1905; Ellis & Bryant, 1920). Currently, the golden trout are classified as one species, *Salmo aguabonita* Jordan, comprised of two subspecies; *S. a. aguabonita* of the Golden Trout Creek, Cottonwood Creek, and South Fork of the Kern River drainages (Curtis, 1935), and *S. a. whitei* Evermann of the Little Kern River basin (Miller, 1950; Shapovalov, Dill, & Cordone, 1959). Populations of *S. a. aguabonita* are distinguished from those of *S. a. whitei* on the basis of less intense spotting, greater brilliance in life colors, and geographic isolation (Evermann, 1905).

Recently, Schreck and Behnke (1971) and Legendre, Schreck, and Behnke (1972) have elaborated not only on the above differences but reported sharp distinctions for a number of meristic characters. Based on their observations, Schreck and Behnke (1971) suggested synonymy of *S. a. whitei* with the Kern River rainbow trout, *S. gairdneri gilberti* Jordan, and thus reclassified *S. a. whitei* to *S. a. gilberti*. However, their revision was based almost entirely on similarities in the number of lateral scale rows between specimens sampled from the Little Kern River basin during 1967–1969 and a few specimens collected from the Little Kern River and the main Kern River in 1893 and 1904. In addition, observations made during a helicopter flight over the Little Kern River basin led them to the erroneous conclusion that no significant barriers to fish migration existed between the main Kern River and the Little Kern River.

Until recently, a complete knowledge of the general topography of the Little Kern River drainage was not available, and an intimate understanding of the locations of natural barriers restricting directional fish migration was lacking. A thorough survey in 1973 (Evans, Smith, & Bell, 1973) has revealed the existence of several natural barriers throughout the watershed, not only near the confluence of the Little Kern River and the Kern River but in most streams tributary to the Little Kern River. The latter findings have two important consequences. First, the presence of barriers restricting fish migration into the Little Kern River basin from the Kern River raises a serious question regarding Schreck and Behnke's contention of unrestricted gene flow between Little Kern and Kern River trout, and hence to their proposed reclassification of *S. a. whitei*. Secondly, the demarcation of tributary streams throughout the basin into several discrete regions suggests the existence of population subdivisions which would require definitive sampling to ascertain population status and distribution.

A second source of confusion regarding the status of the Little Kern golden trout stems from the possible hybridization between endemic golden and rainbow trout, *S. gairdneri* Richardson, introduced for recreational purposes. From 1931–1941, almost 100,000 rainbow fingerlings were planted yearly in various streams in the Little Kern River basin (Dill, 1945). Dill (1945 & 1950) and D. P. Christenson (personal communication) have suggested that the extensive phenotypic heterogeneity which they observed among the Little Kern trout was due to hybridization and subsequent backcrossing of planted rainbow to endemic golden trout. Although no critical evidence supporting successful golden × rainbow hybridization is available, it is generally assumed that extensive crossing occurs (Dill, 1945 & 1950; Needham & Gard, 1959; Schreck, 1969; Schreck & Behnke, 1971). Furthermore, the success of other salmonid hybridizations (Buss & Wright, 1956; Gould, 1966) suggests that isolating mechanisms among salmonids are far from complete.

The purpose of the present investigation was to examine the trout in the Little Kern River basin to discern whether the presumed hybridization between endemic golden and introduced rainbow trout had resulted in significant alterations in or the loss of *S. a. whitei* from the basin. This report presents the results of an analysis based on meristic characteristics; an analysis of the chromosome karyotypes has been presented elsewhere (Gold & Gall, 1975).

Materials and Methods

Model. Studies of hybridization in teleosts have traditionally relied on estimates such as hybrid indices (Hubbs, 1955) and discriminant functions (Smith, 1973) to detect hybrid individuals. These methods require reliable estimates of the parametric values for all characters in each parental population. Since reliable taxonomic data were not available for either *S. a. whitei* or the rainbow trout planted in the Little Kern River basin during 1931–1941, these methods seemed untenable. Furthermore, it was questionable whether these approaches would be valid if taxonomic data were available since about 10 generations had passed since the last rainbow introductions, and backcrossing of hybrid individuals to endemic goldens would surely have occurred.

As an alternative approach, an operational model of population diversity was derived which could be tested through appropriate sampling. The model was based on two observations. First, California Department of Fish and Game personnel and the members of the 1973 Little Kern River basin survey team indicated that while most of the Little Kern trout were phenotypically heterogeneous, several small isolated populations which might represent 'pure' *S. a. whitei* existed in the headwaters of various streams tributary to the Little Kern River. Secondly, Department of Fish and Game records showed that waters inhabited by the subspecies *S. a. aguabonita* had not received plantings of rainbow trout; therefore populations of this subspecies could be assumed to represent *S. aguabonita*.

The model had four premises: 1) If golden by rainbow crossing occurred in the majority of the waters of the Little Kern River basin, as proposed by Dill (1945), then endemic *S. a. whitei* should be represented only by populations into which individuals from introgressed populations could not migrate; 2) A comparison of rainbow-trout free, geographically isolated populations of *S. a. aguabonita* should define the degree of naturally occurring diversity to be expected among golden trout; 3) The diversity among *S. a. aguabonita* populations should be less in relative degree than that expected between *S. a. whitei* and introgressed populations; 4) Isolated *S. a. whitei* populations should be more closely related to their sister subspecies, *S. a. aguabonita*, than to introgressed trout from adjoining waters. It should be noted that this latter premise is in disagreement with that of Schreck and Behnke (1971) who reasoned that *S. a. aguabonita* and the Little Kern golden trouts ". . . represent two independent invasions by already *divergent* forms of the golden trout complex." Most of their 1967–1969 collections, however, came from waters accessible to planted rainbow trout.

SAMPLING. The locations of the collection sites are shown in figures 1, 2, and 3, and detailed descriptions are presented in appendix tables 1 and 2. Within the Little Kern River basin (fig. 2), one sampling was made from the Little Kern River (*LKR*) below the mouth of Soda Springs Creek (Zone 1) and another from lower Soda Springs Creek (*LSSC*) just above the mouth (Zone 2). A third sampling was made near the headwaters of Soda Springs Creek (*USSC*) above a natural barrier to upstream migration (Zone 3). The approximate locations of rainbow trout introductions during 1931–1941 are also shown in figure 2.

The presence of a barrier restricting upstream migration of trout from sites where rainbows were introduced identified the *USSC* sample as a potential population of *S. a. whitei*. The barrier at the mouth of Soda Springs Creek, separating *LSSC* from *LKR*, was constructed by the U.S. Forest Service in 1970. Consequently, trout from both *LSSC* and *LKR* represent the descendants of endemic golden trout and introduced rainbow trout except that *LSSC* might have received more immigrants from *USSC* if downstream migration occurs.

Three populations of *S. a. aguabonita* also were sampled. One was obtained from Golden Trout Creek (*GTC*) at a point adjacent to the South Fork of the Kern River where a second sample (*SFK*) was obtained. These sites are shown in figures 1 and 3 as Zones 4 and 6, respectively. The third

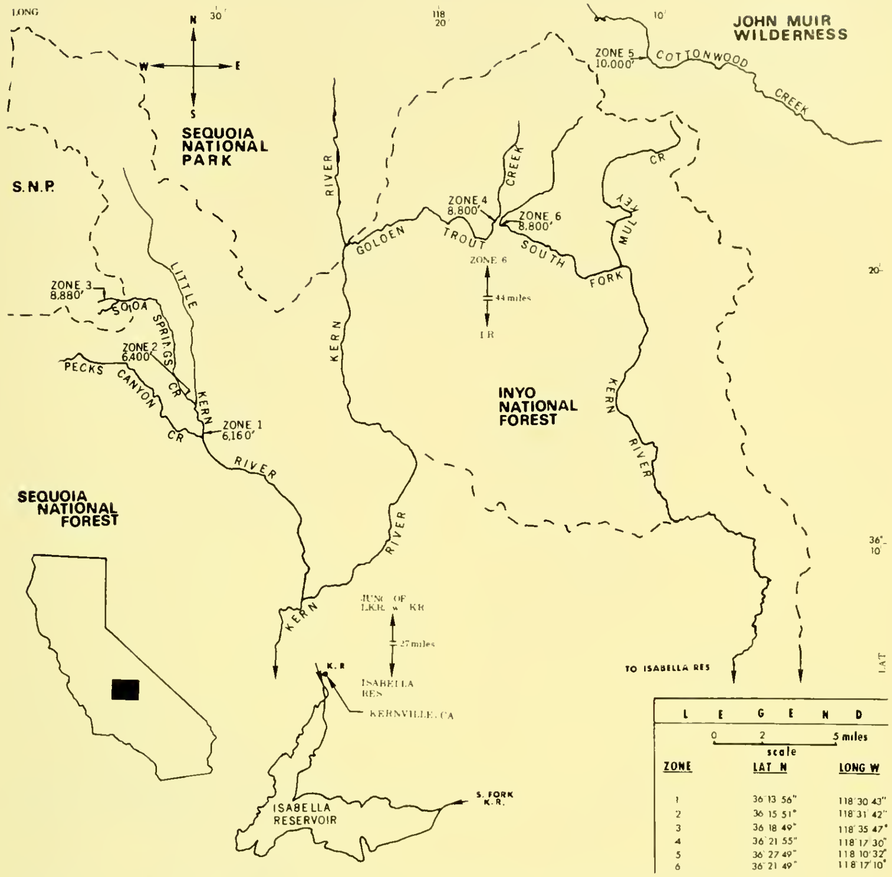

FIGURE 1. A map showing the relative locations of the six populations of golden trout. The collection sites are identified as Zone 1–6.

sample was obtained from Cottonwood Creek (*CWC*) of the Owens River drainage, downstream from the Cottonwood Lakes (Zone 5). Although these three populations are isolated geographically, all share an interrelated history. The low alluvial ridge separating Golden Trout Creek from the South Fork of the Kern River was tunneled in the late 1800's allowing a short period of exchange between the two drainages (Evermann, 1905). Furthermore, at one time the upper South Fork of the Kern was part of the Golden Trout Creek drainage (Lawson, 1904) indicating that trout from these waters may have a common origin. The *CWC* trout are ancestrally related to those of *GTC* and *SFK* since they are descendents of an 1870's 'coffee pot' transplant of 12–13 trout from Mulkey Creek, a tributary of the South Fork of the Kern (Evermann, 1905; Ellis & Bryant, 1920). Since the *CWC* and

FIGURE 2. A map of the Little Kern River basin showing the locations of three collection sites (Zone 1–3), the locations of natural barriers to upstream migration, and the approximate sites of rainbow trout introductions during 1931–41.

Cottonwood Lakes waters were barren of fish prior to the transplant, the *CWC* population was apparently founded by a small sample of fish.

All samples were collected in June, 1973, by electroshock and angling. The specimens were brought live to the trout hatchery at the Fisheries Biology Research Facility at Davis and held until sacrificed. An additional sampling was made at the *USSC* site in August, 1973. All but a few of the specimens were found to be sexually mature.

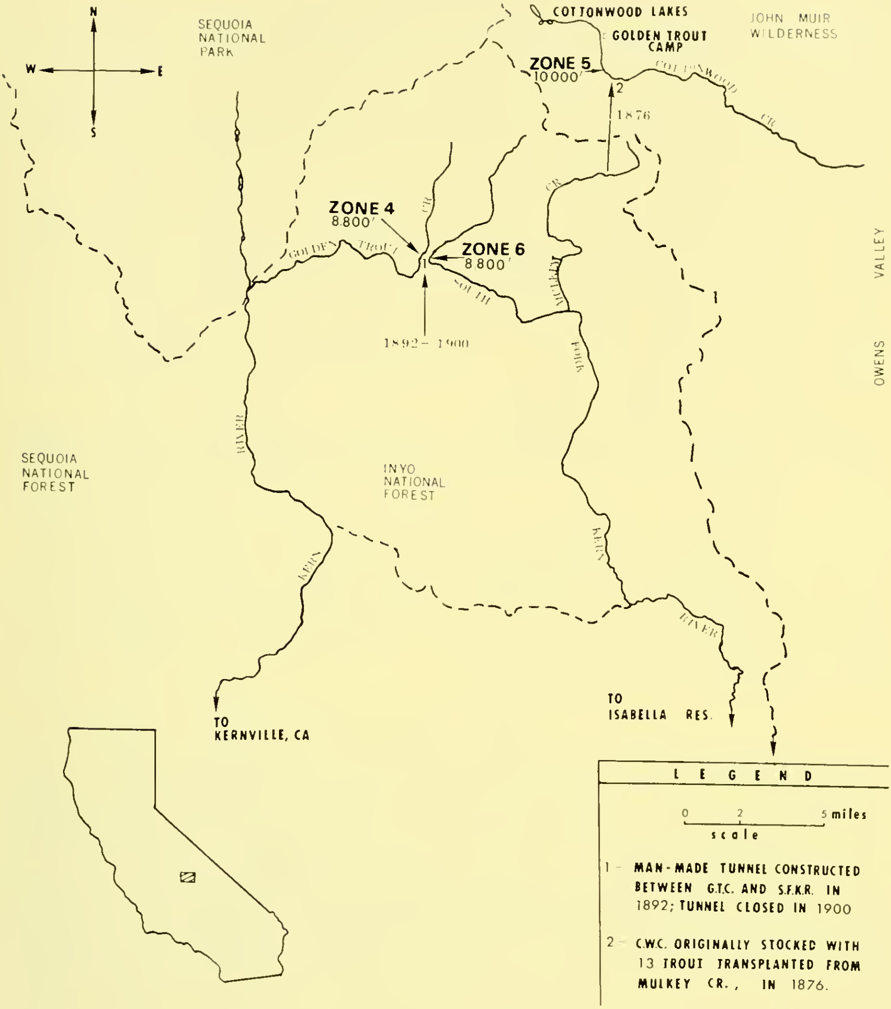

Figure 3. A map of the upper Kern River basin and the Cottonwood Lakes area showing the location of three collection sites (Zone 4–6), the location of an 1890 tunnel, and Mulkey Creek.

Method of analysis. Following sacrifice, specimens were tagged for identification, preserved in 10% formalin for one week, and then transferred to 40% isopropyl alcohol. Measurements and counts of meristic characters were taken from the left side. All specimens were examined in a random sequence and identified only by tag number. The twelve characters analyzed and the methods of scoring were: *Fork length*—the distance in millimeters from the tip of the snout to the fork in the caudal fin; *Pyloric caeca*—each complete tip counted as a single caecum; *BO rays*—all branchiostegal rays including the most anterior (short) rays; *Fin rays*—the principal rays of the ventral (pelvic), dorsal, anal, and pectoral fins, counted under a dissecting microscope; *Vertebrae*—all ossified centra (using radiographs); *Gill rakers*—all gill rakers, including rudiments, on the first gill arch; *Scales along LL*—the number of oblique scale rows, 2–4 rows above the lateral line, from the anteriormost scale touching the shoulder girdle to the last scale at the structural caudal base; *Scales above LL*—the number of scales above the lateral line counted obliquely down from the origin of the dorsal fin to, but not including, the lateral line scale; *Parr marks*—the number of well-defined marks extending both above and below the lateral line.

All data were subjected initially to frequency distribution analysis using the mean, variance, and Fisher's third and fourth moment statistics. Homogeneity of variances among the six samples was tested using Bartlett's method, and homogeneity of means was tested using single classification analysis of variance. If significant heterogeneity among means was detected, mean separation was accomplished using Duncan's multiple range test weighing the least significant ranges for unequal sample sizes (Sokal & Rohlf, 1969). All statistical analyses were carried out by computer using modifications of programs found in Sokal and Rohlf (1969).

RESULTS

DISTRIBUTION OF THE CHARACTERS. Evaluation of the distributions of all 12 characters in each sample indicated that only the number of parr marks was non-normally distributed. Right skewness and leptokurtosis in four of the six samples suggested that the underlying biological phenomenon in parr mark genesis may not follow the assumptions of the normal probability density function. However, the deviations from normality were generally slight, and in the case of *LKR* and *LSSC* resulted from the inclusion of specimens with no visible parr marks. This absence of parr marks on some *LKR* and *LSSC* specimens may indicate the presence of *S. gairdneri* influence since parr marks are not retained into adulthood in that species.

VARIABILITY OF THE CHARACTERS. Estimates of the within sample variances of each of the 12 characters are presented in table 1. The variances among samples were homogeneous for fork length, BO rays, dorsal and pectoral fin rays, gill rakers, and scales above LL. The variances of pyloric caeca, vertebrae, ventral fin rays, and scales along LL were significantly heterogeneous at the 5% level; whereas anal fin rays and parr marks were heterogeneous at the 1% level. Since Bartlett's test is unduly sensitive to even slight

Table 1. *Observed sample variances for six samples of golden trout and the Chi-square probability for test of homogeneity. Numbers in parentheses refer to sample size.*

Character	LKR (56)	LSSC (36)	USSC (93)	GTC (38)	CWC (25)	SFK (40)	P of X^2 (5 df)
Fork length	521.8	453.6	489.3	424.6	219.2	506.4	$.30 > P > .20$
Pyloric caeca	30.35	19.85	14.75	23.12	11.79	22.50	$.05 > P > .02$
BO rays	0.701	0.958	0.717	0.580	0.727	0.666	$.90 > P > .80$
# Vertebrae	1.737	1.018	0.779	1.141	0.573	1.153	$.05 > P > .01$
Fin rays—							
Ventral	0.537	0.593	0.708	0.262	0.577	0.369	$.02 > P > .01$
Dorsal	1.064	0.771	1.070	1.272	0.693	0.820	$.50 > P > .30$
Anal	0.906	1.620	1.012	0.507	0.500	0.404	$P < .01$
Pectoral	0.726	0.730	0.666	0.482	0.673	0.687	$.90 > P > .80$
Parr marks	5.701	4.997	1.448	1.494	1.893	1.563	$P << .01$
Gill rakers	2.200	1.628	1.927	1.563	2.610	1.292	$.50 > P > .30$
Scales along LL	128.7	123.9	83.7	79.0	58.0	155.4	$.05 > P > .02$
Scales above LL	9.579	9.094	8.971	7.400	10.82	9.310	$P = .95$

departures from normality, the significance of these results may have resulted from either small sample sizes or from sampling error. In the case of parr marks, the heterogeneity was undoubtedly due, in part, to the non-normality of the parr mark distribution and raises a serious doubt regarding the validity of number of parr marks as a basis for population separation. Examination of the sample variances for anal fin rays suggested differences in variance between the Little Kern River basin samples and those of *S. a. aguabonita.* Since separation into these two sets correlates with the geographical separation of *S. a. aguabonita* from *S. a. whitei*, this observation may reflect a difference in variability at the subspecies level. Why this should be evident in anal fin ray number alone is unclear.

For the remaining characters with heterogeneous variances, sample variances tended to be higher for *LKR* and *LSSC* than for the other four samples with the exception of the high variance in ventral fin rays in *USSC* and the low variance in pyloric caeca in *LSSC*. The high variability observed for *LKR* and *LSSC* would be expected if the trout from *LKR* and *LSSC* represented 'hybrid' or introgressed populations (Anderson, 1949; Hubbs, 1955).

One notable exception to the above was the high variance in along LL scale row number in the *SFK* sample relative to that observed for *USSC*, *GTC*, and *CWC*. Two seemingly unrelated observations provide a possible explanation for this result. First, during an examination of individual scales, it was noted that the *SFK* specimens possessed an unusually high number of regenerated scales. Secondly, E. P. Pister (personal communication) has informed us that extensive electroshocking has been carried out in the past few years to remove brown trout (*S. trutta*) from the general area of the *SFK* collection site. It is possible that a regenerative response to replace damaged or lost scales caused by heavy electroshocking or excessive handling may have produced the increased variability.

One further result requiring explanation was the reduced variance in fork length observed for the *CWC* sample. Since the Cottonwood Creek region is the most accessible of the six regions sampled and probably the most intensely angled by fishermen, the lower variability and smaller average size (see below) was likely a function of the legal size limit (6 in. or 15 cm.) in effect prior to our sampling.

MEAN VALUES OF THE CHARACTERS. The observed means for the 12 characters in each of the six samples are given in table 2 along with the error mean square obtained in the analysis of variance. The levels of heteroscedasticity observed were considered to be within the limits of the robustness of the analysis of variance for all the characters except number of parr marks. Homogeneity of the parr mark distributions of the six samples was tested by the non-parametric Kruskal-Wallis one-way analysis of variance (Siegel, 1956).

TABLE 2. *Observed means for six samples of golden trout and the error mean square obtained from analysis of variance.* Numbers in parentheses refer to sample size.*

Character	LKR (56)	LSSC (36)	USSC (93)	GTC (38)	CWC (25)	SFK (40)	Error mean square
Fork length	136.9^{a}	136.0^{a}	131.1^{a}	131.5^{a}	117.6^{b}	134.0^{a}	462.1
Pyloric caeca	36.0^{a}	34.6^{a}	32.2^{b}	30.7^{bc}	29.0^{c}	31.1^{bc}	20.34
BO rays	11.1^{ab}	11.1^{ab}	11.3^{a}	10.5^{c}	10.7^{bc}	10.3^{c}	0.720
# Vertebrae	61.4^{a}	61.3^{a}	60.8^{b}	59.7^{c}	59.6^{c}	60.0^{c}	1.077
Fin rays—							
Ventral	9.8^{a}	9.4^{bc}	9.5^{b}	9.2^{c}	9.1^{c}	9.2^{c}	0.544
Dorsal	12.3^{a}	12.2^{ab}	11.9^{bc}	11.6^{cd}	11.1^{d}	11.5^{d}	0.992
Anal	11.4^{a}	11.6^{a}	11.5^{a}	11.1^{a}	11.2^{a}	11.2^{a}	0.873
Pectoral	15.0^{a}	14.9^{a}	15.5^{b}	14.7^{a}	14.6^{a}	14.7^{a}	0.665
Parr marks[†]	10.2	10.4	11.5	9.4	10.3	10.0	——
Gill rakers	17.7^{a}	17.5^{a}	18.2^{a}	17.7^{a}	17.9^{a}	17.7^{a}	1.866
Scales along LL	156.8^{a}	157.7^{a}	181.8^{b}	181.9^{b}	198.5^{c}	180.2^{b}	104.6
Scales above LL	30.2^{a}	31.1^{a}	36.6^{c}	37.7^{c}	42.4^{d}	35.0^{b}	9.103

* Means with identical superscripts are not different at $P \leqslant 0.05$.

[†] Among sample distributions heterogeneous at $P < 0.01$ by Kruskal-Wallis test.

Table 3. *Mean similarity matrix describing the distributions of means among the six samples of golden trout for 10 meristic characters.* Upper values in each comparison refer to the number of characters with similar means; lower values refer to the number of characters with significantly different means ($P < 0.05$).*

Sample	LSSC	USSC	GTC	CWC	SFK
LKR	9	3	3	4	3
	1	7	7	6	7
LSSC		5	4	5	4
		5	6	5	6
USSC			6	2	4
			4	8	6
GTC				8	9
				2	1
CWC					8
					2

* Fork length and number of parr marks were not included.

The corrected H statistic was highly significant ($H = 257$, $X^2 = 11.1$ at $P = .01$ with 5 df) demonstrating that the population distribution for number of parr marks was not the same for all six regions sampled. The heterogeneity was probably the result of both greater variability within the *LKR* and *LSSC* samples, and the higher number of parr marks on the *USSC* fish.

The mean values for 9 of the remaining 11 characters were found to be significantly heterogeneous ($P < .05$); differences were not observed in the numbers of anal fin rays or gill rakers. The significant heterogeneity found for fork length was due solely to the small mean size of the *CWC* fish. Although the differences are not completely consistent for all four characters, the data suggested that trout from the Little Kern River basin, i.e., *LKR*, *LSSC*, and *USSC*, tended to have a larger number of BO rays and a larger number of principal rays in the ventral, dorsal, and pectoral fins than did specimens of *S. a. aguabonita.*

The remaining four characters, pyloric caeca, number of vertebrae, scales along LL and scales above LL, consistently discriminated between the *LKR* and *LSSC* samples and that from *USSC*. The latter had significantly lower numbers of pyloric caeca and vertebrae and a larger number of scales both along LL and above LL. In addition, the pyloric caeca and number of scales observed for the *USSC* sample were very similar to that for *GTC* and *SFK*. A large number of lateral scale rows was a distinctive character of the *CWC* sample, and the *USSC* sample appeared to have a unique number of vertebrae.

Phenetic distance between groups. Mean similarity and Euclidian distance matrices were generated from the data in table 2 in an effort to ex-

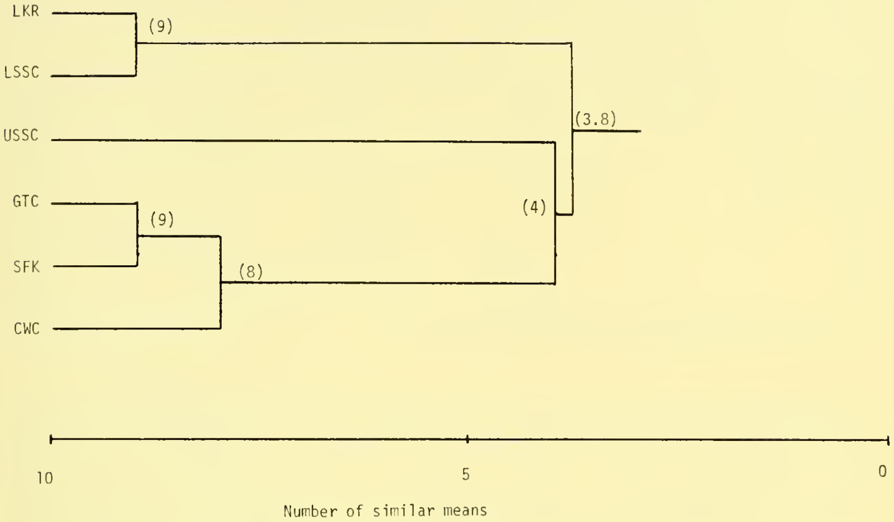

FIGURE 4. Dendrogram from UPGMA average linkage clustering showing the relationship among the six samples of golden trout based on the number of characters with similar mean values. The cophenetic correlation coefficient r_{cs} is 0.911.

press more clearly the collective distributions of the characters among the six samples. Fork length and number of parr marks were omitted as characters in both matrices.

The mean similarity matrix (table 3) provided a qualitative expression of the degree of similarity among the samples. The paired numbers in the matrix represent, for each sample by sample comparison, the number of characters for which the sample means were not found to differ (upper number) and the number of characters for which the sample means did differ (lower number), based on a 5% level of significance. A dendrogram (fig. 4) was derived from the matrix, using the unweighted pair-group method using arithmetic averages (UPGMA) average linkage algorithm outlined in Sneath and Sokal (1973), to pictoralize the degree of association among samples based on the number of characters with similar means.

The method identified two closely aligned groupings or clusters. The *LKR* and *LSSC* samples were similar in mean value for 9 of the 10 characters; the *GTC*, *SFK*, and *CWC* samples shared 8 of 10 character means in common, although *GTC* and *SFK* were more similar to each other than to *CWC*. These two main groupings differed markedly from each other, being similar for only 3–5 of the 10 characters. The *USSC* sample, on the other hand, appeared to be as different from *LKR* and *LSSC* as from *GTC*, *SFK*, and *CWC*, being similar to each of the two main groupings for an average of only 4 of the 10 characters.

TABLE 4. *Euclidian distance matrix of 10 meristic characters* for six samples of golden trout.*

Sample	LSSC	USSC	GTC	CWC	SFK
LKR	4.4	22.4	24.7	38.5	22.7
LSSC		22.2	24.0	38.1	22.0
USSC			10.2	18.3	11.5
GTC				15.6	4.7
CWC					19.0

* Fork length and number of parr marks were not included.

Euclidian distance estimates were obtained for each comparison to provide a quantitative evaluation of the similarities among the samples. This estimation of phenetic distance considers differences in the magnitude of the means as well as the number of means involved. It is important to note that this method does not give equal consideration to all 10 characters but rather gives greatest weight to those characters which show the greatest differences.

The distance estimates were calculated using only those differences which were found statistically significant ($P < .05$) as the remaining differences were attributed to sampling variability. When sample means for a given character were not found to differ (table 2), the best estimate of the mean for each sample involved was calculated as the average of the actual observed means. The sample means were then standardized to remove scaling effects by dividing the deviation of each sample mean from the grand mean of all samples by the standard deviation of a mean. The latter was estimated from the harmonic mean number of observations per sample and the error mean square from the analysis of variance. Finally, the distances shown in table 4 were calculated from the formula:

$$D_{ij} = \left[\sum_{k=1}^{k=10} (Z_{ik} - Z_{jk})^2 \right]^{1/2}$$

where D_{ij} = the distance between the i^{th} and j^{th} sample
Z_{ik} = the value of the k^{th} character in the i^{th} sample
Z_{jk} = the value of the k^{th} character in the j^{th} sample.

The values of D represent the phenetic distance in standard deviation units between any two samples in a 10 dimensional hyperspace (Sokal, 1961; Goodman, 1972).

The resulting dendrogram, obtained using the UPGMA average linkage algorithm, is shown in figure 5. The Euclidian distance estimates identified a close phenetic relationship between *LKR* and *LSSC* (4.4 units), and between

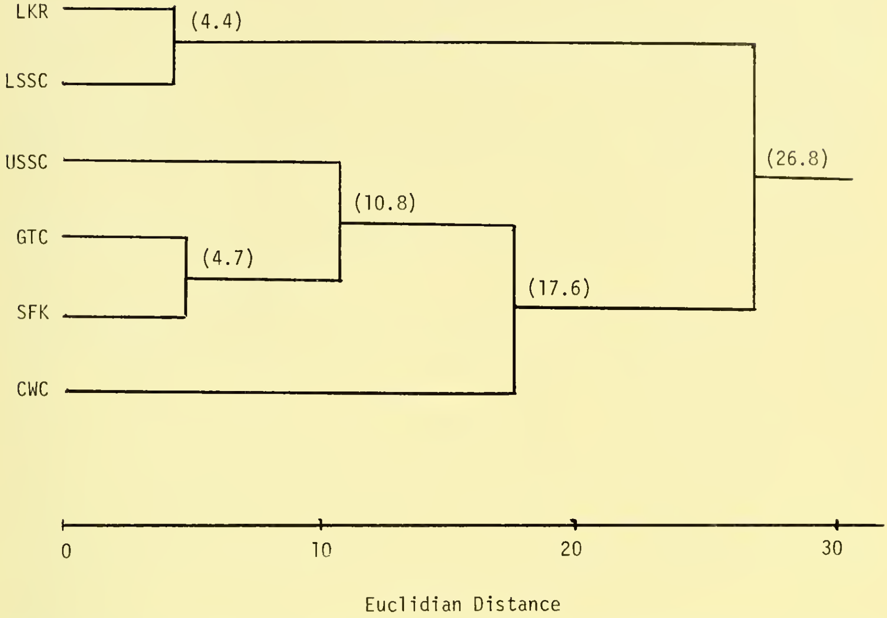

Figure 5. Dendrogram from UPGMA average linkage clustering showing the relationship among the six samples of golden trout based on Euclidian distance. The cophenetic correlation coefficient r_{CS} is 0.860.

GTC and *SFK* (4.7 units). *USSC* was found to be more closely related to the *GTC-SFK* group (10.8 units) than was *CWC* (17.3 units). The latter clustered with the *GTC-SFK-USSC* group at 17.6 units. This is in contrast to the results obtained from the mean similarity matrix which demonstrated *CWC* joining the *GTC-SFK* cluster before *USSC*. This disparity apparently stemmed from the large difference in lateral scale rows between the *CWC* and the *GTC* and *SFK* samples in contrast to their high degree of similarity to the *USSC* sample. Finally, the *LKR-LSSC* group clustered with the *GTC-SFK-USSC-CWC* group at 26.8 units, indicating a marked distinction between the two groups.

Discussion

Sharp distinctions were observed among the six populations of golden trout. Significant differences were found in either the variance, the mean, or both for all meristic characters examined except number of gill rakers. The data indicated discrete groupings from which inference regarding taxonomic classification can be drawn. However, classification in the salmonine fishes, particularly among the subgenus *Parasalmo*, is at best partially subjective. Hubbs (1943) considered that the practical consideration of degree of difference may be the most efficient method. Since there is little or no known genetic incompatibility among most western North American *Salmo* (the subgenus *Parasalmo*), the classifications discussed below are based on "degree of difference" and not on any previous evidence of isolating mechanisms creating genetic incompatibility.

The most evident subgroup comprised trout from *GTC*, *SFK*, and *CWC* which shared common means for 83.3% of the characters studied, but an average of only 38.9% with trout from *LKR*, *LSSC*, and *USSC*. Based on a comparison of these data with the meristic data provided by Schreck (1969) and Schreck and Behnke (1971), the *GTC*, *SFK*, and *CWC* trout were identified as the golden trout subspecies, *S. a. aguabonita*. Also, these trout displayed the brilliant coloration and sparse spotting characteristic of *S. a. aguabonita* (Evermann, 1905; Curtis, 1935).

One notable exception to the classification of *CWC* with *GTC* and *SFK* was the significantly greater number of lateral scale rows on *CWC* trout as compared to both *GTC* and *SFK* trout. Although the number of lateral scale rows for *S. a. aguabonita* is reported to range as high as 210 (Schreck & Behnke, 1971), the large mean value for *CWC* coupled with the low variance raises the question of whether these trout should be given a separate classification. The effect of these differences was evident in the Euclidian distance estimates. The *CWC* trout differed from those of *GTC* and *SFK* in number of scales both along LL and above LL; whereas the latter two differed only in the number above LL. However, separation on this basis alone does not seem warranted. Possible explanations for the large observed difference include: 1) non-random sampling combined with small sample size as only 25 trout were sampled from *CWC*; 2) a 'founder' effect since the Cottonwood Creek was initially founded with only 12–13 trout (Evermann, 1905; Ellis & Bryant, 1920); or 3) environmental modification due to a lower ambient temperature (Garside, 1966; Wallace, 1973) since *CWC* is over 1,000 feet higher in elevation than the *GTC* and *SFK* sites.

It is of interest that despite complete geographic isolation for over 80 years (about 30–40 generations) a high degree of similarity exists among the *S. a. aguabonita* populations. This suggests that the various selection pressures in each region are sufficiently similar to maintain a high degree of homogeneity in meristic characters. The limited distribution and narrow range of *S. a. aguabonita* support this hypothesis.

The situation involving the three samples from the Little Kern River basin is more difficult to interpret. The *LKR* and *LSSC* trout were indistinguishable for 9 of the 10 characters, differing only slightly in number of ventral fin rays, and comprised a second major subgroup. They differed from trout in the other four samples for an average of 61.2% of the characters studied and were found to be only distantly related to them phenetically.

The final subgroup, trout from *USSC*, differed markedly from the other two major subgroups in mean similarity (60% of the characters), but was found to be closely related to *S. a. aguabonita* from *GTC*, *SFK*, and *CWC* in terms of Euclidian distance. It is, therefore, tentatively proposed that the *USSC* trout represent the endemic Little Kern golden trout, *S. a. whitei* Evermann, a conclusion based largely on the close phenetic relationship to *S. a. aguabonita*. However, there also was a remarkable similarity in the coloration and spotting of the *USSC* specimens to the original color plate of *S. whitei* shown in Evermann (1905).

What about the trout from *LKR* and *LSSC*? Originally, the Little Kern River basin was thought to include only golden trout of the subspecies *S. a. whitei*, having differentiated from *S. a. aguabonita* primarily in coloration and spotting (Evermann, 1905). Clearly, the present fish sampled from *LKR* and *LSSC* were only distantly related phenetically to those from *USSC*. Moreover, the means for many of the characters, particularly pyloric caeca, number of vertebrae, and scales along LL and above LL, tended to be intermediate between those observed for *S. a. whitei* and those reported for rainbow trout, *S. gairdneri* (see Needham & Gard, 1959; Schreck & Behnke, 1971). This intermediateness suggested that trout in *LKR* and *LSSC* may have had a hybrid origin.

Schreck and Behnke (1971), following a study of trout from the Little Kern River basin, considered that *S. a. whitei* and the Kern River rainbow trout, *S. gairdneri gilberti* (Jordan & Henshaw, 1878; Evermann, 1905), were synonyms, and thus proposed the classification *S. a. gilberti*. To support this revision they noted that the ranges and means for certain meristic characters, principally oblique lateral scale rows, of trout collected in the Little Kern River in 1893 and the Kern River in 1904 were not apparently different from a limited sample collected from the Little Kern River basin in 1967–69. They further noted that there was no evidence that trout from the Kern River and the Little Kern River were isolated from each other.

For those meristic characters reported, the mean values for the *LKR* and *LSSC* samples were similar to those described for *S. a. gilberti* by Schreck and Behnke (1971). They acknowledged the possibility that these fish were of hybrid origin but dismissed it since some early specimens of *S. a. gilberti* were found to have basibranchial teeth, a character they felt demonstrated a primitive golden trout-like state.

The present finding in upper Soda Springs Creek of an exceptional golden trout population phenetically less similar to the proposed "*S. a. gilberti*", resident only a few miles downstream, than to the geographically distant *S. a. aguabonita*, raises a serious question as to whether the *LKR* and *LSSC* trout are in fact an integral part of the golden trout complex referred to by Legendre, *et al.* (1972). The recent survey of the Little Kern River basin (Evans, *et al.*,

1973) has revealed the existence of significant barriers near the mouth of the Little Kern River which restrict the migration of trout from the Kern River into the Little Kern River. Therefore, there has not been a free exchange of genes between Kern River and Little Kern River populations, at least for an indefinite period of time. Based on these considerations, it is unlikely that the Kern River rainbow, *S. g. gilberti*, is synonymous with *S. a. whitei*.

Further, one of us (JRG) has examined a few of the specimens from the early Kern River and Little Kern River collections, now maintained at the California Academy of Sciences. On one specimen, IU 1113 from the 1904 Little Kern River collection, a lateral scale row count showed in excess of 175 scale rows, a count in sharp disagreement with those of Schreck and Behnke (1971) who reported a mean of 159 and a maximum of 169 lateral scale rows from these trout. However, the condition of most specimens precluded an accurate count and comparison of early specimens with fresh collections seems a dubious prospect.

Finally, no evidence of basibranchial dentition was found on any of the specimens in our collections. Since the same was stated for *S. a. aguabonita* by Schreck and Behnke (1971), it appears that basibranchial dentition may not be a golden trout characteristic.

In summary, the presence of the unique upper Soda Springs Creek golden trout population suggests that a 'pure' Little Kern golden trout still persists in the Little Kern River basin. The origin of the *LKR* and *LSSC* trout is speculative. Their intermediateness between *S. a. whitei* and *S. gairdneri* is strongly suggestive of a hybrid origin. Since numerous *S. gairdneri* were introduced throughout waters of the Little Kern River basin during 1931–1941, hybridization between endemic *S. a. whitei* and the introduced rainbows could have produced the trout now present in the Little Kern River. If the foregoing hypothesis is true, then the impassable barrier separating the upper Soda Springs Creek trout from those downstream has prevented any possible genetic contamination and preserved a vestige population of the original Little Kern golden trout, *S. a. whitei*. Further samplings of other isolated headwater populations throughout the Little Kern River basin should test this hypothesis.

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Appendix Table 1. *Geographic location[*] of collection sites.[†]*

Collection site	Longitude W	Latitude N	Altitude (in feet)	County	Area
ZONE 1 (Little Kern River)	118°30′43″	36°13′56″	6,160	Tulare	Sequoia National Forest
ZONE 2 (Lower Soda Springs Creek)	118°31′42″	36°15′51″	6,400	Tulare	Sequoia National Forest
ZONE 3 (Upper Soda Springs Creek)	118°35′47″	36°18′49″	8,800	Tulare	Sequoia National Park
ZONE 4 (Golden Trout Creek)	118°17′30″	36°21′55″	8,800	Tulare	Inyo National Forest
ZONE 5 (Cottonwood Creek)	118°10′32″	36°27′49″	10,000	Inyo	Inyo National Forest
ZONE 6 (South Fork of the Kern River)	118°17′10″	36°21′49″	8,800	Tulare	Inyo National Forest

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[*] Geographic locations were taken from U.S. Geological Survey, 15 minute series topographic maps, scale 1:62,500.

[†] Fish collections in Zones 1, 3, 4, 5, and 6 were made in about 0.25 miles of stream; collections from Zone 2 were made in about 0.75 miles of stream.

Appendix Table 2. *The linear, cross-country distances (miles) between the collection sites. The three values below the diagonal refer to stream distances (miles).*

Location	ZONE 1 (LKR)	ZONE 2 (LSSC)	ZONE 3 (USSC)	ZONE 4 (GTC)	ZONE 5 (CWC)	ZONE 6 (SFK)
Kernville, California	34	36	40	43	51	43
ZONE 1 (LKR)		2.4	7.1	15.5	25	15.5
ZONE 2 (LSSC)	2.9		4.9	15.0	24	14.9
ZONE 3 (USSC)	9.6	6.7		17.0	25	17.1
ZONE 4 (GTC)					9.7	0.4
ZONE 5 (CWC)						9.7

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THE SCORPAENID FISHES OF THE HAWAIIAN ISLANDS, INCLUDING NEW SPECIES AND NEW RECORDS (PISCES: SCORPAENIDAE)

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Abstract: The number of species of the fish family Scorpaenidae now known from the Hawaiian Islands totals 26. This includes two new species (*Scorpaenopsis brevifrons* and *Scorpaena pele*), and four new records (*Phenacoscorpius nebris, Scorpaenodes corallinus, Scorpaenodes hirsutus,* and *Scorpaenodes littoralis*). In addition, the following are treated as valid Hawaiian species: *Dendrochirus barberi, Ectreposebastes imus, Iracundus signifer, Neomerinthe rufescens, Plectrogenium nanum, Pontinus macrocephalus, Pterois sphex, Rhinopias xenops, Scorpaena ballieui, S. colorata, S. coniorta, S. galactacma, Scorpaenodes kelloggi, S. parvipinnis, Scorpaenopsis altirostris, S. cacopsis, S. diabolus, S. fowleri, Setarches guentheri,* and *Taenianotus triacanthus.* All species are at least briefly described, all are figured, and a key is provided. Synonymies based on Hawaiian references are included for all species; non-Hawaiian references and new Indo-Pacific records are given for a few species.

Table of Contents

Included in brackets are junior synonyms with Hawaiian type localities

Introduction

The shallow-water fish fauna of the Hawaiian Islands is of particular interest because of the high level of endemism associated with its isolated geographic location. The family Scorpaenidae is representative, for nine of a total of 26 species presently are known only from Hawaiian waters. Two species are known only from Hawaii and Japan. The remaining species of scorpaenids occur elsewhere in the Indo-Pacific region and two of these also occur in the Atlantic. Certain groups of scorpionfishes are absent from the Hawaiian Islands but are present in the central and western Pacific; for example, no stonefishes (Synanceiinae) occur in Hawaii.

The scorpionfishes of Oceania are not well known except at the Hawaiian Islands. This is particularly true of those occurring in depths below about 30 meters. We suspect that at least some of the deeper-living species known only from Hawaii will be found at other localities in the Pacific as appropriate depths are sampled.

Many of the scorpaenids which live at depths below about 50 meters were described from specimens collected by the United States Fish Commission steamer *Albatross* in 1901–1902. In the last few years, new material has been taken by the National Marine Fisheries Service vessel *Townsend Cromwell*, and these specimens have been made available to us. Extensive recent collecting in inshore waters to depths of about 200 feet using scuba gear has resulted in additional valuable material. Rather than report solely on the new species and new records of Hawaiian scorpionfishes, we have provided a synopsis of all Hawaiian species. Also, for some species, we have presented new records from other Indo-Pacific localities, as well as comments on possible synonyms or close relatives.

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Persons aiding the study were many. We especially thank Paul J. Struhsaker, National Marine Fisheries Service (NMFS), Honolulu, for making available specimens collected by the *Townsend Cromwell*. John Fowler (NMFS) provided fresh specimens of 2 offshore species collected by the *Townsend Cromwell*. William D. Madden provided information on *Iracundus signifer* and provided the specimens of *Phenacoscorpius megalops*. We wish to thank the following persons for assistance during visits to museums: Alwyne C. Wheeler, British Museum of Natural History (BM (NH)); James E. Böhlke, Academy of Natural Sciences of Philadelphia (ANSP); M. L. Bauchot, Museum National d'Histoire Naturelle (MNHN), Paris; the staff of the United States National Museum of Natural History (USNM); William A. Gosline and George Losey, University of Hawaii (UH); Paul Kausbauer, Naturhistorisches Museum, Wien (NMW); and John R. Paxton, Australian Museum, Sydney (AMS). R. J. McKay, Queensland Museum, Brisbane (QMB), generously loaned the type of *Scorpaenopsis macrochir*. Margaret M. Smith, Rhodes University (RU), Grahamstown, loaned a specimen of *Scorpaenodes littoralis*. Richard Rosenblatt, Scripps Institution (SIO), provided a specimen of *Ectreposebastes niger*. Bruce B. Collette, Systematics Laboratory, National Marine Fisheries Service, arranged for a loan of a specimen of *E. niger* and supplied data on the holotype of that species. We are indebted to various persons for aiding in scuba collections with Randall, particularly Gerald R. Allen, Deetsie Neil Chave, and Paul M. Allen. David T. Anderson assisted in analysis of the humpbacked species of the genus *Scorpaenopsis*. Melissa Barbour, Lillian Dempster, W. I. Follett, Warren Freihofer, Maurice Giles, James Gordon, Tomio Iwamoto, John McCosker, Cherryl Pape, Stuart Poss, Katherine Smith, Pearl Sonoda, and Beverly Wesemann of the California Academy of Sciences (CAS) aided the study as did Helen Randall from the Bernice P. Bishop Museum (BPBM). W. I. Follett and Lillian Dempster provided advice on nomenclatural problems. Kaza V. Rama Rao, Zoological Survey of India, provided comments on the manuscript. We especially thank Lillian Dempster for assistance with literature and for reviewing the manuscript.

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METHODS

Measurements, counts, and terminology of head spines follow Eschmeyer (1969b) with a few modifications. Preorbital spines are here termed lachrymal spines. The last soft ray in the dorsal and anal fins in all Hawaiian species is a double ray, often appearing as two close-set rays. The fraction ½, as in anal rays 5½, is used to draw attention to the fact that the last ray is double and should not be counted as 2 rays.

In MATERIAL EXAMINED sections we list representative specimens from typical habitats and more briefly indicate additional material. The number of specimens followed by the range in standard length is given in parentheses. If only the number of specimens is given, then no fin-ray counts were made on any of the specimens in that lot.

Abbreviations of depositories of specimens are given in the INTRODUCTION with the following exceptions: SU (Stanford University) and GVF (George Vanderbilt Foundation), these specimens now being housed at the California Academy of Sciences. Specimens listed as NMFS uncat. are now at the National Marine Fisheries Service Laboratory, Honolulu, but most of this material eventually will be deposited at the United States National Museum of Natural History. Much of the University of Hawaii collection has been transferred to the Bernice P. Bishop Museum; the specimens reported with both UH and BPBM numbers were transferred, while those with only a UH number remain at the University of Hawaii.

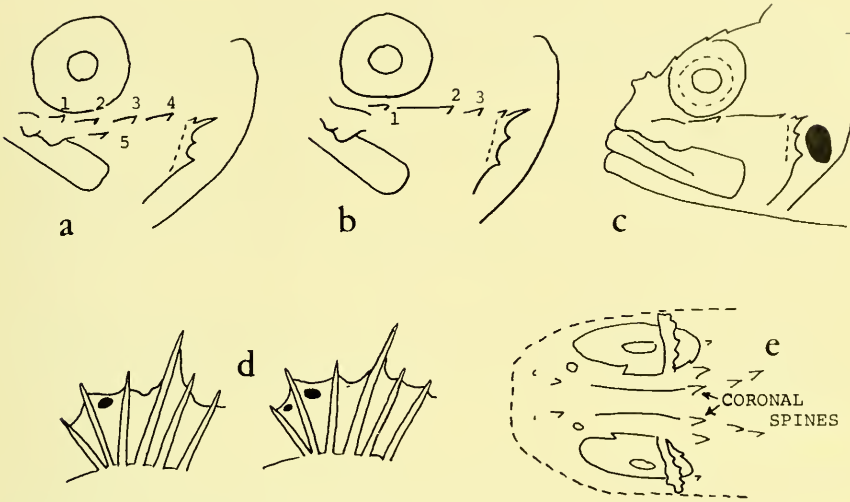

Figure 1. Selected features used in key.

Key to Scorpionfishes of the Hawaiian Islands

Note. Consult figure 1 for diagrams accompanying key. "Deepwater" means that the species occurs deeper than about 50 meters. The coloration for most species is diagnostic and the reader should consult the appropriate figures.

1a. Dorsal spines 13 2
1b. Dorsal spines 12 8

2a. Pectoral rays unbranched; 6½ anal soft rays .... *Pterois sphex* (figure 2a)
2b. Some pectoral rays branched; 5½ anal soft rays 3

3a. Dorsal spines long, longest nearly as long as or longer than depth of body .... *Dendrochirus barberi* (figure 2b)
3b. Dorsal soft rays short, the longest less than ½ depth of body 4

4a. Vertical scale rows (counted 2 or 3 rows above lateral line from above first lateral line scale to end of hypural) fewer than 32; dorsal soft rays usually 8½ 5
4b. Vertical scale rows more than 40; dorsal soft rays usually 9½ (except *Scorpaenodes corallinus* with 8½) 6

5a. Pectoral rays 17–18; suborbital ridge with 4 spines plus extra spine below main ridge (figure 1a) .... *Scorpaenodes hirsutus* (figure 3)
5b. Pectoral rays 18–20, usually 18–19; suborbital ridge usually with 3 spines (figure 1b) .... *Scorpaenodes kelloggi* (figure 4)

6a. Suborbital ridge with more than 5 spinous points (frequently 10 or even 20 or more) .... *Scorpaenodes parvipinnis* (figure 5a)
6b. Suborbital ridge with 3 or fewer spinous points 7

7a. Dorsal soft rays 9½; dusky spot on subopercle behind preopercular spines (figure 1c) .... *Scorpaenodes littoralis* (figure 5b)
7b. Dorsal soft rays 8½; dark spot not present on subopercle behind preopercular spines .... *Scorpaenodes corallinus* (figure 5c)

8a. Pectoral rays 22–23; dorsal soft rays 7½; tenth dorsal spine very short, nearly separated from ninth and eleventh; a deepwater species .... *Plectrogenium nanum* (figure 6)
8b. Pectoral rays fewer than 20; dorsal soft rays 9½ or more; tenth dorsal spine joined by membrane to ninth and eleventh spines 9

9a. Pectoral rays 14–15, usually 14; body strongly compressed, width usually about one-fourth of body depth; body covered with rough papillae instead of normal scales .... *Taenianotus triacanthus* (figure 7)
9b. Pectoral rays 16 or more; body not greatly compressed; body covered with normal scales 10

10a. Fourth dorsal spine especially elongate in specimens over about 60 mm. S.L. (smaller specimens may be identified solely by the next character); black pigment between spines 1–3 or 2–3 (figure 1d) .... *Iracundus signifer* (figure 8)
10b. Fourth dorsal spine not especially elongate; no black spot between spines 1–3 11

11a. Lateral line a more or less continuous trough (covered by thin membranous scales which are usually lost on capture); head cavernous, with ossification weak; scales tiny and cycloid 12
11b. Lateral line normal, scales tubed; head not cavernous, ossification normal; scales cycloid or ctenoid 13

12a. Orbit diameter subequal to interorbital width; pectoral rays 20–22; anal soft rays usually 5½; a deepwater species .... *Setarches guentheri* (figure 9)
12b. Orbit diameter about one-half of interorbital width; pectoral rays 19–20; anal soft rays usually 6½; a deepwater species .... *Ectreposebastes imus* (figure 10)

13a. Enlarged, black melanophores on caudal peduncle as in figure 11; lateral line incomplete, only 4 or 5 tubed scales present anteriorly; a deepwater species .... *Phenacoscorpius megalops* (figure 11)
13b. No enlarged black melanophores on caudal peduncle; lateral line complete 14

14a. Pectoral fin rays unbranched; a deepwater species .... *Pontinus macrocephalus* (figure 12)
14b. Upper pectoral fin rays branched (look carefully at tips) 15

15a. Palatine teeth absent .... genus *Scorpaenopsis* 16
15b. Palatine teeth present 20

16a. Pectoral rays 16 (15 or 17 should be expected occasionally); (a tiny species not exceeding about 30 mm. S.L.) .... *Scorpaenopsis fowleri* (figure 13)
16b. Pectoral rays 17–19, mostly 18 or 19 17

17a. Pectoral rays usually 19; dark spot frequently present at midheight of spinous

portion of dorsal fin between spines 3 or 4 to 6 or 7 ....
.... *Scorpaenopsis brevifrons* new species (figures 14–15)
17b. Pectoral rays usually 17 or 18, rarely 19; no dark spot present on spinous portion of dorsal fin 18

18a. A hump behind head (as in figure 16); (see also figure 17b for coloration inside of pectoral fin) .... *Scorpaenopsis diabolus* (figures 16–17)
18b. Not humpbacked 19

19a. Eye diameter smaller than snout length; numerous tentacles present on lower jaw
.... *Scorpaenopsis cacopsis* (figure 18)
19b. Eye large, nearly 1½ times snout; 1 or 2 tentacles present on lower jaw; a deepwater species .... *Scorpaenopsis altirostris* (figure 19)
20a. Head compressed and orbit elevated; vertical scale rows about 70; a deepwater species .... *Rhinopias xenops* (figure 20)
20b. Head normal; vertical scale rows usually fewer than 50 21

21a. Pectoral rays 18–19; a deepwater species .... *Neomerinthe rufescens* (figure 21)
21b. Pectoral rays 17 or fewer, very rarely 18; most species in shallow water ....
.... genus *Scorpaena* 22

22a. Scales on sides cycloid .... *Scorpaena galactacma* (figure 22a)
22b. Scales on sides ctenoid 23

23a. Pectoral rays usually 16; shallow water 24
23b. Pectoral rays usually 17; deep water 25

24a. Body and fins with conspicuous dark spots; coronal spines absent (not as in figure 1e) .... *Scorpaena coniorta* (figure 22b)
24b. Body and fins without conspicuous dark spots; coronal spines present (figure 1e)
.... *Scorpaena ballieui* (figure 23)

25a. Scales on breast buried (area appears unscaled); 4 spines on suborbital ridge, the first on lateral face of lachrymal bone ....
.... *Scorpaena pele* new species (figures 24, 25a)
25b. Breast with obvious scales; 3 spines on suborbital ridge ....
.... *Scorpaena colorata* (figure 25b)

Genus **Pterois** Oken

Pterois Oken, 1817, p. 1182 [misprinted as p. 1782] (type-species *Scorpaena volitans* Linnaeus by monotypy; based on Cuvier's 'Les Pterois').

Remarks. Generic synonyms are not included. The genus *Pterois* is very closely related to the genus *Dendrochirus*; the 2 genera are separated on the basis of long unbranched pectoral rays (a juvenile feature) in adults of the genus *Pterois*; some rays are branched in adults of the genus *Dendrochirus*. Juveniles are very similar in all features, and separate genera possibly may not be warranted. We do not recognize the genus *Pteropterus* Swainson as distinct from *Pterois* as does Smith (1957b). Only one species occurs in Hawaiian waters.

Pterois sphex Jordan and Evermann.
(Figure 2a.)

Pterois sphex JORDAN & EVERMANN, 1903a, p. 201 (original description; type locality Hawaiian Islands, one specimen from Honolulu; holotype USNM 50650); JORDAN & EVERMANN, 1905, pp. 464–465, fig. 203 (description from Jordan and Evermann, 1903a; figure of holotype); JORDAN & SEALE, 1906, p. 379 (name only; Hawaiian Islands); JORDAN & JORDAN, 1922, p. 56 (listed); FOWLER, 1925, p. 27 (listed); JORDAN & EVERMANN, 1926, p. 10 (listed); FOWLER, 1928, p. 294, pl. 35A (synonymy; description; photograph of colored cast); TINKER, 1944, pp. 270–271, fig. (brief diagnosis; figure from Jordan and Evermann, 1905); SMITH, 1957b, pp. 78, 81 (compared with *P. russelli* and *P. mombasae*); GOSLINE & BROCK, 1960, pp. 284–286, 341, fig. 262 (brief mention; in key; line drawing); GOSLINE, 1965, p. 825 (depth distribution).

MATERIAL EXAMINED. USNM 50650 (1, 112 mm. S.L., holotype of *Pterois sphex*), Oahu, Honolulu, D. S. Jordan and B. W. Evermann, 19 Jan. 1904. BPBM 7812 (1, 36.8), Hawaii, Kona Coast, off Puako, coral bottom in 15 meters, J. E. Randall, 7 Aug. 1969. BPBM 7813 (4, 37.1–68.5), Oahu, Pupakea and Waimea Bay, in 15 meters, rock ledge, J. E. Randall *et al.*, 24 Aug. 1969. BPBM 7814 (1, 148), Oahu, off Makua, at base of ledge in 30 meters, G. R. Allen, 20 March 1969. BPBM 7882 (3, 16.8–27.7), Oahu, Waimea Bay, in 3.5–5.5 meters, G. R. Allen, 30 May 1968. BPBM 7883 (1, 30.0), Oahu, Kaneohe Bay, ledge, J. E. Randall and E. Chave, 10 Oct. 1969. BPBM 9771 (1, 70.0), Oahu, off Makaha Shores Condominium, small caves in reef in 14 meters, J. E. Randall and A. R. Emery, 26 Apr. 1970. BPBM 10625 (1, 44.8), Oahu, Waimea Bay, G. R. Allen, Sept. 1966. CAS 15721 (1, 23.5), Oahu, Waimea Bay, W. P. Davis, 15 July 1967. Additional material is available in the BPBM and CAS collections, and specimens collected by the *Townsend Cromwell* are present in the NMFS collection.

DISTINGUISHING FEATURES. Dorsal fin rays normally XIII, 10½ (sometimes XIII, 11½). Anal fin rays III, 6½. Pectoral fin rays 15–16, usually 16. Pectoral rays all unbranched, very long, and free from membrane distally. Dorsal spines very long, some about as long as body depth. Scales ctenoid, about 50–55 vertical scale rows. Coronal spines present. Most head spines become multiple with growth. Lachrymal and suborbital bones densely covered with spines at specimen length of 100 mm. S. L. Supraocular tentacles banded with black, frequently tentacles absent in large specimens. Coloration (fig. 2a) is also diagnostic (small specimens have fewer bars on pectoral and pelvic fins).

DISTRIBUTION. This species is known only from the Hawaiian Islands. It has been collected by scuba diving in depths from about 3 to 30 meters. These collections were made during daytime hours, and the specimens were found

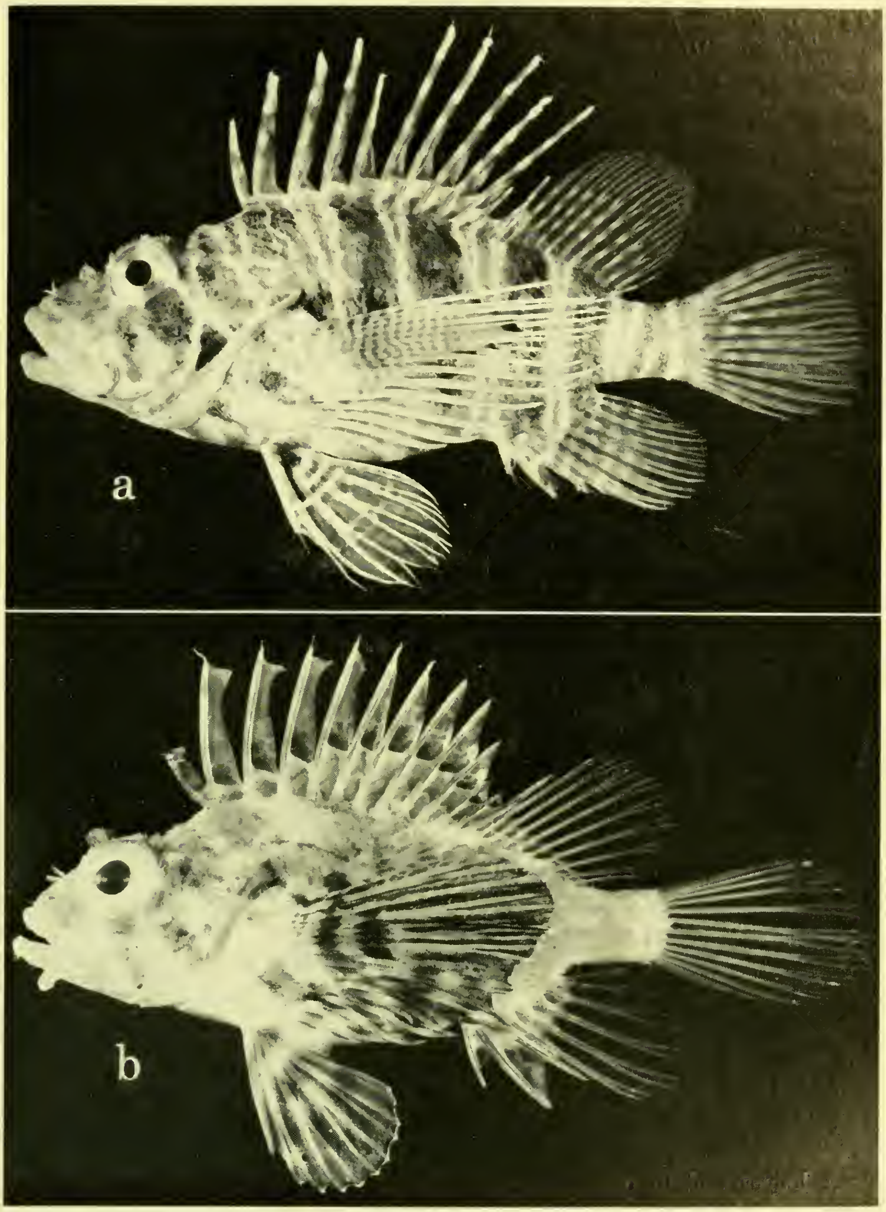

Figure 2. a: *Pterois sphex*, BPBM 7814, 154 mm. S. L., Oahu. (Photograph of fresh specimen.) b: *Dendrochirus barberi*, BPBM 6540, Oahu. (Photograph of preserved specimen.)

TABLE 1. *Counts of dorsal and anal fin rays in Hawaiian scorpionfishes (based only on Hawaiian specimens).*

	Dorsal spines		Dorsal soft rays					Anal spines	Anal soft rays		
	12	13	7½	8½	9½	10½	11½	3	5½	6½	7½
Pterois sphex	—	13	—	—	—	12	1	12	—	13	—
Dendrochirus barberi	—	23	—	1	21	1	—	23	23	—	—
Scorpaenodes hirsutus	—	12	—	11	1	—	—	12	12	—	—
Scorpaenodes kelloggi	—	15	1	14	—	—	—	15	15	—	—
Scorpaenodes parvipinnis[1]	1	15	—	—	16	—	—	16	15	—	—
Scorpaenodes littoralis	—	10	—	—	10	—	—	10	9	1	—
Scorpaenodes corallinus	—	4	—	4	—	—	—	4	4	—	—
Plectrogenium nanum[2]	14	—	13	—	—	—	—	14	14	—	—
Taenianotus triacanthus[3]	12	—	—	1	1	10	—	12	1	10	—
Iracundus signifer	13	—	—	—	12	1	—	13	13	—	—
Setarches guentheri	32	—	—	—	1	31	—	32	31	1	—
Ectreposebastes imus	19	—	—	—	—	18	1	19	—	17	2
Phenacoscorpius megalops	2	—	—	—	2	—	—	2	2	—	—
Pontinus macrocephalus	15	—	—	—	2	13	—	15	15	—	—
Scorpaenopsis diabolus[4]	24	—	—	1	20	2	—	24	23	1	—
Scorpaenopsis cacopsis	11	—	—	1	10	—	—	11	11	—	—
Scorpaenopsis brevifrons[5]	12	—	—	—	13	—	—	13	13	—	—
Scorpaenopsis fowleri	4	—	—	—	4	—	—	4	4	—	—
Scorpaenopsis altirostris	4	—	—	—	4	—	—	4	4	—	—
Rhinopias xenops	4	—	—	—	4	—	—	4	4	—	—
Neomerinthe rufescens	15	1	—	1	14	1	—	16	16	—	—
Scorpaena coniorta	11	—	—	—	10	1	—	11	11	—	—
Scorpaena ballieui	10	—	—	—	10	—	—	10	10	—	—
Scorpaena galactacma[4]	14	—	—	—	12	1	—	14	14	—	—
Scorpaena pele	19	—	—	1	18	—	—	19	19	—	—
Scorpaena colorata	17	—	—	—	17	—	—	17	17	—	—

[1] One with 5 soft anal rays.
[2] Holotype with 6½ soft dorsal rays.
[3] One with 6 soft anal rays.
[4] One with 9 soft dorsal rays.
[5] One with 6 + scaled area + 1 dorsal spines.

under ledges and in or near caves. If the behavior of this species is similar to that of the other members of the genus *Pterois* as observed by G. R. Allen and by us, then the species tends to stay in concealed areas during daylight hours but ranges over adjacent areas while feeding at night. The *Townsend Cromwell* trawled 6 specimens from 5 stations off Molokai in 119–124 meters. These specimens, with one exception, were all taken at night.

Genus **Dendrochirus** Swainson

Brachirus Swainson, 1839, p. 71 (see Remarks).

Dendrochirus Swainson, 1839, p. 180 (see Remarks).

Brachyrus Swainson, 1839, p. 264 (see Remarks; type-species *Pterois zebra* Cuvier by subsequent designation of Swain, 1883, p. 277).

Nemapterois Fowler, 1938a, p. 73 (type-species *Nemapterois biocellatus* Fowler by original designation, monotypic).

Remarks. Swainson (1839) first used the spelling *Brachirus* on p. 71; then on p. 180 he substituted the name *Dendrochirus*, but on p. 264, where species were included, he used the name and spelling *Brachyrus*. Moreover, on p. 303 he used the name *Brachirus* for a genus of sole. We treat *Brachirus* (of p. 71) as an inadvertent spelling error. Bleeker (1876b, p. 42) serves as the first revisor selecting *Dendrochirus* over *Brachyrus*.

Dendrochirus barberi (Steindachner).

(Figure 2b.)

Pterois barberi Steindachner, 1900a, p. 175 (original description; type locality South Pacific [one small specimen found by Captain Barber in the plankton during the trip from Honolulu to Cape Horn, 1896–1897]); Steindachner, 1900b, pp. 491–492, pl. 3, fig. 2 (more complete description including the figure).

Dendrochirus hudsoni Jordan & Evermann, 1903a [April 11], pp. 202–203 (original description; type locality Hawaiian Islands, Oahu, Waikiki; holotype USNM 50652); Snyder, 1904, p. 536 (listed, Honolulu); Böhlke, 1953, p. 120 (location of types).

Dendrochirus chloreus Jenkins, 1903 [July 23], pp. 498–499 fig. 41 (original description; type locality Hawaiian Islands, Honolulu; holotype USNM 50701); Jordan & Snyder, 1904b, p. 126 (one from Honolulu market); Jordan & Evermann, 1905, pp. 465–466, fig. 204 (mostly compiled from Jenkins, 1903; figure of type of *D. chloreus* from Jenkins, 1903); Jordan & Seale, 1906, p. 379 (name only, Hawaiian Islands); Jordan & Jordan, 1922, p. 55 (listed); Böhlke, 1953, p. 120 (location of types).

Dendrochirus barberi: Jordan & Snyder, 1904b, p. 126 (*hudsoni* a synonym of *barberi*); Jordan & Evermann, 1905, p. 465, color pl. 73 (description mostly from Jordan and Evermann, 1903; *hudsoni* as a synonym of *barberi*); Jordan & Seale, 1906, p. 379 (listed, Hawaii; *hudsoni* as a synonym); Jordan & Jordan, 1922, p. 56 (listed).

Brachirus chloreus: Fowler, 1925, p. 27 (listed, Hawaiian Islands).

Dendrochirus zebra (not of Quoy and Gaimard): Fowler, 1928, pp. 294–295 (in part; *barberi* wrongly as young of *zebra*); Wahlert, 1955, p. 326 (type of *barberi* in Übersee Museum, Bremen).

Dendrochirus brachypterus (not of Cuvier): Fowler, 1928, p. 295 (in part; *hudsoni* and *chloreus* included in synonymy); Pietschmann, 1930, p. 18 (Kaneohe Bay, Oahu); Fowler, 1931, p. 349 (in part; two specimens from Kona, Hawaii); Fowler, 1934, p. 430 (in part; one specimen from Kewalo Bay, Oahu); Pietschmann, 1938, pp. 5, 30–31 (brief description; color like *chloreus*; one from French Frigate Shoal); Tinker, 1944, p. 271, fig. 9 on pl. 6, text fig. (brief description; figure of type of *chloreus* from Jenkins, 1903); Gosline & Brock, 1960, p. 341 (wrongly included *barberi* in synonymy).

Remarks. The type specimen of *D. barberi* is in the Übersee Museum in Bremen, West Germany (Wahlert, 1955). It has not been examined by us.

Table 2. *Counts of left pectoral fin rays in Hawaiian scorpionfishes (specimens from Hawaii only; footnotes are used when the left or right fin-ray count differed such that the count for one side was unusual for the species).*

	14	15	16	17	18	19	20	21	22	23	24
Pterois sphex	—	1	12	—	—	—	—	—	—	—	—
Dendrochirus barberi	—	—	—	2	21	—	—	—	—	—	—
Scorpaenodes hirsutus	—	—	—	4	8	—	—	—	—	—	—
Scorpaenodes kelloggi	—	—	—	—	5	9	1[a]	—	—	—	—
Scorpaenodes parvipinnis	—	—	—	—	13[b]	3	—	—	—	—	—
Scorpaenodes littoralis	—	—	—	3	4	3	—	—	—	—	—
Scorpaenodes corallinus	—	—	—	1	3[b]	—	—	—	—	—	—
Plectrogenium nanum	—	—	—	—	—	—	—	—	4	9	1
Taenianotus triacanthus	11	1	—	—	—	—	—	—	—	—	—
Iracundus signifer	—	—	—	4[c]	9	—	—	—	—	—	—
Setarches guentheri	—	—	—	—	—	—	4	23	5[d]	—	—
Ectreposebastes imus	—	—	—	—	—	10	8	1[e]	—	—	—
Phenacoscorpius megalops	—	—	—	2	—	—	—	—	—	—	—
Pontinus macrocephalus	—	—	2	13	—	—	—	—	—	—	—
Scorpaenopsis diabolus	—	—	—	2[c]	22	—	—	—	—	—	—
Scorpaenopsis cacopsis	—	—	—	1[c]	10[ab]	—	—	—	—	—	—
Scorpaenopsis brevifrons	—	—	—	—	1	10	2[a]	—	—	—	—
Scorpaenopsis fowleri	—	—	4	—	—	—	—	—	—	—	—
Scorpaenopsis altirostris	—	—	—	1	3	—	—	—	—	—	—
Rhinopias xenops	—	—	—	—	3	1	—	—	—	—	—
Neomerinthe rufescens	—	—	—	—	12[a]	4[c]	—	—	—	—	—
Scorpaena coniorta	—	1	10	—	—	—	—	—	—	—	—
Scorpaena ballieui	—	—	9	1	—	—	—	—	—	—	—
Scorpaena galactacma	—	1[f]	11	2	—	—	—	—	—	—	—
Scorpaena pele	—	—	1[b]	18	—	—	—	—	—	—	—
Scorpaena colorata[1]	—	—	1[b]	13[g]	2[b]	—	—	—	—	—	—

[a] One with 19 on right.
[b] One with 17 on right.
[c] One with 18 on right.
[d] 23 on right in one specimen.
[e] 20 on right.
[f] 16 on right.
[g] Two with 18 on right.
[1] One abnormal specimen with 15 + 16.

The type was reported as 31 mm. in standard length and was reportedly taken in the plankton during the trip from Hawaii to Cape Horn. A 61-mm. S. L. specimen came to a nightlight station and was captured by G. R. Allen at Hanalei Bay, Kauai, so we know that small specimens can be found in surface waters. Because of this and because the species is otherwise known only from the Hawaiian Islands, we suspect the small holotype was collected very soon after leaving port in the Hawaiian Islands.

Material examined. USNM 50652 (1, 33.4, holotype of *Dendrochirus hudsoni*), Oahu, Waikiki Beach, U. S. Bureau of Fisheries, 1901. USNM 50701 (1, 97.4, holotype of *Dendrochirus chloreus*), Oahu, Honolulu, O. P. Jenkins,

1889. SU 23294 (5, about 35–55.3, paratypes of *D. chlorcus*) and SU 23315 (1, 72.8, paratype of *D. chlorcus*), Oahu, Honolulu, O. P. Jenkins, 1889. USNM 126089 (1, 43.5), Oahu, Honolulu, *Albatross*, 1902. SU 7467 (2, 33.8–37.5, paratypes of *D. hudsoni*), Oahu, Honolulu, U. S. Fish Commission, 1901. ANSP 87600 (1, 62.9), Honolulu, J. W. Thompson, 1910. ANSP 104663 (1, 72.7), Honolulu, C. M. Cooke, 16 Oct. 1923. BPBM 6540 (1, 50.3), Oahu, Moku Manu, north side in 49 meters, base of vertical dropoff, J. E. Randall *et al.*, 9 Oct. 1968. BPBM 7975 (1, 66.7), Oahu, Pokai Bay, in 9 meters, J. E. Randall *et al.*, 29 July 1969. CAS 15690 (2), Oahu, west side of Waimea Bay, in 6–9 meters, J. E. Randall *et al.*, 25 Aug. 1969. CAS 15693 (9, 36.8–54.2), Oahu, off rocky islet at SW. end of Waimea Bay, in 1–10.5 meters, J. E. and L. A. Randall and P. M. Allen, 27 July 1970. CAS 15714 (1, 80.8), Hawaiian Leeward Islands, reef on NW. side of Laysan, 25°46′27″N., 171°44′37″W., GVF Reg. no. 26, V. E. Brock, R. R. Harry *et al.*, 3 July 1951. SU 7846 (2, 40.0–114), Oahu, Honolulu, U. S. Fish Commission, 1901. SU 8420 (2, 98.5–116), Honolulu, E. L. Berndt, 1902. Additional material is available in the ANSP, BPBM, CAS, and USNM collections.

Distinguishing features. Dorsal fin rays normally XIII, 9½. Anal fin rays normally III, 5½. Pectoral fin rays 17–18, mostly 18. Pectoral fin large, upper rays branched distally. Dorsal fin spines longer than ½ body depth, membranes deeply incised. Scales ctenoid, about 50–55 vertical scale rows. Coronal spines present. Some branching of head spines in large specimens. Suborbital ridge a single row of spines, not as broad patch of tiny spinules. Supraocular tentacle when present short, less than orbit diameter, and usually absent; not banded with black.

Distribution. *Dendrochirus barberi* is known only from the Hawaiian Islands. It has been collected in depths from near shore to about 50 meters.

Genus **Scorpaenodes** Bleeker

Scorpaenodes Bleeker, 1857, p. 371 (type-species by monotypy, *Scorpaena polylepis* Bleeker, 1851).

Generic synonyms and a discussion of the limits of the genus *Scorpaenodes* are given by Eschmeyer (1969a, pp. 2–3).

Five species of *Scorpaenodes* occur in Hawaiian waters; all are widespread Indo-Pacific species.

Scorpaenodes hirsutus (Smith).

(Figure 3.)

Parascorpaenodes hirsutus Smith, 1957a, p. 63, fig. 5, pl. 1E (original description; as type of new genus; type locality western Indian Ocean, Bazaruto, 21°30′S., 35°30′E.; four paratypes, from Pinda, Bazaruto, and Aldabra; comparisons with *S. kelloggi*).

No Hawaiian references apply to this species.

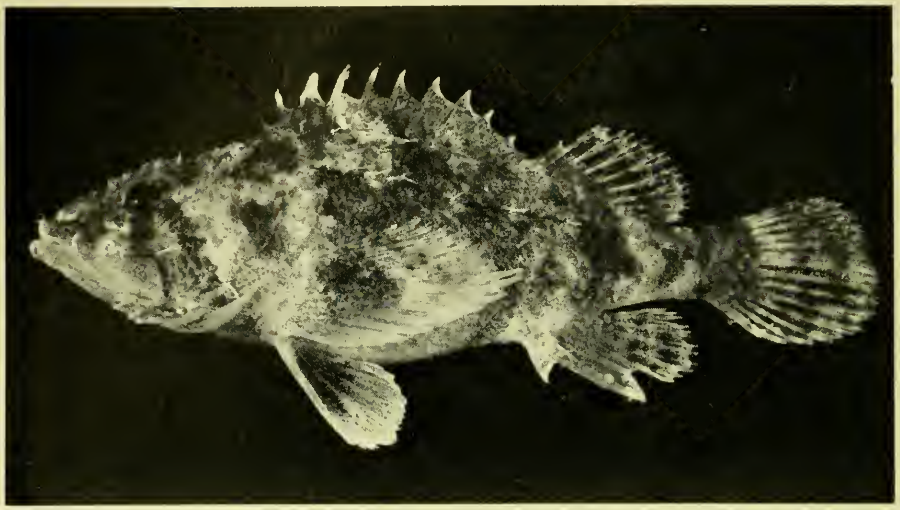

Figure 3. *Scorpaenodes hirsutus*, BPBM 13913, 39 mm. S. L., Rarotonga. (Photograph of fresh specimen.)

Material examined. BPBM 13742 (12, 30.6–41.8), Oahu, Kahe Point, E. Chave, 9 March 1968. CAS 13473, formerly UH 1644 (1, 33.3), Oahu, Hauula Park, W. A. Gosline *et al.*, 11 May 1952.

Distinguishing features. Dorsal fin rays normally XIII, 8½. Anal fin rays III, 5½. Pectoral rays 17–18, usually 17. Vertical scale rows about 30 (as in *S. kelloggi*; see key couplet 5 to separate *hirsutus* and *kelloggi*). Suborbital ridge usually with 4 spines, first on lateral face of lachrymal bone; usually 1 additional spine below suborbital ridge at level between second and third spines. Interorbital spines present. No small spines at midline between tympanic spines.

Distribution. Until now this species has been known only from the type specimens from the western Indian Ocean and a recent listing from Tahiti (Randall, 1973), but it appears that *Scorpaenodes hirsutus* is a widespread Indo-Pacific species. We can report it from the following localities besides Hawaii: Johnston Island (BPBM 13740), Palmyra (BPBM 7787) and Fanning (BPBM 7548) in the Line Islands, Tahiti (BPBM 7809), the Ryukyu Islands (BPBM 8703), Rarotonga (BPBM 13913), and Mauritius (BPBM 16384). CAS specimens are from Ifaluk and Kapingamarangi in the Caroline Islands, Comoro Islands, Chagos Archipelago, Red Sea, and Taiwan. Depths of capture where available are from near shore to 40 meters, and the habitat of this species appears to be coral reef areas.

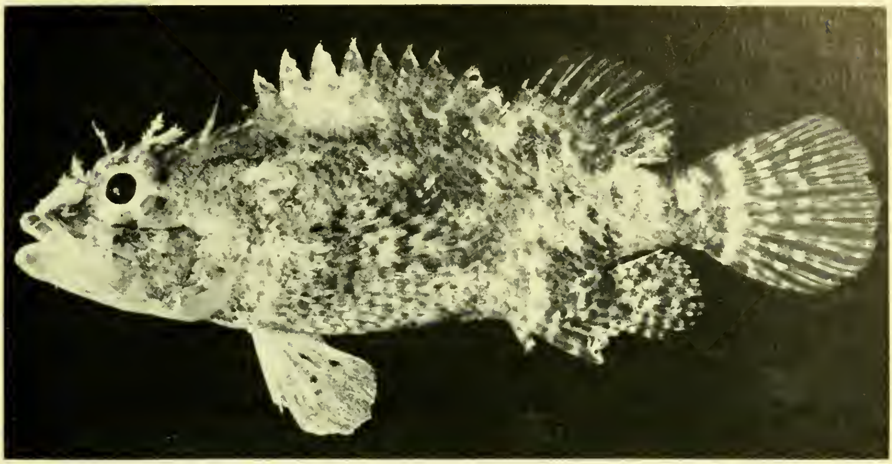

FIGURE 4. *Scorpaenodes kelloggi*, BPBM 8593, 39 mm. S. L., Oahu. (Photograph of fresh specimen.)

Scorpaenodes kelloggi (Jenkins).

(Figure 4.)

(Synonymy based only on Hawaiian references.)

Sebastopsis kelloggi JENKINS, 1903, pp. 492–493, fig. 37 (original description; type locality coral rocks on reef at Honolulu, Hawaii; holotype USNM 50694); SNYDER, 1904, p. 535 (listed, Honolulu); JORDAN & EVERMANN, 1905, pp. 462–463, fig. 202 (description; additional Hawaiian specimens; figure from Jenkins, 1903); JORDAN & SEALE, 1906, p. 374 (abundant at Hawaii; compared with *S. guamensis* and *S. scaber*); BÖHLKE, 1953, p. 124 (location of types).

Scorpaenodes kelloggi: JORDAN & JORDAN, 1922, p. 54 (listed; common on reefs); JORDAN & EVERMANN, 1926, p. 10 (listed); BORODIN, 1930, p. 59 (listed, Pearl Harbor); FOWLER, 1928, p. 290 (synonymy; brief description); FOWLER, 1934, p. 430 (listed); PIETSCHMANN, 1938, pp. 5, 30, pl. 18 (brief description; one specimen from Kaneohe Bay [second specimen and figure possibly *S. hirsutus*]); TINKER, 1944, pp. 266–267, fig. (brief diagnosis; figure of type from Jenkins, 1903); FOWLER, 1949, p. 107 (compiled synonymy); SMITH, 1957a, p. 63 (compared with *S. hirsutus*); SCHULTZ, 1966, pp. 35–36, fig. 142 (figure of type from Jenkins, 1903; remainder of account deals with Marshall and Marianas Islands specimens).

Scorpaenodes guamensis (not of Quoy and Gaimard): TANAKA, 1928, p. 826 (*S. kelloggi* in synonymy).

Scorpaenodes parvipinnis (not of Garrett): GOSLINE & BROCK, 1960, p. 340 (*S. kelloggi* in synonymy).

MATERIAL EXAMINED. USNM 50694 (1, 37.7, holotype of *Sebastopsis kelloggi*) and SU 23306 (1, about 24, paratype of *S. kelloggi*), Oahu, coral rocks at Honolulu, O. P. Jenkins, 1889. BPBM 8593 (9, 21.0–37.5), Oahu, Waimea Bay, in 6–9 meters, J. E. Randall *et al.*, 25 Aug. 1969. BPBM 8594 (1, 32.9), Oahu, Kahe Point, E. Chave, 9 Mar. 1968. BPBM 9787 (5, 19.2–31.9), Oahu, off Makaha Shores Condominium, in 14 meters, small caves in reef, J. E. Randall and A. R. Emery, 26 Apr. 1970. BPBM 10967 (5), Oahu, off Waikiki, in 7.5 meters, sand and small coral head and coral rubble, J. E. Randall, E. Chave, and students, 30 Mar. 1969. BPBM 12288 (4), Oahu, off Pokai Bay in 24 meters, J. E. Randall *et al.*, 29 July 1969. CAS 15689 (3), Oahu, artificial reef off Aina Haina, in 23 meters, J. E. Randall *et al.*, 12 Sept. 1969. Additional Hawaiian material is present in the BPBM and CAS collections.

DISTINGUISHING FEATURES. Dorsal fin rays normally XIII, 8½. Anal fin rays III, 5½. Pectoral fin rays usually 18–19, rarely 20. Vertical scale rows about 30 (as in *S. hirsutus*; see key couplet 5). Suborbital ridge with 3 or 4 spines in a single row. Interorbital spines present. No small spines at midline between tympanic spines.

DISTRIBUTION. *Scorpaenodes kelloggi* is a small species inhabiting coralline areas in depths from near shore to at least 24 meters. It appears to be widespread in the Indo-Pacific. We can report this species from Tahiti (BPBM 8650, 8368), and localities represented by CAS specimens include Palmyra, Raiatea, Palau Islands, Gilbert Islands, Caroline Islands, and Taiwan.

Scorpaenodes parvipinnis (Garrett).

(Figure 5a.)

(Synonymy based only on Hawaiian references.)

Scorpaena parvipinnis GARRETT, 1864, pp. 105–106 (original description; type locality Sandwich Islands [Hawaii]); GÜNTHER, 1873, p. 75, fig. D on pl. 52 (description; Hawaii and Raiatea).

Sebastopsis guamensis (not of Quoy and Gaimard): FOWLER, 1900, p. 535 (one specimen, ANSP 12207).

Sebastopsis parvipennis: SEALE, 1902, p. 20 (specific name misspelled; listed).

Sebastopsis parvipinnis: SNYDER, 1904, p. 535 (listed, Honolulu); JORDAN & EVERMANN, 1905, pp. 462–463 (description; brief synonymy; one specimen taken by the *Albatross*); JORDAN & SEALE, 1906, p. 374 (compiled).

Scorpaenodes parvipinnis: JORDAN & JORDAN, 1922, p. 54 (listed; very rare); JORDAN & EVERMANN, 1926, p. 10 (listed); FOWLER, 1928, p. 290 (synonymy; description; Hawaiian specimens); FOWLER, 1941, p. 257 (one from Hawaii); TINKER, 1944, p. 266 (compiled); FOWLER, 1949, p. 107 (synonymy); GOSLINE & BROCK, 1960, pp. 284, 287, 341, fig. 264 (brief description; in key; line drawing; *S. kelloggi* included in synonymy); GOSLINE, 1965, p. 825 (depth distribution).

MATERIAL EXAMINED. BPBM 7818 (1, 50.8), Oahu, off Waikiki, in 24 meters in coral, J. E. Randall and S. Swerdloff, 3 Sept. 1969. BPBM 7822 (1, 45.0), Oahu, Moku Manu, in 26 meters, J. E. Randall and W. J. Baldwin, 6

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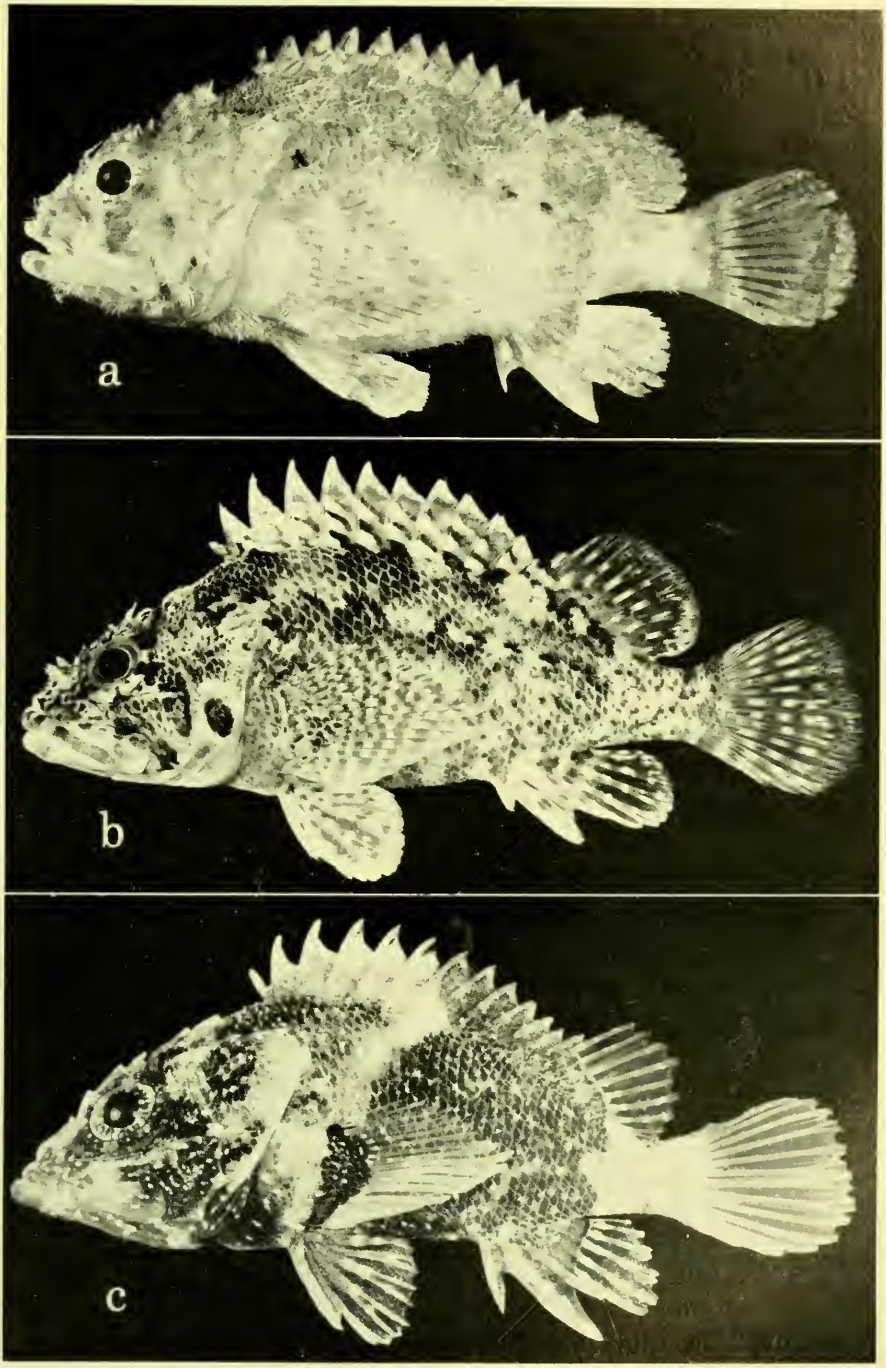
FIGURE 5. a. *Scorpaenodes parvipinnis*, BPBM 7823, 69 mm. S. L., Hawaii. b. *Scorpaenodes littoralis*, BPBM 13732, 80 mm. S. L., Oahu. c. *Scorpaenodes corallinus*, BPBM 13730, 36 mm. S. L., Oahu. (Photographs of fresh specimens.)


a
b
c

Oct. 1969. BPBM 7823 (1, 66.5), Hawaii, Kona Coast, off point at north end of Honaunau Bay, in 43–49 meters, J. E. Randall *et al.*, 16 Aug. 1969. BPBM 7892 (1, 91.3), Oahu, Diamond Head Park, in 2 meters, G. R. Allen, 6 Mar. 1966. BPBM 9859 (3, 48.8–63.6), Oahu, off Lahilahi Point, in 27 meters, J. E. Randall and P. M. Allen, 11 July 1970. BPBM 13741 (1, 94.3), Hawaii, Mauna Loa, lava flow kill, H. Moore on *O'Malley*, 3 June 1950. CAS 13478, formerly UH 1644 (8, 50.4–92.5), Oahu, Hauula Park, W. A. Gosline *et al.*, 11 May 1952. CAS 15696 (2), Oahu, off rocky islet at SW. end of Waimea Bay, 1–10.5 meters J. E. and L. A. Randall and P. M. Allen, 27 July 1970. CAS 15712 (2), Oahu, Waikiki, ½ mi. off Niumalu Hotel, in 7.5–9 meters, W. A. Gosline *et al.*, GVF Reg. no. 54, 7 Sept. 1951. Additional Hawaiian material is available in the BPBM collection.

DISTINGUISHING FEATURES. Dorsal fin rays normally XIII, 9½. Anal fin rays III, 5½. Pectoral fin rays 17–19, usually 18. Scales very strongly ctenoid; vertical scale rows 45–55; interorbital area and snout scaled. Small spines at midline between tympanic spines frequently present. Interorbital spines present. Extra spines usually present on upper rear margin of eye after supraocular spine. Dorsal spines short, usually none longer than orbit diameter. Body often covered with small skin flaps (as in fig. 5a).

This species is distinguished from other species of *Scorpaenodes* by having the suborbital ridge with more than 5 spinous points, usually with 10 or more in adults.

DISTRIBUTION. *Scorpaenodes parvipinnis* has been taken in depths from near shore to about 45 meters in Hawaii. This species occurs widely in the Indo-Pacific from Africa and the Red Sea to the central Pacific.

Scorpaenodes littoralis (Tanaka).

(Figure 5b.)

Sebastella littoralis TANAKA, 1917, p. 10 (original description; type locality Misaki, Japan).

Hawaiian reference:

?*Scorpaenodes guamensis* (not of Quoy and Gaimard): GOSLINE & BROCK, 1960, pp. 284, 287, 341 (brief description; Hawaii).

Scorpaenodes guamensis was reported from Hawaii by Gosline and Brock (1960), but this species does not occur in Hawaiian waters. At least some specimens in the University of Hawaii collection available to Gosline and Brock and labeled *S. guamensis* are specimens which appear to be referable to *S. littoralis* (Tanaka), the type locality of which is Japan.

MATERIAL EXAMINED. BPBM 10059 (2, 41.8–69.0), Oahu, off Pupukea on north shore, in 21 meters, rock and sand bottom, from small cave, J. E. Randall, 9 Aug. 1970. BPBM 10174 (4, 50.0–73.6), Oahu, off Kahana Bay, west side, ¼ mi. out, cave in 26 meters, J. E. Randall, 27 Sept. 1970. BPBM 13731 (2, 55.8–60.9), Oahu, artificial reef off Pokai Bay, in 26 meters, J. E. Randall *et* *al.*, 21 June 1969. BPBM 13732 (2, 67.7–76.5), Oahu, Waimea Bay, west side, large boulders and some sand, J. E. Randall *et al.*, 25 Aug. 1969. CAS 13476, formerly UH 360 (2, 61.3–63.9), Oahu, Hauula Park, W. A. Gosline and class, 28 June 1949. CAS 13477 (1, 73.0), Oahu, Kaena Point, W. A. Gosline and class, 4 Mar. 1950.

Distinguishing features. Dorsal fin rays normally XIII, 9½. Anal fin rays normally III, 5½. Pectoral rays 17–19, usually 18–19. Vertical scale rows about 45. Suborbital ridge with single row of 3 spines. Interorbital spines usually present, sometimes not well marked; small spines at midline between tympanic spines sometimes present.

This species is distinguished from other Hawaiian species of *Scorpaenodes* by the dark spot on the subopercle behind the preopercular spines. General body coloration also is diagnostic.

Distribution. *Scorpaenodes littoralis* has been collected at Hawaii in depths to 26 meters. Habitat appears to be rocky or coral areas and caves. *S. englerti* Eschmeyer and Allen, 1971 (Easter Island) is closely related. We also can report *littoralis*-like specimens from a variety of localities in the Indo-Pacific: Rapa (BPBM 11242, 11247, 11249, 11251, 11255) in depths from about 3 to 27 meters, the Marquesas (BPBM 11111, 11134, 11147) in depths from 4.5–9 to 35–41 meters, Taiwan (USNM uncat.), One Tree Island off Australia (CAS 13855), and Africa (RU 970–142). This complex needs additional study.

Scorpaenodes corallinus Smith.

(Figure 5c.)

Scorpaenodes corallinus Smith, 1957a, pp. 64–65, 68, fig. 5, pl. 3E (original description; type locality western Indian Ocean, Baixo Pinda; paratypes from Mozambique, Matemo, Tekomazi, Zanzibar, Pemba, Kenya, Aldabra, and Assumption).

No Hawaiian references apply to this species.

Material examined. BPBM 6451 (2, 38.2–53.6), Oahu, Moku Manu, west side, cave in 18 meters, rocky bottom, J. E. Randall, E. Reese, G. S. Losey, and L. Harris, 30 Sept. 1968. BPBM 13730 (1, 34.5), Oahu, Kahe Point, Waianae Coast, in 12 meters, G. R. Allen, 7 Sept. 1969. CAS 15724 (1, 34.8), Hawaii, Keahuolu Point, N. of Kailua, 19°38′45″N., 156°01′30″W., in 7.5–12 meters, *Te-Vega* cruise 8, station 366, R. L. Bolin *et al.*, 15 Aug. 1965. Additional BPBM lots from Oahu are available.

Distinguishing features. Dorsal fin rays XIII, 8½. Anal fin rays III, 5½. Pectoral fin rays 17–18. Vertical scale rows in low 40's. Suborbital ridge with 3 spinous points in a single row. Interorbital spines absent or present as a lump; small spines at midline between tympanic spines present.

Body coloration (see figure 5c and Smith, 1957a, pl. 3E) is sufficient to distinguish this species from all other species of *Scorpaenodes*.

DISTRIBUTION. *Scorpaenodes corallinus* was previously known only from the type specimens from the western Indian Ocean and a recent listing from Tahiti (Randall, 1973). Besides the Hawaiian specimens reported above we also can report this species from Moorea in the Society Islands (CAS 15804) at a depth of 9–12 meters, and from the Mentawei Islands in Indonesia (CAS 15805) in .5–2 meters. Depths of capture for the Hawaiian examples are 7.5–12 to 18 meters. Little is known of its habitat or habits. Smith (1957a, p. 64) reported that the species was rather rare, occurred only in coral, and normally was found well below the low tide mark, usually in 1–5 fathoms (2–9 meters).

Genus **Plectrogenium** Gilbert

Plectrogenium GILBERT, 1905, p. 634 (type-species by original designation, *Plectrogenium nanum* Gilbert, 1905).

Plectrogenium is a monotypic genus which Matsubara (1934) treats in a separate subfamily, Plectrogeniinae.

Plectrogenium nanum Gilbert.

(Figure 6.)

Synonymy based only on Hawaiian references:

Plectrogenium nanum GILBERT, 1905, pp. 634–635, fig. 248 (original description; type locality Hawaiian Islands, off north coast of Maui, *Albatross* station 4082, in 220–238 fathoms [435 meters]; holotype USNM 51598; paratypes from *Albatross* stations 3952, 4079–82, 4132); JORDAN & SEALE, 1906, p. 378 (listed); JORDAN & JORDAN, 1922, p. 55 (listed); JORDAN & EVERMANN, 1926, p. 10 (listed); FOWLER, 1928, p. 291 (compiled from Gilbert, 1905); TINKER, 1944, p. 269, fig. (compiled; figure of type from Gilbert, 1905); FOWLER, 1949, p. 107 (compiled); BÖHLKE, 1953, pp. 120–121 (location of types); GOSLINE & BROCK, 1960, pp. 285, 288, 341 (in key; compiled); CLARKE, 1972, p. 313 (submarine observation in 380 meters, off Barbers Point, Oahu).

MATERIAL EXAMINED. USNM 51598 (1, 56.3, holotype of *Plectrogenium nanum*), Maui, north coast off Puniawa Point, in 402–445 meters, bottom of gray sand, 10-ft. Blake trawl, *Albatross* station 4082, 21 July 1902. SU 8652 (4, paratypes of *P. nanum*), Hawaiian Islands, *Albatross*, no other data. BPBM 13738 (10, 46.3–55.4), CAS 15704 (18) and CAS 31300 (2, cleared and stained), Lanai, Kealaikahiki Channel, 20°38.1′–41.3′N., 155°41.1′–41.0′W., in 292 meters, shrimp trawl, *Townsend Cromwell* cruise 33, station 38, 9 Nov. 1967. CAS 15700 (3, 49.1–52.3) and CAS 15702 (1, cleared and stained), Hamakua, off coast of Hawaii, 19°54′–57′N., 155°03.1′–04.8′W, in 280 meters, shrimp trawl, *Townsend Cromwell* cruise 35, station 8, 29 Mar. 1968. Additional paratypes are present in the USNM collection. Additional *Townsend Cromwell* specimens are in the NMFS collection.

DISTINGUISHING FEATURES. Dorsal fin rays normally XII, 7½. Anal fin rays III, 5½. Pectoral fin rays 22–24. Scales ctenoid, about 30–35 vertical scale rows. Suborbital ridge with very well developed flat spines (somewhat

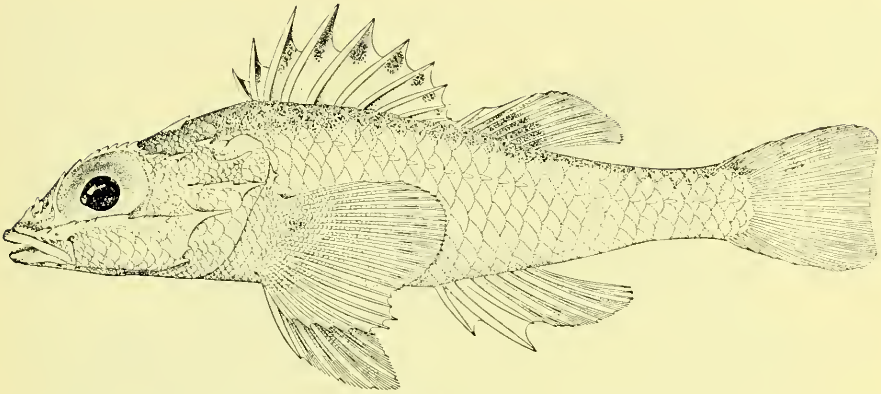


FIGURE 6. *Plectrogenium nanum*, USNM 51598, off north coast of Maui. (Figure from Gilbert, 1905, fig. 248, but modified by addition of more dusky pigment.)

as in platycephalids). A number of extra spines on head, particularly on lachrymal bone and above orbits. Dorsal fin divided into 2 fins, second fin headed by 2 spines. Mouth somewhat ventral in location.

Body shape is diagnostic for this species. The normal presence of 7½ soft dorsal rays together with the high pectoral ray count characterizes this species.

DISTRIBUTION. *Plectrogenium nanum* is a small species and apparently is very common in the Hawaiian Islands in the depth range of 274 to 640 meters; Struhsaker (1973) indicates a peak in abundance at depths of 300 to 450 meters based on *Townsend Cromwell* trawling operations. This species is also known from Japan (Matsubara, 1943, pp. 330–335).

Genus **Taenianotus** Lacépède

Taenianotus LACÉPÈDE, 1802, p. 304 (type-species *Taenianotus triacanthus* Lacépède, by subsequent designation of Cuvier *in* Cuvier & Valenciennes, 1829, p. 371).

Taenianotus triacanthus Lacépède.

(Figure 7.)

Taenianotus triacanthus LACÉPÈDE, 1802, pp. 305, 308 (original description; no type locality). Hawaiian references:

Taenianotus garretti GÜNTHER, 1873, p. 83, fig. C on pl. 57 (original description; type locality Hawaiian Islands); JORDAN & EVERMANN, 1905, p. 471 (compiled from Günther, 1873); JORDAN & SEALE, 1906, p. 378 (name only); JORDAN & JORDAN, 1922, p. 55 (listed); SCHULTZ, 1938, p. 206 (suggested *garretti* may be distinct from *triacanthus* if Günther's figure were accurate).

Taenianotus citrinellus GILBERT, 1905, pp. 636–637, pl. 81 (original description; type locality Hawaiian Islands, south of Molokai, in 43–73 fathoms, *Albatross* station 3849; holotype USNM 51634); JORDAN & SEALE, 1906, p. 378 (name only); JORDAN & JORDAN, 1922, p. 55 (listed; compiled locality data); BORODIN, 1930, p. 59 (Pearl Harbor record; reference to Fowler).

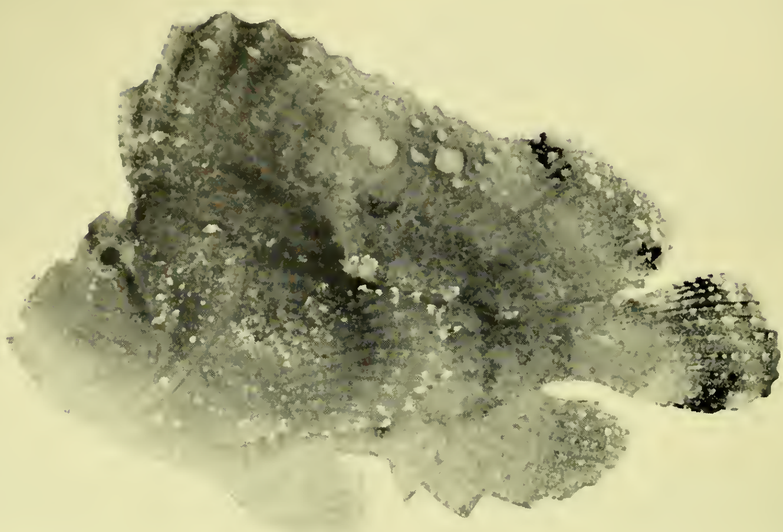


FIGURE 7. *Taenianotus triacanthus*, BPBM 6205, 47 mm. S. L., Oahu. (Photograph of fresh specimen.)

Taenianotus triacanthus: FOWLER, 1923, p. 387 (listed; Honolulu); FOWLER, 1925, p. 27 (listed); JORDAN, 1925, p. 21 (listed); FOWLER, 1928, pp. 296–297 (synonymy; *garretti* and *citrinellus* in synonymy; Hawaiian specimens); FOWLER, 1934, p. 431 (reference to Borodin, 1930); SCHULTZ, 1938, p. 206 (brief description; color phases; *citrinellus* a synonym); TINKER, 1944, p. 272, fig. (brief description; figure from Gilbert, 1905); GOSLINE & BROCK, 1960, pp. 284, 285, 341 (in key; brief description; synonymy); GOSLINE, 1965, p. 825 (depth distribution).

The type localities of *garretti* and *citrinellus* are Hawaii. They have been recognized as color phases of *Taenianotus triacanthus* for a number of years.

MATERIAL EXAMINED. USNM 51634 (1, 35.8, holotype of *Taenianotus citrinellus*), south coast of Molokai, N. 71° and W. 21.9′ from Lae-o Ka Laau Light, 10-ft. Blake trawl in 134–79 meters, bottom of coarse sand, broken shells and coral, *Albatross* station 3849, 8 April 1902. BPBM 4405 (1, 60.5), Oahu, Kahala, C. M. Cooke, Jr., 17 March 1919. BPBM 4406 (2, 51.2–56.6), Oahu, C. M. Cooke, Jr., 3 Dec. 1923. BPBM 4891 (1, 59.4), Oahu, Laie, C. M. Cooke III, 15 Jan. 1939. BPBM 6203 (1, 45.3), Oahu, Ala Moana Reef, 200 feet from shore in .5 meters, S. M. Trefz, 17 April 1966. BPBM 6984 (1, 38.2), Oahu, Diamond Head Park, in 2 meters, G. R. Allen, March 1968. BPBM 8821 (1, 37.9), Oahu, Makua, in 12 meters, G. R. Allen, March 1968. BPBM 9777 (1, 41.0), Oahu, off Makaha Shores Condominium, small caves in reef, in 14 meters, J. E. Randall and A. R. Emery, 26 April 1970. BPBM 10628 (2, 56.5–59.7), Oahu, Hanauma Bay, G. R. Allen, June 1965. BPBM 10950 (1, 29.0), Oahu, Waimea Bay, in 3–6 meters, G. R. Allen, July 1970. CAS 15691 (2, 35.7–52.8), Oahu, Waimea Bay, among large boulders with some sand, at west side of Waimea Bay, in 6–9 meters, J. E. Randall *et al.*, 25 Aug. 1969. Additional Hawaiian material is available in the BPBM and NMFS collections.

Distinguishing features. Dorsal fin rays usually XII, 10½. Anal fin rays III, 6½ (sometimes III, 5½). Pectoral rays usually 14 (sometimes 15), all rays unbranched. Dorsal fin high, 3rd or 4th spine longest. Scales as small spiny papillae. Suborbital ridge without spines, or with lump at end of ridge. Preopercle with 2 indistinct spines only.

This species is characterized by having the body extremely compressed, the soft dorsal fin attached to the caudal fin, and the fewest pectoral rays (usually 14) of any Hawaiian scorpionfish.

Distribution. *Taenianotus triacanthus* is a widespread, shallow water Indo-Pacific species occurring from Africa to the central Pacific. Depths of capture in Hawaii ranged from .5 to 14 meters, with one trawled from 79–134 meters.

Remarks. The coloration of this species is variable, from nearly all yellow, to red, brown, or nearly black, and variously mottled with darker pigment. Coloration evidently is related partly to shedding of a cuticular layer containing algae (see Wickler and Nowak, 1969).

Genus **Iracundus** Jordan and Evermann

Iracundus Jordan & Evermann, 1903b, pp. 209–210 (type-species *Iracundus signifer* Jordan and Evermann, 1903b, by original designation, monotypic).

Iracundus signifer Jordan and Evermann.

(Figure 8.)

Iracundus signifer Jordan & Evermann, 1903b, p. 210 (original description; type locality Hawaiian Islands; one specimen from coral reef at Honolulu; holotype USNM 50886); Jordan & Snyder, 1904b, p. 126 (one specimen from Honolulu market); Jordan & Evermann, 1905, pp. 470–471, fig. 207 (mostly compiled from Jordan and Evermann, 1903b, additional Hawaiian specimens; figure of holotype); Jordan & Seale, 1906, p. 374 (name only; Hawaii); Jordan & Jordan, 1922, p. 55 (listed); Fowler, 1923, p. 387 (listed; Honolulu); Fowler, 1925, p. 27 (listed); Jordan, 1925, p. 20 (listed); Jordan & Evermann, 1926, p. 10 (listed); Fowler, 1928, p. 292 (synonymy; description; Hawaiian specimens); Tinker, 1944, p. 269, fig. (compiled; figure of type from Jordan and Evermann, 1905); Fowler, 1949, p. 107 (compiled); Gosline & Brock, 1960, pp. 284, 286, 341 (in key; compiled); Gosline, 1965, p. 825 (listed); Madden, 1973, p. 145 (from salvaged vessel; luring behavior); Shallenberger & Madden, 1973, pp. 33–47, figs. 1–6 (luring behavior; aspects of biology).

Non-Hawaiian reference:

Iracundus signifer rarotongae Whitley, 1965, pp. 113–114 (original subspecies description; type locality Cook Islands, Rarotonga; holotype AMS IA5226).

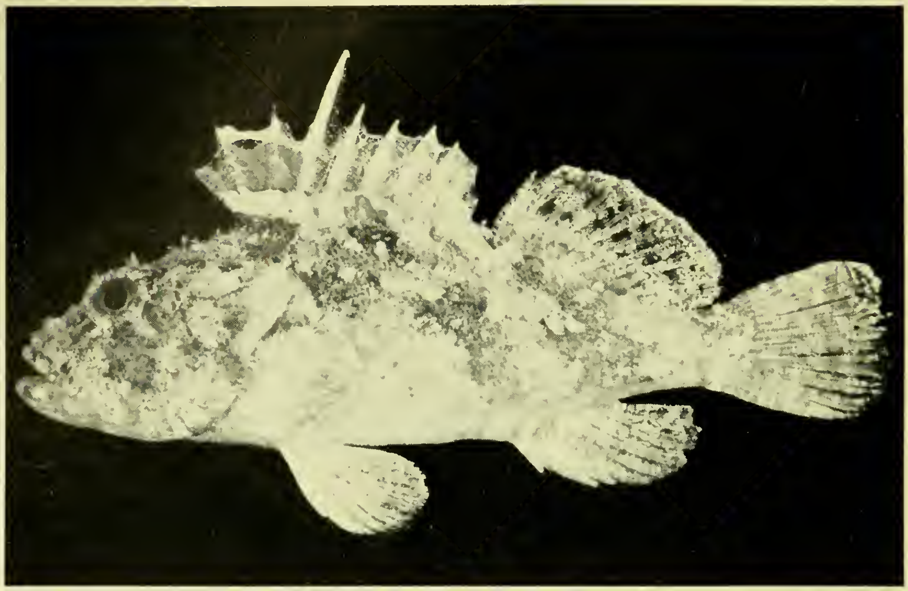


FIGURE 8. *Iracundus signifer*, BPBM 6354, 91 mm. S. L., Oahu. (Photograph of fresh specimen.)

REMARKS. Whitley (1965, pp. 113–114) described *Iracundus signifer rarotongae* from Rarotonga Island in the Cook Islands. The type (AMS IA5226) was examined by Eschmeyer. The differences reported by Whitley between *I. s. rarotongae* and *I. s. signifer* do not appear to be valid ones. Whitley reported that his subspecies had one more pectoral ray (18), but we find many Hawaiian examples with 18 pectoral rays. Whitley reported 39 scale rows above the lateral line but Eschmeyer counts about 70 vertical scale rows for Whitley's type. Whitley gives the gill rakers as 6 + 10, but the type has 6 or 7 + 11, including rudiments. Other differences reported by Whitley seem to result from incorrect interpretation of Jordan and Evermann's account of this species. At the time of Whitley's description of *I. signifer rarotongae, I. signifer* was known only in Hawaiian waters; we now know that the species is widespread in the Indo-Pacific (see below). We feel that the Cook Island population is not subspecifically distinct.

MATERIAL EXAMINED. USNM 50886 (1, 77.8, holotype of *Iracundus signifer*), Oahu, reef at Honolulu, U. S. Fish Commission. BPBM 6354 (3, 86.9–97.4), Oahu, Kahe Point Beach State Park, reef in 10.5 meters, J. E. Randall, G. R. Allen, *et al.*, 30 March 1968. BPBM 7319 (2, 45.2–53.4), Oahu, off Lahilahi Point, near cave in 27–30 meters, coral rubble, J. E. Randall and University of Hawaii students, 10 Aug. 1968. BPBM 7924 (6, 54.8–78.3), Oahu, Moku Manu, in 49 meters, J. E. Randall, W. J. Baldwin, and A. Stark, 9 Oct. 1968. CAS 24990 (18), Oahu, SE. of Poka Bay, Waianae coast, caves adjacent to coral rubble and sand in 21–30 meters, J. E. Randall *et al.*, 20 July 1969. SU 8602 (1), Oahu, Honolulu, E. L. Berndt. Additional Hawaiian material is available in the BPBM collection.

Distinguishing features. Dorsal fin rays usually XII, 9½. Anal fin rays III, 5½. Pectoral rays usually 18 (sometimes 17; 19 should be expected). Palatine teeth absent. Scales ctenoid; about 65–75 vertical scale rows. Lachrymal bone with 2 spines over maxillary; first points forward; second broad, pointing out and to rear. Suborbital ridge without spines except one at rear before preopercle. Preopercular spines short, usually only 3 developed; no supplemental preopercular spine at base of first spine.

This species is characterized by a dark spot on the spinous dorsal fin between spines 1 or 2 and 3, and vertical scale rows of about 70. The fourth dorsal spine is characteristically elongate in specimens over about 50 or 60 mm. S. L.

Distribution. *Iracundus signifer* occurs in Hawaiian waters in coral rubble areas, particularly in or near concealed locations beneath ledges or in caves, in depths from about 10.5 to 61 meters. William D. Madden (1973, p. 141, and pers. comm.) reports capture of specimens inside a sunken hull raised from 67 meters. Although this species is known in the literature only from the Hawaiian Islands and from the Cook Islands (type of *I. s. rarotongae*), we suspect it is widely distributed in the Indo-Pacific. Randall has taken specimens from several localities in French Polynesia and from Mauritius.

Genus **Setarches** Johnson

Setarches Johnson, 1862, p. 177 (type-species *Setarches güntheri* Johnson, 1862, by monotypy).

This genus has been treated on a world basis by Eschmeyer and Collette (1966, pp. 355–356).

Setarches guentheri Johnson.

(Figure 9.)

Setarches güntheri Johnson, 1862, pp. 177–179, pl. 23 (original description; type locality Madeira).

Synonymy of Hawaiian references only:

Scorpaena remigera Gilbert & Cramer, 1897, pp. 404, 418–419, pl. 40 (original description; type locality off Hawaiian Islands, in 298 fathoms, *Albatross* station 3476, holotype USNM 47726); Böhlke, 1953, p. 121 (location of types).

Setarches remiger: Gilbert, 1905, p. 634 (brief description; new combination; additional specimens from Hawaii); Jordan & Seale, 1906, p. 377 (name only, Hawaii); Jordan & Jordan, 1922, p. 55 (listed; common in deepwater); Fowler, 1928, pp. 291–292 (synonymy; description from Gilbert and Cramer); Tinker, 1944, p. 270, text fig. (compiled; figure from Gilbert and Cramer, 1897); Fowler, 1949, p. 107 (compiled);

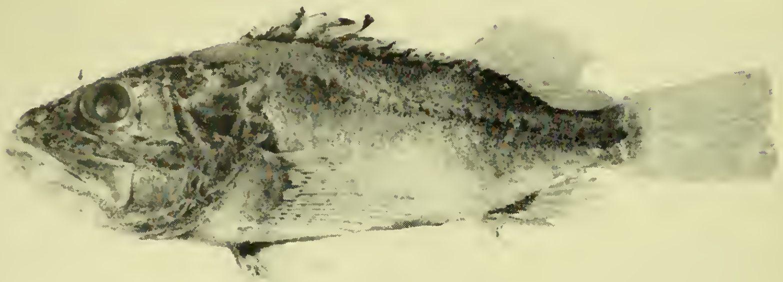


FIGURE 9. *Setarches guentheri*, BPBM 29322, 109 mm. S. L., north of Maui. (Photograph of preserved specimen.)

GOSLINE & BROCK, 1960, pp. 285, 341 (in key; compiled); CLARKE, 1972, p. 313 (submarine observation in 310 meters, off Barbers Point, Oahu).

Setarches guentheri: ESCHMEYER & COLLETTE, 1966, pp. 358–360 (*remigera* in synonymy; description; distribution; remarks).

The reader is referred to Eschmeyer and Collette (1966) for a thorough treatment of this species.

MATERIAL EXAMINED. USNM 47726 (1, 83.2, holotype of *Scorpaena remigera*), south of Oahu, 21°09′N., 157°53′W., in 545 meters *Albatross* station 3476, 6 Dec. 1891. BPBM 14109 (16, 66.3–88.0) and CAS 29322 (16, 68.6–92.5), north of Maui, 21°10.1′–10.6′N., 156°25.8′–33.2′W., 41-ft. shrimp trawl in 494–512 meters, *Townsend Cromwell* cruise 35, station 17, 1 April 1968. Additional specimens are available in the BPBM, USNM, and NMFS collections; paratypes of *S. remigera* are present in the USNM and SU collections. (Counts in tables 1 and 2 based on BPBM 14109 and CAS 29322, not from Eschmeyer and Collette, 1966.)

DISTINGUISHING FEATURES. Dorsal fin rays normally XII, 10½. Anal fin rays III, 5½. Pectoral fin rays in Hawaiian specimens 20–22, mostly 21. Body covered by tiny cycloid scales. Lateral line more or less a continuous trough covered by thin membranous scales (these covering scales usually lost during capture) as in *E. imus*. Body grayish or pinkish in coloration. Distinguishable from *E. imus* by having 5½ rather than 6½ anal soft rays, higher average number of pectoral rays, and orbit diameter about equal to interorbital width rather than about ½ interorbital width.

Distribution. *Setarches guentheri* occurs in offshore areas from Hawaii circumtropically west to the western Atlantic (Eschmeyer and Collette, 1966). In Hawaiian waters the *Albatross* took specimens at 14 stations (see Gilbert, 1905) between about 350 and 550 meters (with one station in 177–364 and one in 351–644 meters). The *Townsend Cromwell* captured a total of 184 specimens from 21 stations in the depth range 238–686 meters (Struhsaker, 1973). *Setarches guentheri* is a bottom or near-bottom species which may feed only on pelagic organisms (Eschmeyer and Collette, 1966).

Genus **Ectreposebastes** Garman

Ectreposebastes Garman, 1899, p. 53 (type-species *Ectreposebastes imus* Garman, 1899, by monotypy).

This genus has been treated on a world basis by Eschmeyer and Collette (1966, pp. 366–367).

Ectreposebastes imus Garman.

(Figure 10.)

Ectreposebastes imus Garman, 1899, pp. 53–55, pls. 7, 9, fig. 1 on pl. 71 (original description; type locality Galapagos Islands, *Albatross* station 3403, 702 meters).

Hawaiian references:

Ectreposebastes imus: Eschmeyer, 1969b, p. 104 (new record for Hawaii based on personal communication from P. Struhsaker); Collette & Uyeno, 1972, pp. 26–28, fig. 1 (*Pontinus niger* Fourmanoir, 1970, as a synonym; range including Hawaii; first record for Japan; various comments; good figure).

The reader is referred to Eschmeyer and Collette (1966) for a more thorough treatment of this species, and to Collette and Uyeno (1972) for recent range extensions and references.

Pontinus niger Fourmanoir, type locality near the Marquesas Islands, was placed in the genus *Ectreposebastes* and synonymized with *E. imus* by Collette and Uyeno (1972). Examination by Eschmeyer of a specimen from the south central Pacific at 10°51′–29′S., 123°28′–48′W. (SIO 73–43), the specimen reported by Collette and Uyeno from near New Caledonia at 22°02′S., 167°57′E. (USNM 206500), along with notes made by Collette on the holotype of *P. niger*, indicate that *E. niger* possibly is a valid species differing most notably in having scales noticeably larger than in specimens of *E. imus* from other areas. There also may be differences in depth of the caudal peduncle, pectoral fin length, and length of lachrymal and preopercular spines. A detailed comparison of specimens from different populations is needed.

Material examined. BPBM 14110 (18, 82.5–140) and CAS 29321 (33, 76.3–135), Kaiwi Channel between Oahu and Molokai, 21°08.8′–07.4′N., 157° 42.2′–49.6′W., in 585–640 meters, 41-ft. shrimp trawl, *Townsend Cromwell*

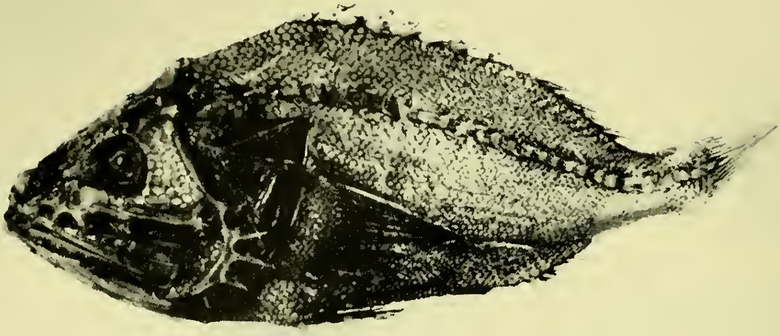


FIGURE 10. *Ectreposebastes imus*, CAS 29321, 88.7 mm. S. L., between Oahu and Molokai. (Photograph of preserved specimen.)

cruise 36, station 31, 6 May 1968. Additional Hawaiian specimens are available in the NMFS collection.

DISTINGUISHING FEATURES. Dorsal fin rays usually XII, 10½. Anal fin rays III, 6½. Pectoral fin rays usually 19 or 20. Body delicate, flabby, with weak fin spines and poor ossification. Scales tiny and cycloid. Lateral line more or less a continuous trough covered by thin membranous scales (these covering scales usually lost during capture) as in *S. guentheri*. Juveniles black, adults maroon and black.

This species may be distinguished from all species except *Setarches guentheri* on the basis of its characteristic lateral line. It differs from *Setarches guentheri* in having 6½ rather than 5½ anal rays, 3 rather than 2 prominent lachrymal spines, and interorbital width about twice orbit rather than about equal to orbit.

DISTRIBUTION. *Ectreposebastes imus* is known from the eastern and western Atlantic, the southeastern Pacific off the Galapagos Islands and Peru, Hawaii, and Japan.

It is an offshore, near-bottom species occurring in depths of about 150 to about 850 meters, excluding those depths deeper than 850 meters where the specimens may have been captured during retrieval of nets. Some captures have been made by midwater trawl hauls well off the bottom, and Eschmeyer and Collette (1966) suggest that this fish is the most modified of scorpionfishes for life in midwater. Struhsaker (1973) states that the species may occur near bottom during the day and undertake vertical feeding migrations into midwater areas at night. In Hawaiian waters the *Townsend Cromwell* took specimens at five bottom trawl stations in depths between 567 and 686 meters. Two hundred twenty-one specimens were taken on cruise 36 at station 31 (see Material examined) in 622 meters during daytime hours while a repeat tow in the same area at night resulted in only 2 specimens (Struhsaker, 1973).

Genus **Phenacoscorpius** Fowler

Phenacoscorpius FOWLER, 1938a, pp. 69–70 (type-species *Phenacoscorpius megalops* Fowler, 1938a, by original designation).

This genus has been discussed by Eschmeyer (1965b, pp. 522–523).

Phenacoscorpius megalops Fowler.

(Figure 11.)

No Hawaiian literature applies to this species.

Phenacoscorpius megalops FOWLER, 1938a, pp. 70–71, fig. 30 (original description; type locality Philippine Islands, *Albatross* station 5387, in 209 fathoms, 11 March 1909; plus a series of paratypes from the Philippines and East Indies); Böhlke, 1953, p. 120 (location of types); ESCHMEYER, 1965b, pp. 522–523 (compared with an Atlantic species).

MATERIAL EXAMINED. BPBM 13761 (1, 29.3), Oahu, 6 miles off Makapuu Point in direction of Molokai, depth of 366 meters, collected with pink coral, W. D. Madden, 5 May 1972. BPBM 16416 (1, about 51, poor condition), Oahu, Kaiwi Channel off Makapuu Pt., depth 366 meters, collected with pink coral from submarine, presented by W. D. Madden, 11 Feb. 1974. (The holotype, USNM 98903, and some paratypes, SU 40198–40200, of *Phenacoscorpius megalops* were examined.)

DISTINGUISHING FEATURES. (Based also on specimens from the Philippines.) Dorsal fin rays XII, 9½. Anal fin rays III, 5½. Pectoral fin rays usually 17. Palatine teeth absent. Scales on sides weakly ctenoid; about 55 (?) vertical scale rows. Lachrymal bone with 2 spines over maxillary; first as a broad lobe, second as a broad spine pointing down. Suborbital ridge well marked, with 5 or 6 or more spines. Second preopercle spine small or absent.

This species is easily distinguished from other Hawaiian scorpionfishes by having only the anterior 4 or 5 tubed lateral line scales present, with the remainder of the lateral line absent. The large melanophores on the caudal peduncle are also characteristic.

Coloration in life is mostly red.

DISTRIBUTION. *Phenacoscorpius megalops* is known from the Philippine Islands and the East Indies and now from Hawaii in reported depths of 68–622 meters. A wider distribution in the central Pacific Ocean is expected when these depths are sampled more thoroughly.

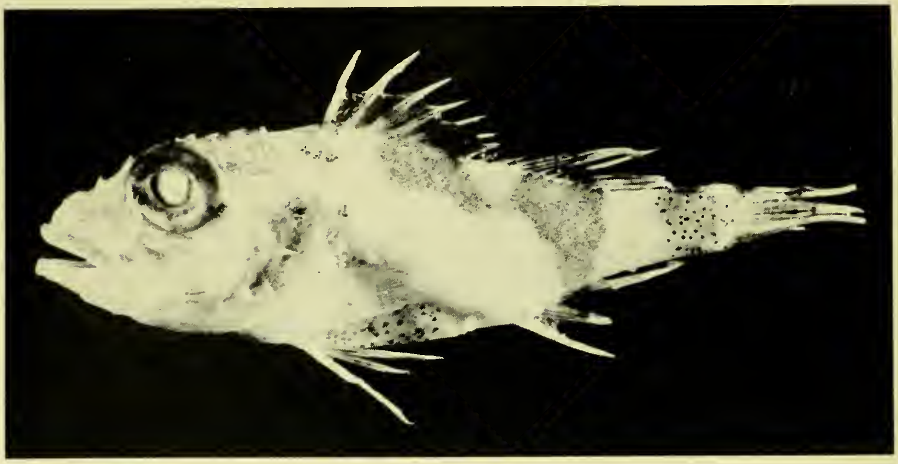


FIGURE 11. *Phenacoscorpius nebris,* BPBM 13761, 29.3 mm. S. L., Oahu. (Photograph of preserved specimen.)

Genus **Pontinus** Poey

Pontinus POEY, 1860, p. 172 (type-species *Pontinus castor* by inference from text (see Eschmeyer, 1965b, p. 527) or by subsequent designation of Jordan and Gilbert, 1883, p. 669).

Generic synonyms and nomenclatural problems are discussed by Eschmeyer (1965b, pp. 526–528).

Pontinus macrocephalus (Sauvage).

(Figure 12.)

Sebastes macrocephalus SAUVAGE, 1882, pp. 169–170 (original description; type locality Hawaiian Islands, collected by Ballieu).

Merinthe macrocephala: SNYDER, 1904, p. 535 (brief description; 2 specimens from Honolulu); JORDAN & EVERMANN, 1905, p. 461, pl. 55 (description; two specimens from Hawaii); JORDAN & SNYDER, 1907, p. 217 (common in winter market; brilliant orange with sparse dots and mottlings); JORDAN & JORDAN, 1922, p. 55 (name; size; deep-water); JORDAN, 1925, p. 20 (variation in skin appendages; color description); FOWLER, 1925, p. 27 (listed); JORDAN & EVERMANN, 1926, p. 10 (listed); FOWLER, 1928, p. 291 (synonymy; description); FOWLER, 1931, p. 349 (description of 2 specimens from Honolulu market); TINKER, 1944, p. 267, fig. (compiled brief description; figure from Jordan and Evermann, 1905); FOWLER, 1949, p. 107 (compiled literature reference); GOSLINE & BROCK, 1960, pp. 285, 288, 341, fig. 266 (in key; brief characterization; figure from Jordan and Evermann, 1905); GOSLINE, 1965, p. 825 (depth distribution).

Pontinus spilistius GILBERT, 1905, pp. 633–634, fig. 247 (original description; type locality Hawaiian Islands, off Maui, in 174–238 meters, *Albatross* station 4077; Holotype USNM 51644); JORDAN & SEALE, 1906, p. 377 (listed); JORDAN & JORDAN, 1922, p. 55 (listed); JORDAN & EVERMANN, 1926, p. 10 (listed); FOWLER, 1928, p. 291 (compiled from Gilbert, 1905); BORODIN, 1930, p. 59 (listed, Oahu); TINKER, 1944, p. 268, fig. (brief

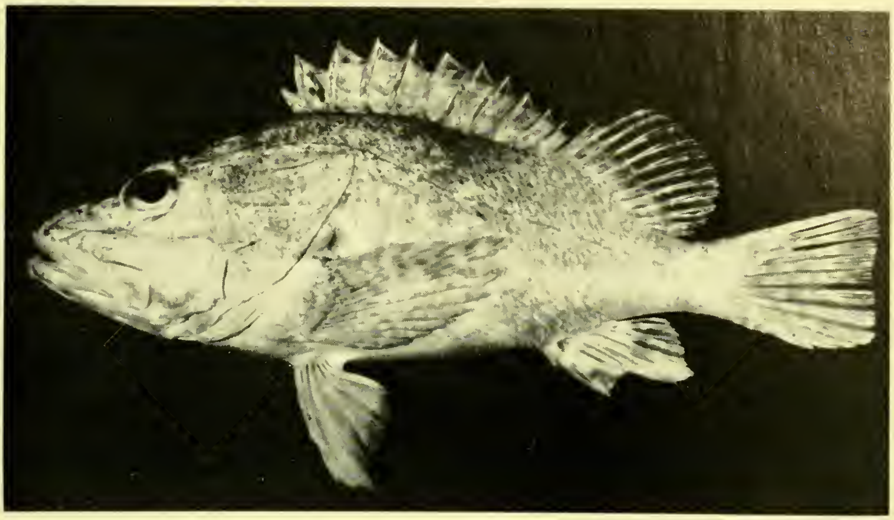


Figure 12. *Pontinus macrocephalus*, BPBM 10573, 285 mm. S. L., Honolulu fish market. (Photograph of fresh specimen.)

description compiled; figure of type from Gilbert, 1905); Fowler, 1949, p. 107 (compiled literature reference); Böhlke, 1953, p. 121 (location of types); Gosline & Brock, 1960, pp. 285, 289, 342 (in key; compiled).

Pontinus macrocephalus: Eschmeyer, 1969b, p. 24 (*spilistius* a synonym; *macrocephalus* restricted to Hawaii); Clarke, 1972, p. 313 (submarine observations and gill-net capture, off Oahu, in 120–300 meters).

Remarks. *Pontinus spilistius* appears to be based on juveniles of *Pontinus macrocephalus*. Specimens under about 100 mm. S. L. have a dark spot on the spinous dorsal fin but this is absent or not well marked in large specimens. Small specimens have the eye almost as large as the snout while the eye is proportionally smaller in large specimens. The supraocular tentacle often is absent; when present it may be two or more times the size of the eye.

Material examined. MNHN A. 4165 (1, about 365, holotype of *Sebastes macrocephalus*), Hawaii, collected by Ballieu, no other data. USNM 51644 (1, 67.7, holotype of *Pontinus spilistius*), Maui, off north coast, Puniawa Point, S. 45°45′, E. 6.1′, in 181–194 meters, bottom of fine coral sand and foraminifera, 10-ft. Blake trawl, *Albatross* station 4077, 21 July 1902. USNM 51663 (1, 47.1, paratype of *P. spilistius*) and SU 8638 (1, 44.3, paratype of *P. spilistius*), Maui, off north coast, Puniawa Point, S. 52°30′, E. 6.5′, in 174–238 meters bottom of coral, sand and foraminifera and rock, 10-ft. Blake Trawl, *Albatross* station 4098. ANSP 66366–67 (2, 192–210), Oahu, Honolulu, R. Wehrl, 1929. BPBM 4386 (2, 270–360), Oahu, Honolulu, J. W. Thompson. BPBM 7944 (1, 340), Oahu, Campbell Park, Waianae, in 183 meters, gill net, T. A.

Clarke, and P. Struhsaker, 11 Dec. 1968. BPBM 8150 (1, 127), Oahu, off Campbell Industrial Park, Barber's Point, in 183–219 meters, T. A. Clarke, 14–15 Dec. 1968. BPBM 10573 (1, 285), Oahu, Honolulu fish market, J. E. and H. A. Randall, 7 Oct. 1969. BPBM 13736 (2, 67.2–99.5), CAS 15703 (2, 67.3–103) and USNM 214048 (3, 60.0–82.5), off Hawaii, Hamakua coast, 20°07.2–08.3′N., 155°24.7–28.2′W., in 238–252 meters, shrimp trawl, *Townsend Cromwell* cruise 35, station 12, 30 Mar. 1968. USNM 88259 (2, 205–206), Oahu, Honolulu, H. W. Fowler. USNM 151639 (1, 196), Oahu, Honolulu, E. K. Jordan.

DISTINGUISHING FEATURES. Dorsal fin rays normally XII, 10½, sometimes XII, 9½. Anal fin rays III, 5½. Pectoral fin rays 16–17, usually 17. Scales ctenoid; about 45–50 vertical scale rows. Lachrymal bone with 2 spines over maxillary, first points out and back, second points mostly back. Suborbital ridge with 3 or 4 spines. Second preopercular spine usually absent in large specimens. Mostly red in life.

The pectoral rays are unbranched in adults of this species (as in *Taenianotus* and *Pterois*). *Pterois* differs in having 13 dorsal spines and *Taenianotus* in having 15 or fewer pectoral rays, among other features. Most difficulty comes in separating small specimens of *Pontinus* from *Scorpaena* or *Scorpaena*-like specimens, such as ones of *Neomerinthe rufescens,* when the specimens are at a size at which their pectoral rays are still unbranched (usually under 30 or 40 mm. S. L.). Useful characters for separating small specimens include counts (tables 1–2), presence or absence of a dark spot on the spinous dorsal fin (present in juveniles of *P. macrocephalus* and a few other species), as well as general coloration, depth of capture, and lachrymal and suborbital spination. See also the account of *Neomerinthe rufescens.*

DISTRIBUTION. *Pontinus macrocephalus* is an upper slope species. Depths of capture range from about 180 to 250 meters, with one collection from the range 174–278 meters. We know this species only from the Hawaiian Islands (see Eschmeyer, 1969b, p. 24).

Genus **Scorpaenopsis** Heckel

Scorpaenopsis HECKEL, 1837, p. 159 (type-species *Scorpaena gibbosa* Schneider *in* Bloch and Schneider, 1801, by subsequent designation of Bleeker, 1876, p. 4; not an originally included species but Bleeker synonymized it with *nesogallica* Cuvier *in* Cuvier and Valenciennes on p. 28 of the same work; see Article 69(a)(iv), International Code of Zoological Nomenclature, 1964).

Scorpaenichthys BLEEKER, 1856, pp. 388, 402 (type-species *Scorpaena gibbosa* Schneider *in* Bloch and Schneider, 1801, by subsequent designation of Jordan, 1919, p. 267; preoccupied by *Scorpaenichthys* Girard, 1854, p. 161, a genus of cottid fishes).

Dendroscorpaena SMITH, 1957a, pp. 51, 60 (replacement name for *Scorpaenichthys* Bleeker, 1856; therefore taking the same type-species as *Scorpaenichthys* Bleeker, despite the statement by Smith on p. 60 "Genotype *Perca cirrhosa* Thunberg, 1793"; see Article 67(i), International Code of Zoological Nomenclature, 1964).

The genus *Scorpaenopsis* consists of two groups of species: humpbacked ones and non-humpbacked ones. Smith (1957a) recognized each group as a separate genus, *Scorpaenopsis* for the former and *Dendroscorpaena* for the latter. As discussed in the synonymy above, Smith wrongly thought the type-species of *Dendroscorpaena* was the non-humpbacked species *cirrhosa* when in fact the type-species was the humpbacked species *gibbosa*. We agree, however, with Matsubara (1943) that all species should be placed in one genus. Of the four humpbacked species, one has only a slight hump (*S. neglecta*).

The differences between *Scorpaenopsis* and *Scorpaena* are few, the major difference being that species of *Scorpaena* have palatine teeth while species of *Scorpaenopsis* lack palatine teeth. We suspect that palatine teeth have been lost more than once in different *Scorpaena*-like species. Most of the species usually referred to *Scorpaenopsis* seem more closely related to each other than to the species in various subgroups of *Scorpaena*, but there are a few species which stand apart. They are usually placed in *Scorpaenopsis* because they lack palatine teeth. Among these are *S. fowleri* and *S. altirostris* from Hawaii. On the other hand, there are a few species of the genus *Scorpaena* which seem perhaps more closely related to species of *Scorpaenopsis* than to subgroups of *Scorpaena*, for example, *Scorpaena orgila* from Easter Island. So the limits of *Scorpaenopsis* and *Scorpaena* are unclear, as are the differences between them. We have allocated the Hawaiian species for now solely on the basis of presence or absence of palatine teeth.

The non-humpbacked species are poorly known. For example, there are several species which are usually confused under the name *Scorpaenopsis cirrhosa*. Among the humpbacked ones, there are four species as discussed under the account of *Scorpaenopsis diabolus*.

Scorpaenopsis fowleri (Pietschmann).

(Figure 13.)

Scorpaenodes fowleri Pietschmann, 1934, pp. 99–100 (original description; type locality Hawaiian Islands, Makaua, Oahu [see lectotype designation below]); Pietschmann, 1938, pp. 5–6, 30, pl. 9 (redescription; figure of one type); Fowler, 1949, p. 107 (compiled synonymy; no specimens; questioned Pietschmann's generic placement, thought related to *asperella*).

Scorpaena ballieui (not of Sauvage): Gosline & Brock, 1960, p. 342 (in part; questionably included *fowleri* in synonymy).

Remarks. Pietschmann described this species from 3 small specimens (NMW 6341–6343); these specimens were examined briefly by Eschmeyer and one (NMW 6341) was loaned to him for more detailed study. We designate NMW 6341 as the lectotype of *S. fowleri*. We are unable to determine if this was the specimen figured by Pietschmann (1938, pl. 9).

Placement of this species in the genus *Scorpaenopsis*, rather than in *Scorpaena*, is based on the absence of palatine teeth, but the limits of the

FIGURE 13. *Scorpaenopsis fowleri*, BPBM 14968, 24 mm. S. L., Society Islands. (Photograph of fresh specimen.)

genera *Scorpaenopsis* and *Scorpaena* are uncertain as was discussed under the account of *Scorpaenopsis*. (This species does not belong in *Scorpaenodes* as placed by Pietschmann.)

Except for a recent listing from Tahiti (Randall, 1973), *Scorpaenopsis fowleri* (Pietschmann) has not been recognized as a valid species since its description in 1938. The three types and subsequent specimens reported here are all less than 30 millimeters in standard length. Attempts by us to identify this species with the young stages of other species failed. Dissection showed that two of our specimens were egg-laiden mature females, and this left no doubt that the species is a valid one. This species almost certainly matures at the smallest size (about 25 mm. S. L.) of any scorpaenid now known. As discussed in the distribution section, collections by Randall have resulted in capture of specimens from areas outside the Hawaiian Islands.

MATERIAL EXAMINED. NMW 6341 (1, 28.1, lectotype of *Scorpaenodes fowleri*), Oahu, Makaua, collected by T. T. Dranga, Dec. 1927. NMW 6342–43 (2, paralectotypes of *S. fowleri*), same data as lectotype (not examined in detail). BPBM 7853 (1, 24.6), Oahu, Moku Manu, off north side in 23 meters at entrance to cave, bottom of sand and coral rubble, J. E. Randall, W. J. Baldwin, and G. S. Losey, 3 Oct. 1968. BPBM 7854 (1, 25.8), Oahu, Moku Manu, in 26 meters, bottom of sand, coral rubble, and reef, J. E. Randall and W. J. Baldwin, 6 Oct. 1968. CAS 30738 (1, 27.0), Hawaii, Kona coast at south end of Kailua Airport, between Keahole and Puhili Points, in 14 meters, coral and rocky bottom, J. E. Randall, 7 Nov. 1972.

Distinguishing features. A very small species, probably not exceeding 30 or perhaps 35 mm. in standard length (about 40–45 mm. total length). Dorsal fin rays XII, 9½. Anal fin rays III, 5½. Pectoral fin rays 16, unbranched in available specimens. Vertical scale rows about 35; scales on sides ctenoid. Palatine teeth absent. Lachrymal bone with 2 spines over maxillary, first points forward, second points down and slightly forward. Suborbital ridge without spines or with a low spine at rear end. Nasal spine small, sometimes absent.

This species differs from other species of *Scorpaenopsis* by having only 16 pectoral rays rather than 17 or more. It differs from species of *Scorpaena* by lacking palatine teeth. The posterior lachrymal spine over the maxillary points forward, a feature characteristic for the species and rare in scorpionfishes generally.

Preserved specimens are mostly pallid; frequently one or two small dark bars radiate back from rear of orbit. In life, body and fins mottled with red and white.

Distribution. No data on depth of capture are available for Pietschmann's types. Subsequent collections of this species in Hawaii have been in depths from 14 to 26 meters. We also can report this species from the Tuamotu Archipelago at Mangareva Island (BPBM 13576) in 12 meters and Takaroa Island (BPBM 11159) in 9 to 15 meters, Tetiaroa in the Society Islands (BPBM 14968), from American Samoa at Tutuila (BPBM 17246) in 27 meters, and from Enewetak (formerly Eniwetok) in the Marshall Islands (CAS 31807, 31808, collected by R. S. Nolan). A wider distribution in the central Pacific is expected.

Scorpaenopsis brevifrons Eschmeyer and Randall, new species.

(Figures 14–15.)

Sebastapistes asperella (not of Bennett): Pietschmann, 1938, pp. 27–28 (five specimens from French Frigate Shoal in the Hawaiian Islands; brief description); Fowler, 1949, p. 106 (in part; reference to Pietschmann, 1938).

Scorpaenopsis cacopsis (not of Jenkins): Edmondson, 1946, pp. 344–345, fig. 211b (color notes; fairly good figure).

Material examined. *Holotype*: BPBM 10958 (103 mm. S. L.), Oahu, reef in Kaneohe Bay, in 1 meter, J. E. Randall, A. H. and D. Banner, R. E. and J. Brock, 14 July 1971.

Paratypes: ANSP 84921 (1, 98.6), Honolulu, collected by J. W. Thompson. BPBM 4350 (1, 119), Honolulu, J. W. Thompson. BPBM 7816 (3, 27.4–53.8), Oahu, Waimea Bay, in 6–9 meters, rock with some sand, J. E. Randall *et al.*, 25 Aug. 1969. BPBM 10182 (1, 108), Oahu, off channel to Kaneohe Bay, in 30 meters, cave at base of small dropoff, J. E. Randall and

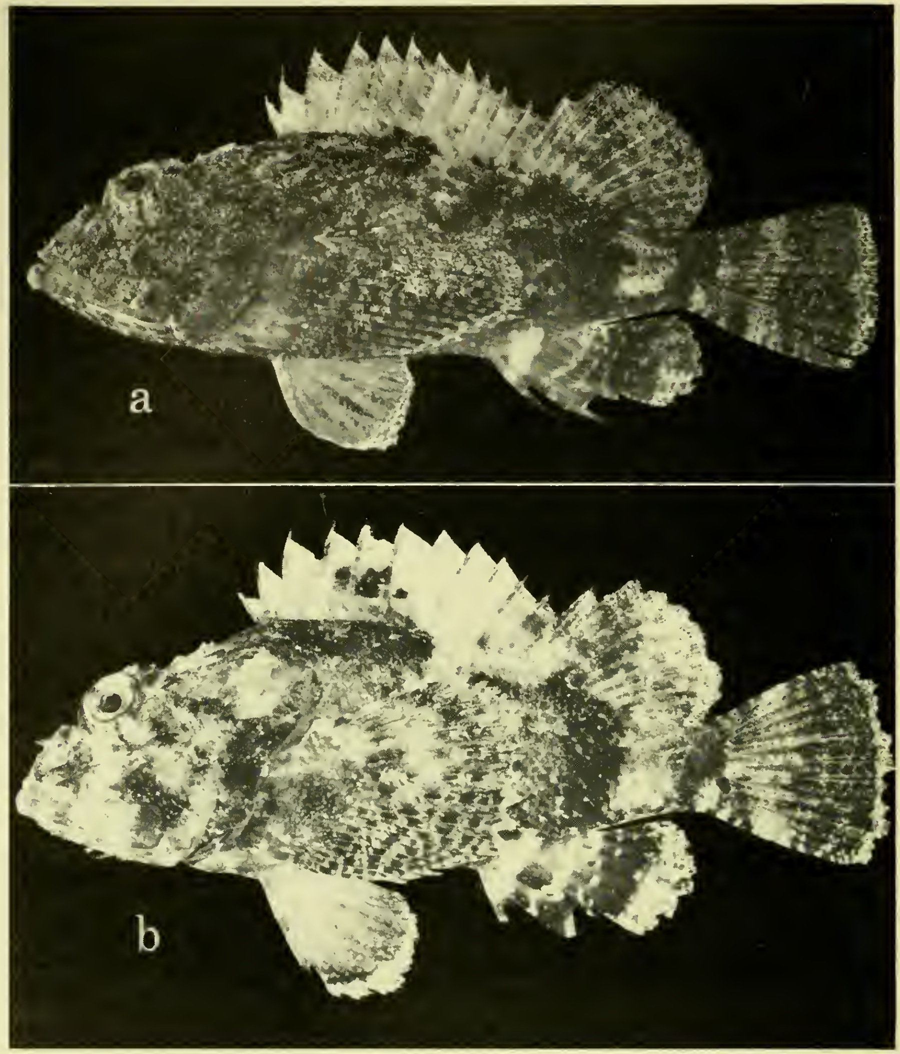


FIGURE 14. *Scorpaenopsis brevifrons.* a. BPBM 6491, paratype, 95.5 mm. S. L., lacking dark spot on spinous dorsal fin, Oahu. b. BPBM 10958, holotype, with dark spot on dorsal fin, Oahu. (Photographs of fresh specimens.)

E. Chave, 29 Sept. 1970. BPBM 11985 (1, 81.3), Oahu, ½ mile off Niumalu Hotel, Waikiki, E. S. Herald, R. R. Rofen, V. E. Brock, W. A. Gosline, *et al.*, 7 Sept. 1951. BPBM 13350 (1, 116), Oahu, off Makua, in 18 meters, bottom mostly of coral rock and rubble, J. E. Randall, 9 Sept. 1972. BPBM 13351 (1, 57.8), Oahu, Makua, rocky shore in 6 meters, J. E. Randall, G. S. Losey

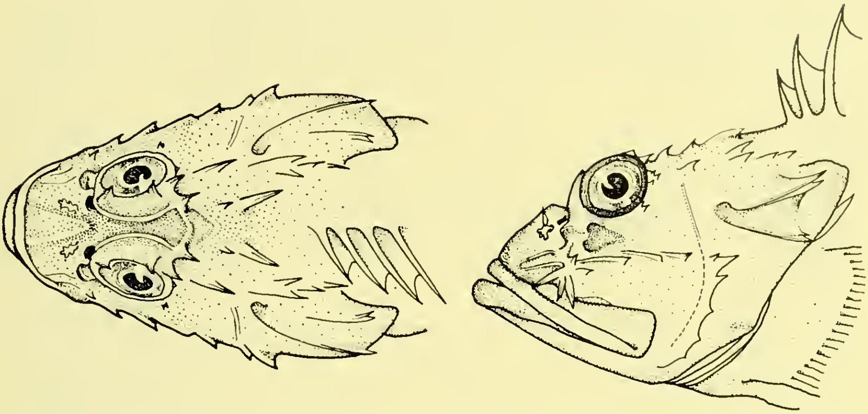


Figure 15. *Scorpaenopsis brevifrons*, diagram of head spines, based mostly on BPBM 6491.

and class, 9 Sept. 1972. CAS 30231, formerly BPBM 6491 (2, 54.4–95.5), Oahu, off Lahilahi Point, near cave in 27–30 meters, coral rubble and rock, J. E. Randall and University of Hawaii students, 10 Aug. 1968. USNM 214047 (1, 89.5), Pokai Bay, 60 meters seaward from deep dropsite, ledge in 24 meters, W. A. Gosline *et al.*, Aug. 1969.

Additional material. NMW 4996–5000 (5, 87.5–99.5), French Frigate Shoal [no other data; these specimens reported as *Sebastapistes asperella* by Pietschmann, 1938].

Diagnosis. A species of *Scorpaenopsis* with pectoral fin rays usually 19 (18–20), a blunt head profile, long jaw (21–27% S. L.), no hump behind head, longest dorsal spines 4–6, and normally 5 spines on the suborbital ridge and 3 on the lachrymal bone overlying the maxillary. (See also Comparisons below.)

Description. Measurements and counts summarized in table 3; body shape and coloration as in figures 14–15.

Dorsal fin rays XII, 9½, longest spines the third through sixth. Anal fin rays III, 5½, third anal spine extends beyond second when depressed. Pectoral fin rays usually 19 (18–20), rays 1 or 2 through 6 or 7 branched in larger specimens, branching begins at specimen length of just under 30 mm S. L. Gill rakers, including rudiments, on outside of first arch 14–16, 4–6 on upper arch, 8 plus 2 or 3 indistinct rudiments on lower arch.

Head spination as in figure 15. Lachrymal bone usually with 3 spines over maxillary, first points forward, posterior two close set and point mostly down (specimens under about 50 mm. S. L. usually with only 2 spines). Suborbital ridge usually with 5 spines, first 2 on lachrymal. Preopercle with supplemental and 5 preopercular spines. Other spines include nasal, pre-

Table 3. *Counts and measurements for type specimens of* Scorpaenopsis brevifrons *(percent standard length in parentheses).*

	BPBM 7816			CAS 30231	BPBM 13351	BPBM 11985	USNM 214047
Standard length	27.4	43.3	53.8	54.4	57.8	81.3	89.5
Dorsal rays	XII, 9½	VI-I, 9½	XII, 9½	XII, 9½	XII, 9½	XII, 9½	XII, 9½
Anal rays	III, 5½	III, 5½	III, 5½	III, 5½	III, 5½	III, 5½	III, 5½
Pectoral rays	19+19	19+19	18+18	19+19	19+19	19+19	19+19
Gill rakers (upper, lower; r=rudiments)	4, 8+r	4, 8+r	5, 8+r	4, 8+r	3, 8+r	5, 8+3	4, 10
Head length	12.8(47)	19.5(45)	23.4(43)	24.7(45)	25.0(43)	36.3(45)	42.2(47)
Snout length	3.3(12)	5.1(12)	6.7(12)	6.8(12)	6.8(12)	10.0(12)	11.8(13)
Orbit diameter	3.0(11)	4.4(10)	4.9(09)	5.2(10)	5.5(10)	7.5(09)	8.5(09)
Interorbital width	1.8(07)	2.2(05)	2.2(04)	2.8(05)	2.7(05)	4.8(06)	4.8(05)
Upper jaw length	6.0(22)	9.2(21)	11.4(21)	12.7(23)	12.6(22)	19.1(23)	22.3(24)
Predorsal-fin length	11.9(44)	17.2(40)	21.6(40)	22.6(41)	22.3(39)	32.9(40)	36.9(41)
Body depth	9.6(35)	13.6(31)	17.8(33)	18.2(33)	18.1(31)	27.7(34)	31.8(35)
Pectoral fin length	8.9(32)	14.0(32)	17.2(31)	16.9(32)	18.0(32)	25.8(32)	28.7(32)
Pelvic fin length	7.0(26)	11.8(27)	14.9(28)	15.1(28)	15.4(27)	21.4(26)	25.2(28)
Caudal fin length	8.9(32)	13.2(30)	16.1(30)	16.6(30)	17.4(30)	23.1(28)	26.4(29)
Length 3rd dorsal spine	4.1(15)	6.0(14)	8.4(16)	7.8(14)	8.8(15)	10.7(13)	11.8(13)
Length 11th dorsal spine	2.9(11)	—	5.9(11)	5.5(10)	5.9(10)	8.3(10)	8.9(10)
Length 12th dorsal spine	4.3(16)	6.1(14)	7.9(15)	8.1(15)	8.7(15)	11.2(14)	13.8(15)
Length 1st anal spine	3.0(11)	5.1(12)	6.4(12)	6.5(12)	6.4(11)	8.6(11)	9.6(11)
Length 2nd anal spine	5.5(20)	9.0(20)	11.4(21)	11.5(21)	11.3(20)	15.8(19)	19.1(21)
Length 3rd anal spine	5.2(19)	7.9(18)	10.5(20)	10.4(19)	10.7(19)	15.0(18)	17.8(20)

Table 3 (continued)

	CAS 30231	ANSP 84921	BPBM 10958	BPBM 10182	ANSP 130800	BPBM 4350
Standard length	95.5	98.6	103	108	116	119
Dorsal rays	XII, 9½	XII, 9½	XII, 9½	XII, 9½	XII, 9½	XII, 9½
Anal rays	III, 5½	III, 5½	III, 5½	III, 5½	III, 5½	III, 5½
Pectoral rays	19+19	19+19	19+19	19+19	20+20	20+19
Gill rakers (upper, lower; r=rudiments)	4, 8+r	3, 8+r	5, 11	4, 8+r	4, 10	4, 10
Head length	44.5(47)	46.0(47)	46.5(45)	49.0(45)	53.8(46)	53.8(45)
Snout length	12.8(13)	14.1(14)	14.3(14)	15.0(14)	16.6(14)	16.8(14)
Orbit diameter	8.0(08)	8.9(09)	9.2(09)	9.4(09)	10.5(09)	10.3(09)
Interorbital width	4.9(05)	5.7(06)	6.1(06)	6.6(06)	8.4(07)	5.4(04)
Upper jaw length	22.7(23)	24.2(24)	25.0(24)	28.1(26)	31.1(27)	29.7(24)
Predorsal-fin length	39.0(40)	40.3(41)	42.8(41)	44.4(41)	45.9(40)	47.2(40)
Body depth	32.6(34)	35.8(36)	38.7(36)	40.0(37)	44.1(38)	39.3(33)
Pectoral fin length	32.7(34)	—	37.3(36)	37.5(35)	35.0(30)	39.5(33)
Pelvic fin length	26.4(28)	—	28.3(27)	30.4(28)	30.7(26)	30.5(26)
Caudal fin length	27.2(28)	—	29.5(28)	32.4(30)	33.8(29)	33.3(28)
Length 3rd dorsal spine	14.5(15)	—	13.9(13)	13.9(13)	14.6(13)	14.8(12)
Length 11th dorsal spine	12.1(13)	—	12.0(12)	12.0(11)	12.8(11)	11.3(09)
Length 12th dorsal spine	15.0(16)	—	16.1(16)	16.5(15)	16.9(15)	14.9(12)
Length 1st anal spine	12.4(13)	—	10.0(10)	11.8(11)	13.5(12)	11.6(10)
Length 2nd anal spine	18.6(19)	—	18.2(18)	20.7(19)	21.8(19)	19.5(16)
Length 3rd anal spine	18.5(19)	—	18.3(18)	19.2(18)	20.1(17)	19.4(16)

supra-, and postocular, tympanic, nuchal, parietal, upper and lower posttemporal, opercular (2, sometimes double), sphenotic (multiple), pterotic, supracleithral, and cleithral. Also small spines (postorbital) behind eye. Occiput with a shallow pit.

Scales on sides ctenoid; head before eye unscaled, otherwise with cycloid scales. Vertical scale rows about 45; lateral-line scales 23 + 1 on caudal fin. Vertebrae 24. Head and body with skin appendages. Supraocular tentacle variable, about equal to eye as maximum, frequently absent. Small flaps present on most head spines, pectoral fin, some body scales, a few on eye, and on the lower jaw and underside of head.

Measurements are summarized in table 3. Orbit smaller than snout, orbit into snout 1.1–1.6, large specimens with proportionally smaller orbits; orbit into head 3.9–5.6, large specimens with lower values.

Color in alcohol similar to that in figure 14 taken of fresh specimen. Body and head marked with dark patches on a pale background, darkest usually below middle of spinous dorsal fin, below soft dorsal fin, and at base of caudal fin. Fins usually with some dark pigment, especially at center of anal fin and as a broad bar across the caudal fin. Dark spot on spinous dorsal fin present or absent, when present usually between spines 4 through 7 at about midheight of fin. Color in life variable. Upper part of body and most of head brownish to gray with bluish-green to green areas and some yellow, mottled with white. Lower parts with more red and orange. Pelvic fin red, streaked with white, mostly white distally. Anal fin with prominent white bar across anterior base, greenish in middle, otherwise red streaked with white. Dorsal fin mostly pale, mottled with brown, orange, and green.

COMPARISONS. This species is rather typical for a *Scorpaenopsis*: of moderate size, robust, well colored, with a large mouth and strong spination. It lacks the humpback found in some species (see account of *S. diabolus*). It has a smaller eye, a longer maxillary, and a blunter head profile than most species of *Scorpaenopsis* of the Indo-Pacific.

In Hawaiian waters, *S. brevifrons* most likely would be confused with *S. cacopsis* and *S. diabolus*—all brightly colored, moderate to large species. *S. diabolus* has a characteristic color pattern on the inside of the pectoral fin (fig. 17b), is humpbacked, and has the interorbital width greater than the eye diameter. *S. cacopsis* has a more pointed snout and usually 18 rather than 19 pectoral rays; the longest dorsal spine in *S. cacopsis* usually is the third while the longest dorsal spines in *S. brevifrons* are near the middle of the fin (4–6).

DISTRIBUTION. This species is known only from Hawaii in depths from 1 to 30 meters, usually in coral or rocks.

NAME. The species name is a noun in apposition formed by the combination of the Latin words 'brevis' (short) plus 'frons' (brow, forehead), referring to the steep head profile in this species as compared to the more pointed, longer snout found in most species of *Scorpaenopsis.*

Scorpaenopsis diabolus Cuvier.

(Figures 16–17.)

Scorpaenopsis diabolus Cuvier *in* Cuvier and Valenciennes, 1829, p. 312 (original description; type locality "le grand Océan oriental").

Hawaiian references:

Scorpaenenopsis diabolus: Fowler, 1900, p. 515 (generic name misspelled; dried skin from Hawaii [could be *cacopsis*]).

Scorpaena gibbosa (not of Schneider): Steindachner, 1900b, p. 491 (one from Honolulu).

Scorpaenopsus gibbosa (not of Schneider): Seale, 1902, p. 18 (generic name misspelled; Honolulu).

Scorpaenopsis catocala Jordan & Evermann, 1903a, pp. 201–202, pl. 56 (original description; type locality Hawaiian Islands, holotype (USNM 50651) from Honolulu, paratypes from Honolulu and Hilo); Snyder, 1904, p. 536 (listed; Hawaii); Jordan & Snyder, 1904a, p. 946 (coloration; Honolulu); Jordan & Evermann, 1926, p. 10 (listed; Hawaii).

Scorpaenopsis gibbosa (not of Schneider): Jordan & Evermann, 1905, pp. 468–470, pl. 56, fig. 206 (description; good figures, pl. 56 wrongly with *catocala* as caption; synonymy); Jordan & Seale, 1906, pp. 178, 375 (in part; *catocala* in synonymy; common about Hawaii); Jordan & Jordan, 1922, p. 55 (synonymy; abundant); Fowler, 1925, p. 27 (listed); Gosline & Brock, 1960, pp. 284, 287, 341 (in key; brief description); Gosline, 1965, p. 825 (depth distribution).

Scorpaenopsis gibbosus: Fowler, 1925, p. 27 (listed; Hawaii); Fowler, 1928, pp. 286–287 (in part; *diabolus* and *catocala* in synonymy; Hawaiian specimens listed); Tinker, 1944, p. 264, fig. (brief description; figure from Jordan & Evermann, 1905); Edmondson, 1946, p. 344 (brief description; coloration; reefs of Hawaiian Islands); Fowler, 1949, p. 106 (in part; reference to Fowler, 1938; record from Hawaii).

Remarks. The species of *Scorpaenopsis* which have a humpback have at times been recognized as a separate genus as discussed by us under the genus *Scorpaenopsis.* We follow a broader interpretation of the genus. Within the humpbacked subgroup, there are four species: *Scorpaenopsis diabolus, S. gibbosa* (Schneider *in* Bloch and Schneider, 1801), *S. macrochir* Ogilby, 1910, and *S. neglecta* Heckel, 1837. *Scorpaenopsis diabolus* and *S. gibbosa* frequently are confused, and *S. macrochir,* type locality northeastern Australia, is widespread in the central Pacific based on CAS and BPBM specimens, but has not been reported from there (so far only reported from Australia). *Scorpaenopsis neglecta* is an Oriental species characterized by serrated ocular spines and the inside of the pectoral fin marked about as in figure 17d. *Scorpaenopsis macrochir* also has the pectoral fin markings as in figure 17d, but *macrochir* has unserrated ocular spines among other differences. *Scorpaenopsis gibbosa* (with *S. nesogallica* (Cuvier) a synonym) apparently is restricted to the Indian Ocean and *S. diabolus,* the only humpbacked species occurring in Hawaii, is widespread in the Indo-Pacific faunal region. *Scorpaenopsis diabolus* and *S. gibbosa* may be separated easily on the basis of

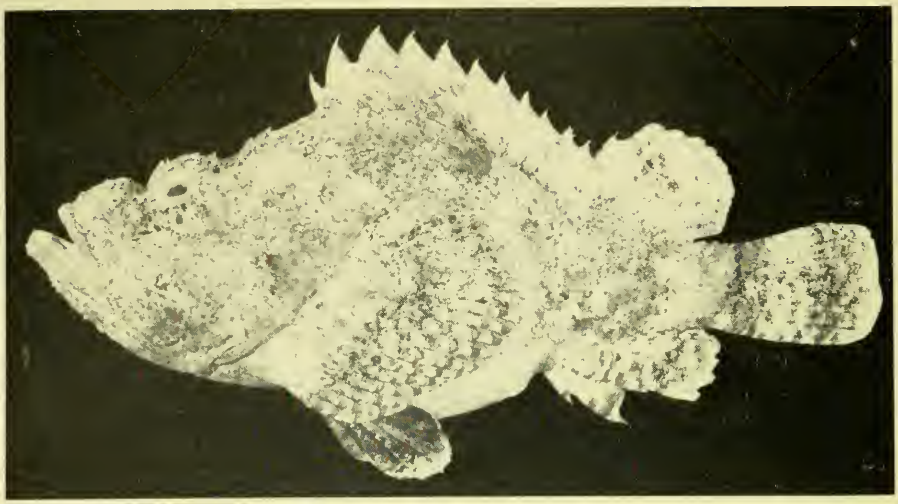


FIGURE 16. *Scorpaenopsis diabolus*, BPBM 7815, 175 mm. S. L., Oahu. (Photograph of fresh specimen.)

pectoral fin coloration (see figure 17a-c); *S. diabolus* also has a longer snout and wider interorbit than *S. gibbosa*, and usually 18 rather than 17 pectoral rays.

MATERIAL EXAMINED. USNM 50651, formerly SU 7754 in part (1, 185, holotype of *Scorpaenopsis catocala*), Oahu, Honolulu, U. S. Fish Commission. SU 7754 (5, 56.3–152) and SU 7466 (5, 115–181), paratypes of *S. catocala*, Oahu, U. S. Fish Commission. CAS 17488 (1, 58), Leeward Is., Laysan Is., 25°46′27″N., 171°44′37″W., in depths to 3.5 meters. SU 19344 (1, 150), Oahu, Honolulu, D. S. Jordan. SU 23393 (2, 95.2–101), Oahu, Honolulu, E. K. Jordan. Counts are also included for the following Hawaiian specimens: CAS 389 (1), CAS 996 (1), CAS 11073 (1), CAS 11088 (1), CAS 17485 (1), CAS 17486 (1), CAS 17487 (1), CAS 31393 (1) and SU 8406 (1). Much additional Hawaiian material is available in the BPBM collection.

NOTE. The type specimens of *S. catocala* were to be distributed to a number of museums (Jordan and Evermann, 1903a, p. 202) but they were not sent and are now found in SU 7466 and 7754. The specimens bear separate field numbers so it will be possible to distribute them as originally intended, and this will be done at the time of publication of this paper.

DISTINGUISHING FEATURES. Dorsal fin rays XII, 9½. Anal fin rays III, 5½. Pectoral fin rays usually 18. Back arched (see figure 16). Scales ctenoid; about 45 vertical scale rows. Lachrymal bone with 2 or 3 spines over maxillary, first points forward, followed by 1 or by 2 closeset spines which point down and back. Suborbital ridge with 4 or more spinous points, usually

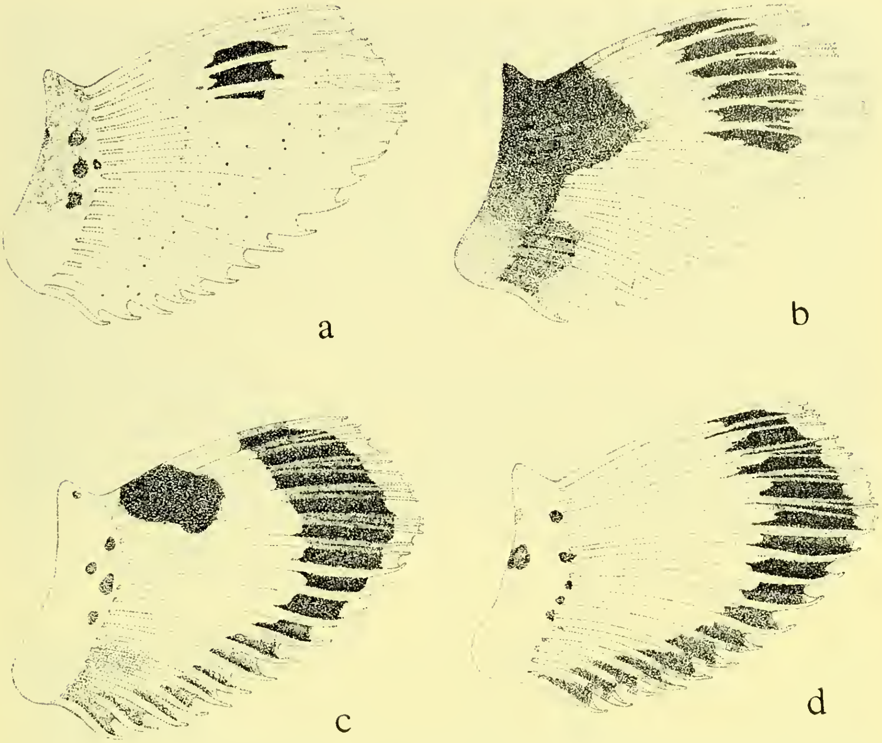


Figure 17. Coloration on inside of pectoral fin in humpbacked species of the genus *Scorpaenopsis*. a. *S. diabolus* (restricted dark patch distally); b. *S. diabolus*, Hawaiian island populations (dark patch distally, note dark pigment at base of fin); c. *S. gibbosa*; d. *S. macrochir* and *S. neglecta* (band complete, no black patch as in c).

more than 8 or 10 points, not in a row and of various sizes. A shallow pit below front corner of eye.

This species is most likely to be confused with *Scorpaenopsis cacopsis* and *S. brevifrons*. The arched back distinguishes *S. diabolus* (fig. 16) along with the characteristic coloration on the inside of the pectoral fin (fig. 17b). *Scorpaenopsis brevifrons* usually has 19 instead of 18 pectoral rays, while *S. diabolus* and *S. cacopsis* usually have 18 pectoral rays. The interorbital width is greater than the orbit diameter in *S. diabolus* but smaller than the orbit diameter in *S. brevifrons* and *S. cacopsis* (in very large specimens, over 200 mm S. L., of *cacopsis* the interorbital width is about equal to the orbit diameter).

Distribution. *Scorpaenopsis diabolus* is the most widespread species in the genus, occurring from the Red Sea and eastern Africa to the central Pacific as far east as the Society Islands. Specimens from Hawaii seem to represent a distinct and recognizable population based on the pectoral fin coloration (fig. 17c). In Hawaii, specimens of the species have been taken in depths from .5 to 10.5 meters.

Scorpaenopsis cacopsis Jenkins.

(Figure 18.)

Scorpaena cookii GÜNTHER, 1873, pl. LV (in part; plate only; plate based on a Hawaiian specimen).

Scorpaenopsis cacopsis JENKINS, 1901, pp. 400–402, figs. 13–14 (original description; type locality Hawaiian Islands, Honolulu; holotype USNM 49690); SEALE, 1901, p. 11, fig. 5 (description; good figure; two specimens from Honolulu); JENKINS, 1903, p. 497 (one specimen from Hawaii); JORDAN & EVERMANN, 1905, pp. 467–468, figs. 205, 205a, color pl. 71 (description; 14 specimens from Hawaii; figs. 205 and 205a copied from Jenkins, 1901); JORDAN & SEALE, 1906, p. 375 (listed, Hawaii and Tahiti); JORDAN & JORDAN, 1922, p. 55 (listed); JORDAN & EVERMANN, 1926, p. 10 (listed); FOWLER, 1928, p. 286, pl. 34B (synonymy; Hawaiian specimens; *altirostris* wrongly in synonymy); TINKER, 1944, pp. 263–264, fig. (brief description; compiled range as Society Islands and Hawaii; figure copied from Jenkins, 1901); FOWLER, 1949, p. 106 (reference); GOSLINE & BROCK, 1960, pp. 284, 288, 341 (brief description and synonymy); GOSLINE, 1965, p. 825 (depth distribution).

Scorpaenopus cacopsis: SEALF, 1902, p. 22 (generic name misspelled; listed).

MATERIAL EXAMINED. USNM 49690 (1, 330, holotype of *Scorpaenopsis cacopsis*), Hawaiian Islands, collected by T. D. Wood, no other data. BPBM 4387 (1, about 330), Oahu, Haleiwa Bay, Waialua, in 3.5 meters, E. Y. Hosaka, 2 Aug. 1932. BPBM 7852 (2, about 300–360), Oahu, Honolulu, J. W. Thompson, no other data. BPBM 10527 (1, 222), Oahu, Moku Manu, in 26 meters, J. E. Randall and W. J. Baldwin, 6 Oct. 1969. BPBM 13352 (2, 74.3–143), Oahu, Makua, rocky shore in 6 meters, J. E. Randall, G. S. Losey and class, 9 Sept. 1972. BPBM 13733 (1, 41.1), Oahu, Waimea Bay, in 4.5 meters, G. R. Allen, 2 July 1967. BPBM 13739, formerly UH 2095 (1, 22.5), Maui, Baldwin Packer's property, about 3 miles W. of Lahaina, W. A. Gosline and E. Hunter, 5 Aug. 1955. BPBM 13744 (1, 227), Oahu, off Pakai Bay, in 9 meters, J. E. Randall, S. N. Swerdloff and D. Chave, 29 July 1969. SU 23263 (1, 220), Honolulu, *Albatross*.

DISTINGUISHING FEATURES. Dorsal fin rays XII, 9½. Anal fin rays III, 5½. Pectoral fin rays normally 18 (17–19). Scales ctenoid; about 50–55 vertical scale rows. Lachrymal bone with 2 spines over maxillary; first points down and forward, second points down and back, sometimes second split distally into 2 points. Suborbital ridge usually with 5 spines, sometimes some spines split in larger specimens. See also the distinguishing features sections of *Scorpaenopsis brevifrons* and *S. diabolus*.

DISTRIBUTION. This species is confined to the Hawaiian Islands. Available depths of capture are from near shore to 26 meters.

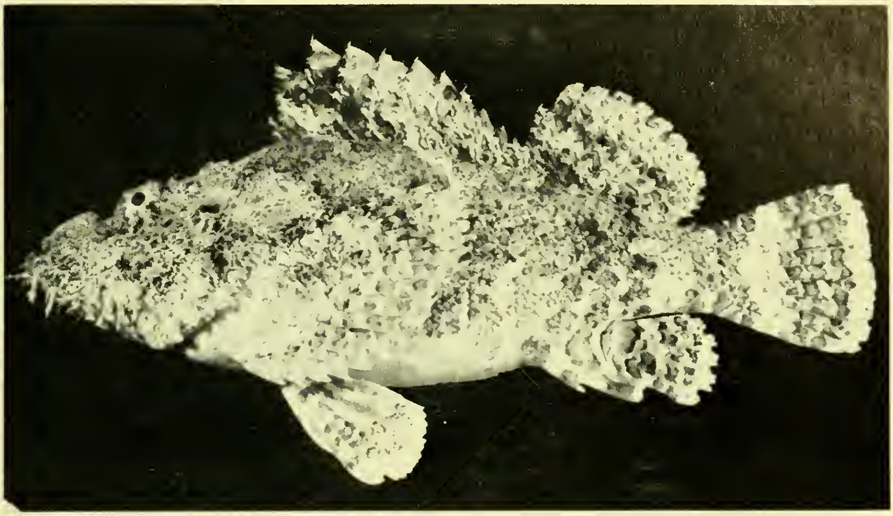


Figure 18. *Scorpaenopsis cacopsis*, BPBM 13744, 243 mm. S. L., Oahu. (Photograph of fresh specimen.)

Scorpaenopsis altirostris Gilbert.

(Figure 19.)

Scorpaenopsis altirostris Gilbert, 1905, pp. 628–630, fig. 244 (original description; type locality Hawaiian Islands, off Molokai, *Albatross* station 3849; holotype USNM 51636); Jordan & Seale, 1906, p. 376 (name only); Jordan & Jordan, 1922, p. 55 (name; suggested may belong in a genus separate from *Scorpaenopsis*); Jordan & Evermann, 1926, p. 10 (listed); Böhlke, 1953, p. 121 (location of types); Gosline & Brock, 1960, pp. 285, 289, 342 (compiled); Gosline, 1965, p. 825 (compiled depth distribution).

Remarks: See Remarks under the genus *Scorpaenopsis* regarding generic placement of this species.

Material examined. USNM 51636 (1, 45.6, holotype of *Scorpaenopsis altirostris*), USNM 51671 (3, 32.0–39.9, paratypes of *S. altirostris,* poor condition) and SU 8620 (2, 33.0–39.2, paratypes of *S. altirostris*), off south coast of Molokai, N. at 71°, W. 21.9′ from Lae-o Ka Laau Light, in 134–79 meters, 10-ft. Blake trawl, bottom of coarse sand, broken shells, and coral, *Albatross* station 3849, 8 April 1902.

Distinguishing features. Dorsal fin rays XII, 9½. Anal fin rays III, 5½. Pectoral fin rays 17–18, mostly 18. Scales ctenoid; about 45 vertical scale rows. Lachrymal bone with 2 spines over maxillary; anterior spine points forward and down, posterior spine points down and back. Suborbital ridge usually with 4 spines, first on lachrymal below main suborbital ridge,

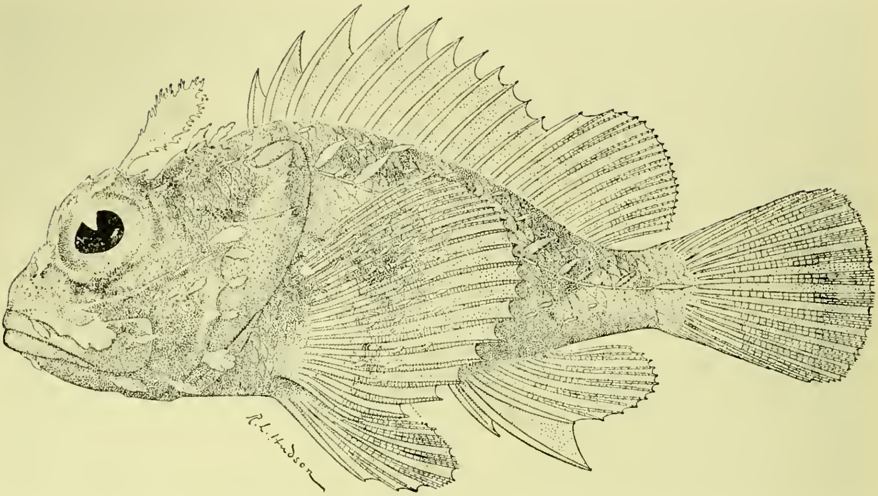


Figure 19. *Scorpaenopsis altirostris*, USNM 51636, holotype, 45.6 mm. S. L. (Figure from Gilbert, 1905, fig. 244.)

second under eye and below main ridge, third and fourth to rear. A slight occipital pit present.

This species and *S. fowleri* resemble species of *Scorpaena* more than species of *Scorpaenopsis* but they lack palatine teeth (see Remarks under the genus *Scorpaenopsis*). *Scorpaenopsis fowleri* has only 16 pectoral rays as opposed to 17–18 in *altirostris*, and *S. fowleri* is a near-shore species while *S. altirostris* occurs in deeper water.

Distribution. *Scorpaenopsis altirostris* is an upper slope species known only from the type specimens listed in the material examined section. Depth of capture was between 79–134 meters.

Remarks. *Scorpaenopsis cotticeps* Fowler, 1938, from the Philippines might prove to be the same species. Fowler wrongly described it as having 14 pectoral fin rays but the type (USNM 98891) has 17. The type specimen is only 27.4 mm. S. L.

Genus **Rhinopias** Gill

Rhinopias Gill, 1905, p. 225 (type-species *Scorpaena frondosa* Günther, 1891, by original designation).

Peloropsis Gilbert, 1905, p. 630 (type-species *Peloropsis xenops* Gilbert, 1905, by original designation).

The genus *Rhinopias* has been treated in detail by Eschmeyer, Hirosaki, and Abe (1973).

Figure 20. *Rhinopias xenops*, BPBM 13988, 116 mm. S. L., Oahu. (Photograph of fresh specimen which had been kept in an aquarium for 2 months.)

Rhinopias xenops (Gilbert).

(Figure 20.)

Synonymy based only on Hawaiian references:

Peloropsis xenops Gilbert, 1905, pp. 630–631, fig. 245 (original description; type locality Hawaiian Islands, between Maui and Lanai, *Albatross* station 3872; holotype USNM 51604); Jordan & Seale, 1906, p. 379 (listed); Jordan & Jordan, 1922, p. 55 (listed; compiled locality data); Jordan & Evermann, 1926, p. 10 (listed); Fowler, 1928, p. 287 (compiled); Tinker, 1944, pp. 262–263, fig. (compiled; figure of type copied from Gilbert, 1905); Gosline & Brock, 1960, pp. 284, 286, 341 (in key; compiled); Gosline, 1965, p. 825 (depth distribution compiled).

Rhinopias xenops: Eschmeyer, Hirosaki, & Abe, 1973, pp. 288, 292–295, figs. 3–4 (synonymy; additional Hawaiian specimen and Japanese material; description; comparisons; shedding of cuticle; figure of holotype copied from Gilbert, 1905; second Hawaiian specimen figured).

Material examined. USNM 51604 (1, 110 mm. S. L., holotype), Auau Channel, between Maui and Lanai islands, in 59 to 79 meters, *Albatross* station 3872, 12 Apr. 1902. BPBM 13988 (1, 115), Oahu, off Haleiwa, in 110 meters, shrimp trawl, *Robert May*, Oct. 1972 [kept alive in an aquarium for 2 months]. UH 3102 (1, 153), Oahu, off Waikiki, otter trawl in 73 meters, P. S. Lobel, 9 Feb. 1974. USNM 209415 (1, 107), Hawaii, Haleiwa, 21°39.6′–42′N., 158°07.3′–05′W., shrimp trawl, in 95–110 meters, *Townsend Cromwell* cruise 36, station 19, 3 May 1968.

DISTINGUISHING FEATURES. Dorsal fin rays XII, 9½. Anal fin rays III, 5½. Pectoral fin rays 18. Scales cycloid; vertical scale rows about 70–75. Palatine teeth absent. Lachrymal bone with 2 rounded lobes over maxillary. Suborbital ridge with 3 or 4 spines, not well marked and sometimes split, first spine on lateral face of lachrymal bone.

This species is distinguished from other Hawaiian species by its compressed head and body, somewhat elevated rostrum, long snout, and coloration. A complete description is given by Gilbert (1905) and by Eschmeyer, Hirosaki, and Abe (1973).

The specimen figured differs from previously known specimens in having a dark spot on the spinous dorsal fin and it lacks dusky pigment at the base of the soft dorsal fin. When fresh it was reddish with large areas of light purple. In other features it agrees with other specimens of *R. xenops*. UH 3102 differs from previously known specimens by having 19 pectoral rays and the third dorsal spine is not elongate.

DISTRIBUTION. We know this offshore species at Hawaii only from the holotype and 3 additional specimens as given in our "Materials examined" section. One additional specimen was taken off Molokai in 124 meters by the *Townsend Cromwell* (Paul Struhsaker, pers. comm.) but this specimen was lost. Depths of capture were 59–79, 73, 95–110, and 124 meters. *Rhinopias xenops* is known also from Japan (see Eschmeyer, Hirosaki, and Abe, 1973).

REMARKS. William D. Madden and Randall observed the feeding of the specimen shown in figure 20 when it was maintained in an aquarium. Live *Gambusia* were introduced into the tank as food. The *Rhinopias* moved very slowly and intermittently towards its prey by "creeping" on its lower pectoral rays which were in contact with the bottom. The dorsal fin was held fully erect. Occasionally the *Rhinopias* moved a little to and fro, reminiscent of the rocking of *Taenianotus*. When it came to within about 2.5 cm. of the prey, it engulfed the small fish with incredible rapidity. Just prior to striking the prey, the dorsal fin was slowly folded back.

Genus **Neomerinthe** Fowler

Neomerinthe FOWLER, 1935, pp. 41–42 (type-species *Neomerinthe hemingwayi* Fowler, 1935, by original designation).

Eschmeyer (1969b, p. 93) remarked that the Hawaiian species described as *Helicolenus rufescens* Gilbert did not belong in the genus *Helicolenus* of the subfamily Sebastinae but should be classified instead in the subfamily Scorpaeninae. The species *rufescens* seems to be referable to the genus *Neomerinthe* Fowler. *Neomerinthe* is a genus which contains *Pontinus*-like species, but unlike species of *Pontinus* those of *Neomerinthe* have some

Figure 21. *Neomerinthe rufescens*, BPBM 13737, 93 mm. S. L., off Kauai. (Photograph of preserved specimen.)

branched pectoral rays. Previously, only two Atlantic species have composed the genus *Neomerinthe.*

Neomerinthe rufescens (Gilbert).

(Figure 21.)

Helicolenus rufescens Gilbert, 1905, pp. 631–633, fig. 246 (original description; type locality Hawaiian Islands, holotype (USNM 51628) from near Kauai at *Albatross* station 4133, paratype from off Maui at *Albatross* station 4074); Jordan & Seale, 1906, p. 378 (listed); Jordan & Jordan, 1922, p. 54 (name; locality data compiled); Jordan & Evermann, 1926, p. 10 (listed); Fowler, 1928, p. 291 (synonymy; brief description compiled from Gilbert, 1905); Tinker, 1944, pp. 267–268, fig. (compiled; figure of type from Gilbert, 1905); Böhlke, 1953, p. 120 (location of types); Gosline & Brock, 1960, pp. 285, 289, 342 (in key; compiled); Gosline, 1965, p. 825 (depth distribution).

Material examined. USNM 51628 (1, 83.4, holotype of *Helicolenus rufescens*), off Kauai, S. at 40° and W. 4.4′ from Hanamaulu warehouse, in 75–302 meters, bottom of fine gray sand and rubble, 8-ft. Albatross-Blake trawl, station D. 4133, 1 Aug. 1902. BPBM 13737 (5, 59.1–90.8), CAS 15697 (9, 61.3–92.4) and CAS 15689 (3, 75.0–100, cleared and stained), all off Molokai, 21°14.4′–15.6′N., 157°07.8′–13.5′W., shrimp trawl in 124 meters, *Townsend Cromwell* cruise 40, station 106, 28 Nov. 1968. SU 8619 (1, 59.5, paratype of *Helicolenus rufescens*), north coast of Maui, S. at 70° and E. 8.5′ from Puniawa Point, in 143–155 meters, bottom of coral, sand, and foraminifera, 8-ft. Tanner beam trawl, staton D. 4074, 19 July 1902. Additional Hawaiian material is available in the NMFS collection.

DISTINGUISHING FEATURES. Dorsal fin rays XII, 9½. Anal fin rays III, 5½. Pectoral fin rays usually 18, sometimes 19. Palatine teeth present. Scales ctenoid; about 50 vertical scale rows. Lachrymal bone with 2 spines over maxillary, both point back and down. Suborbital ridge with 2–4, usually 3, spines; one on lateral face of lachrymal bone usually absent. No occipital pit.

This species is most likely to be confused with species of *Scorpaena* or *Pontinus*. *Neomerinthe rufescens* has 18 or 19 pectoral rays while all Hawaiian species of *Scorpaena* and *Pontinus* usually have 17 or fewer pectoral rays (*S. colorata* sometimes with 18). Upper pectoral rays in *N. rufescens* branch when specimens reach about 70 mm. S. L., but in *Pontinus macrocephalus* they never branch; specimens of *rufescens* usually have 9½ soft dorsal rays and *macrocephalus* usually 10½. Species of *Scorpaenopsis* differ in lacking palatine teeth.

DISTRIBUTION. *Neomerinthe rufescens* is an offshore species known only from the Hawaiian Islands. *Townsend Cromwell* operations captured a total of 63 specimens from 18 stations in depths between 108 and 124 meters (Struhsaker, 1973). The holotype was taken somewhere between 75 and 302 meters and the paratype between 143 and 155 meters by the *Albatross*.

Genus **Scorpaena** Linnaeus

Scorpaena LINNAEUS, 1758, p. 266 (type-species *Scorpaena porcus* Linnaeus, 1758, by subsequent designation of Bleeker, 1876; see Opinion 77 and "Official List of Generic Names").

Problems of the limits of this genus and generic synonyms have been mentioned by Eschmeyer (1965a, p. 89; 1969b, p. 54) and Eschmeyer and Allen (1971, p. 521). Some of the Hawaiian species are referable to *Sebastapistes,* but we follow Matsubara (1943) in treating *Sebastapistes* as a synonym of *Scorpaena*. It is likely that the genus *Scorpaena* is a 'catch-basket' genus, and a more thorough treatment on a world basis is needed. See also our remarks under the genus *Scorpaenopsis*.

Scorpaena galactacma (Jenkins).

(Figure 22a.)

Sebastapistes galactacma JENKINS, 1903, pp. 496–497, fig. 40 (original description; type locality Hawaiian Islands, coral reef at Honolulu; holotype USNM 50692); JORDAN & EVERMANN, 1905, pp. 455, 459–460, fig. 201 (description mostly from Jenkins, 1903; figure of type from Jenkins, 1903); JORDAN & JORDAN, 1922, p. 54 (listed; common on reefs).

Sebastapistes galactacme: JORDAN & SEALE, 1906, p. 377 (species name misspelled; listed).

Sebastapistes albobrunneus (not of Günther): FOWLER, 1928, p. 287 (in part; *galactacma* in synonymy).

?*Sebastopsis galactma*: BORODIN, 1930, p. 59 (species name misspelled; specimens from Oahu; compared with type).

Scorpaena ballieui (not of Sauvage): GOSLINE & BROCK, 1960, p. 342 (in part; *galactacma* in synonymy).

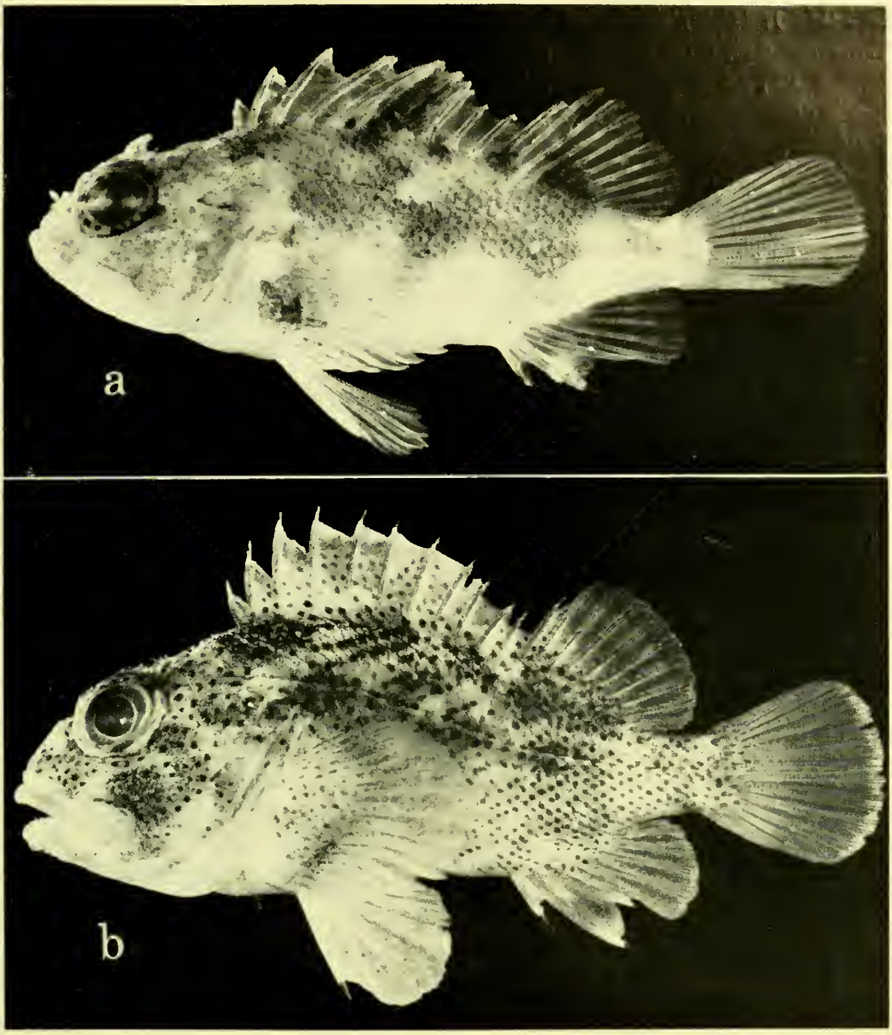


Figure 22. a. *Scorpaena galactacma*, BPBM 7925, 33 mm. S. L., Oahu (Photograph of a preserved specimen). b. *Scorpaena coniorta*, BPBM 6464, 47 mm. S. L., Oahu. (Photograph of fresh specimen.)

Material examined. USNM 50692 (1, 49.3 mm. S. L., holotype of *Sebastapistes galactacma*), and USNM uncat. (2, about 36–40, paratypes of *S. galactacma*), Oahu, Honolulu, O. P. Jenkins, 1889. BPBM 7835 (7, 33.4–47.8), Oahu, off Waikiki, in 7.5 meters, J. E. Randall, E. Niel, and students, 30 Mar. 1969. BPBM 7925 (1, 32.8), Oahu, Waimea Bay, in 6–9 meters, J. E. Randall, W. F. Smith-Vaniz, *et al.*, 25 Aug. 1969. BPBM 13470 (3, 33.5–36.4), Oahu, off Waikiki in 29 meters, from vicinity of small ledge, J. E. Randall, 30 Sept. 1972. CAS 13471, formerly UH 2484 (10), Kauai, Port Allen, in 24–29 meters, *Miss Honolulu,* 10 Sept. 1959. CAS 13472, formerly UH 2481 (40), Kauai, Port Allen, in 10.5–24.5 meters, *Miss Honolulu,* 12 Sept. 1959. CAS 15725 (2), Maui, dredged off Lahaina, in 18–64 meters, E. M. Ehrhorn. SU 7615 (6), Oahu, Honolulu, U. S. Fish Commission, 1901. Additional material is present in the BPBM collection.

DISTINGUISHING FEATURES. Dorsal fin rays XII, 9½. Anal fin rays III, 5½. Pectoral fin rays 15–17, usually 16. Coronal spines absent. Virtually no occipital pit. Vertical scale rows about 45. Lachrymal bone with 2 widely diverging spines over maxillary, first points forward, second back. Suborbital ridge with 2 or 3 poorly marked spines, usually one under eye below main ridge, one at end, and sometimes one on lachrymal bone below main ridge. A dark smudge sometimes present between dorsal spines 6–7 to 9.

This species differs from other Hawaiian species of the genus *Scorpaena* by having cycloid to emarginate scales; the other species have ctenoid scales at least on their flanks.

DISTRIBUTION. This small species appears to inhabit coral and rubble areas in depths from near shore to 29 meters (one collection from 18 to 64 meters).

Scorpaena coniorta (Jenkins).

(Figure 22b.)

Sebastapistes strongia (not of Cuvier): STREETS, 1877, pp. 62–63 (description; Honolulu); FOWLER, 1900, p. 515 (one from Hawaii; fin formula).

Sebastapistes coniorta JENKINS, 1903, pp. 495–496, fig. 39 (original description; type locality Hawaiian Islands, coral rocks on reef at Honolulu; holotype USNM 50693); SNYDER, 1904, p. 536 (listed; Honolulu); JORDAN & EVERMANN, 1905, pp. 455, 458–459, fig. 200 (description; brief synonymy; figure from Jenkins, 1903); JORDAN & SEALE, 1906, p. 376 (listed); JORDAN & JORDAN, 1922, p. 54 (listed; common on reefs); FOWLER & BALL, 1925, p. 20 (Pearl and Hermes Reef); JORDAN & EVERMANN, 1926, p. 10 (listed); BÖHLKE, 1953, p. 122 (location of types); SCHULTZ, 1966, p. 28 (*coniorta* distinct from *albobrunneus*).

Sebastapistes albobrunneus (not of Günther): FOWLER & BALL, 1925, p. 20 (Pearl and Hermes Reef); FOWLER, 1928, p. 287 (in part; *S. coniorta* in synonymy; listed some Hawaiian specimens); PIETSCHMANN, 1938, pp. 28–29, pl. 3 (description; specimens from Pearl and Hermes Reef [some misidentified]; photograph of 7 specimens; year-groups by length frequencies [based on misidentifications]); TINKER, 1944, pp. 264–265, fig. (brief description; figure of type of *coniorta* from Jenkins, 1903); EDMONDSON, 1946, p. 344, fig. 211a (brief description).

Sebastapistes albo-brunneus: FOWLER, 1941, p. 257 (one specimen from Mogua Reef).

Scorpaena coniorta: GOSLINE, 1955, pp. 461–462 (described in key, Johnston Island); GOSLINE & BROCK, 1960, pp. 285, 288, 341 (brief diagnosis; in key; brief synonymy); GOSLINE, 1965, p. 825 (vertical zonation).

MATERIAL EXAMINED. USNM 50693 (1, 49.8 mm. S. L., holotype of *Sebastapistes coniorta*), Oahu, off Honolulu, reefs, O. P. Jenkins, 1889. SU 23589

(57, paratypes of *S. coniorta*) and SU 23330 (122, paratypes of *S. coniorta*), Oahu, reefs off Honolulu, O. P. Jenkins. BPBM 6464 (4, 40.5–45.8), Oahu, western end of Waimea Bay, in 6 meters, all from head of *Pocillopora meandrina*, J. E. Randall, 28 Sept. 1968. BPBM 9987 (1, 35.3) and CAS 15695 (4), Oahu, off rocky islet at SW. end of Waimea Bay, in 1–10.5 meters, J. E. Randall, L. A. Randall and P. M. Allen, 27 July 1970. CAS 13480, formerly UH 809 (10), Oahu, Diamond Head, W. A. Gosline and class, 16 May 1950. CAS 15710 (16) and CAS 15711 (3, 28.5–47.8, cleared and stained), Oahu, Waikiki Beach, about ½ mi. off Niumalu Hotel, in 7.5–9 meters, W. A. Gosline *et al.*, GVF Reg. no. 54, 7 Sept. 1971. UH uncat. (5, 30.2–53.7), Wake Island, near wreck, 0–6 meters, W. A. Gosline and J. E. Randall, 9 June 1953. Additional material is available in the BPBM and CAS collections.

Distinguishing features. Dorsal fin rays normally XII, 9½. Anal fin rays III, 5½. Pectoral fin rays usually 16 (15–17). Coronal spines absent. No occipital pit. Scales ctenoid; about 50–55 vertical scale rows. Lachrymal bone with 4 spines; two spines lie over the maxillary, first points forward, second points back; a spine above each of these. A small spine sometimes present at base of first spine over maxillary in large specimens. Suborbital ridge more or less a double ridge; a spine at end; sometimes a spine under eye; fourth spine on lachrymal bone is far below level of suborbital ridge and not counted as part of suborbital ridge. Supplemental preopercular spine well above first preopercular spine. Well-marked spines at upper rear of orbit in area of sphenotic.

The coloration of this species is diagnostic: body and fins with scattered small dark spots, no dark spot on spinous portion of dorsal fin; see figure 22b.

Distribution. This species is known from the Hawaiian Islands and from Johnston Island and the Line Islands (e.g., CAS 13479). Other *coniorta*-like species occur in the Indo-West Pacific area as discussed below. In Hawaii the species occurs in shallow water in depths from near shore to about 24.5 meters.

Remarks. *Scorpaena coniorta* belongs in the subgroup *Sebastapistes* within *Scorpaena*. Within this subgroup, it appears to be related to the widespread Indo-Pacific *Scorpaena albobrunnea* Günther. *Scorpaena coniorta* also seems closely related to the little-known Asian *S. tinkhami* Fowler (1946), and to BPBM specimens of a similar species taken by Randall in French Oceania. A more thorough study is needed of this complex.

Scorpaena ballieui Sauvage.

(Figure 23.)

Scorpoena ballieui Sauvage *in* Vaillant and Sauvage, 1875, pp. 278–279 (original description; type locality Iles Sandwich [Hawaiian Islands]; generic name misspelled).

Scorpaena ballieui: Sauvage, 1878, pp. 123–124, fig. 4 on pl. 2 (description; good figure); Jordan & Seale, 1906, p. 376 (listed); Gosline & Brock, 1960, pp. 285, 289, 341–342 (in key; brief description; *galactacma* and *fowleri* included in synonymy); GOSLINE, 1965, p. 825 (depth distribution).

Sebastapistes corallicola JENKINS, 1903, pp. 493–495, fig. 38 (original description; type locality Hawaiian Islands, Honolulu; holotype USNM 50691); SNYDER, 1904, p. 535 (listed from Honolulu and Hilo); JORDAN & EVERMANN, 1905, pp. 455–458, fig. 199 (mostly after Jenkins, 1903; figure from Jenkins, 1903); JORDAN & SEALE, 1906, p. 376 (thought might be same as *asperella*); JORDAN & JORDAN, 1922, p. 54 (compiled); FOWLER & BALL, 1925, p. 19 (Pearl and Hermes Reef, Ocean Island, and Laysan); PIETSCHMANN, 1938, pp. 5, 29–30 (brief description; Pearl and Hermes Reef); BÖHLKE, 1953, p. 122 (location of types); SCHULTZ, 1966, pp. 29–32, figs. 138b, 140 (name used for Marshall and Marianas specimens; figure of holotype of *corallicola* from Jenkins, 1903).

Sebastapistes ballieui: JORDAN & EVERMANN, 1905, pp. 455–456, color pl. 72 (lengthy description; Honolulu, Waikiki, Hilo); JORDAN & JORDAN, 1922, p. 54 (name; rather common); FOWLER & BALL, 1925, p. 19 (Pearl and Hermes Reef).

Sebastapistes albobrunneus (not of Günther): FOWLER, 1928, p. 287 (in part; *coniorta* and *galactacma* wrongly in synonymy; Hawaiian specimens among others listed).

Sebastapistes asperella (not of Bennett): FOWLER, 1931, pp. 348–349 (color description of Honolulu specimens); FOWLER, 1949, p. 106 (in part; references).

Sebastapistes nuchalus (not of Günther): SCHULTZ, 1943, p. 174 (in part; type of *corallicola* only); FOWLER, 1949, p. 107 (in part; *corallicola* wrongly included in synonymy).

Scorpaena peruana HILDEBRAND, 1946, pp. 445–448, fig. 86 (original description; type locality Peru [in error, see remarks below]).

MATERIAL EXAMINED. MNHN 6883 (2, about 32 and 86.0), MNHN 8993 (1, 79.5), and MNHN 9557 (2, 62.4–74.3), all syntypes of *Scorpaena ballieui*, Hawaii, collected by Ballieu. USNM 50691 (1, about 95, holotype of *Sebastapistes corallicola*), Oahu, Honolulu. SU 7729 (1, paratype of *Sebastapistes corallicola*), Oahu, Honolulu, O. P. Jenkins. BPBM 4369 (1, 64.5), Oahu, C. M. Cooke, Jr., 5 May 1923. BPBM 7817 (2, 47.3–61.5), Oahu, off Waikiki, in 7.5 meters, J. E. Randall, E. Niel, and students, 30 Mar. 1969. BPBM 9338 (1, about 67), Oahu, off Kewalo Basin, in about 1 meter, P. M. Allen, 20 Mar. 1970. CAS 13470, formerly UH 264 (15), Oahu, Waianae coast, W. A. Gosline and class, 22 Feb. 1949. CAS 15692 (8), Oahu, large boulders and some sand at west side of Waimea Bay, in 6–9 meters, J. E. Randall *et al.*, 25 Aug. 1969. CAS 15694 (8), Oahu, off rocky islet at SW. end of Waimea Bay, 1–10.5 meters, J. E. and L. A. Randall and P. M. Allen, 27 July 1970. CAS 15709 (2), Oahu, ½ mi. off Waikiki Beach, in 7.5–9 meters, GVF Reg. no. 54, W. A. Gosline *et al.*, 7 Sept. 1951. CAS 22841 (44) and CAS 15688 (3, 40.9–79.8, cleared and stained), Kauai, Kapaa, P. R. Needham and J. P. Walsh, 8 Aug. 1949. Additional material is present in the BPBM and CAS collections.

DISTINGUISHING FEATURES. Dorsal fin rays normally XII, 9½. Anal fin rays III, 5½. Pectoral fin rays 16. Coronal spines present. Virtually no occipital pit. Scales ctenoid; about 40–45 vertical scale rows. Lachrymal bone with 3 spines over maxillary, posterior 2 closeset and pointing down

Figure 23. *Scorpaena ballieui*, BPBM 7817, 64 mm. S. L., Oahu. (Photograph of fresh specimen.)

and to rear, first points mostly forward. Suborbital ridge with one spine at posterior end of ridge.

This is the only Hawaiian species which has coronal spines (fig. 1e). A dark spot frequently is present on the spinous dorsal fin between about spines 7–10.

Distribution. *Scorpaena ballieui* occurs in or near coral at depths from near shore to about 10.5 meters. We know it definitely only from Hawaii but similar species occur in the Pacific and need study.

Remarks. *Scorpaena asperella* Bennett (1829) was the first scorpaenid described from the Hawaiian Islands, but it still remains unidentifiable in our opinion. The type specimen is lost. This problem has been discussed by Gosline (1955) and mentioned by Springer (1967). No Hawaiian species fits Bennett's description well. The capture site of a blenny described by Bennett from Hawaii actually was off South America (see Springer, 1967), and this adds doubt to the provenance of the specimen described as *asperella* by Bennett. The collections used by Bennett originated from a cruise of the *Blonde*, which stopped at Madeira, several areas on the Pacific coast of South America, Hawaii, and other ports in the Pacific. We have been unable to link Bennett's brief description of *asperella* with any scorpaenid from the localities visited by the *Blonde* and we retain it for now as an unidentifiable species.

Scorpaena peruana Hildebrand (1946) is a synonym of *S. ballieui*; the type specimens of *peruana* had incorrect locality data accompanying them (see Greenfield, MS).

Scorpaena pele Eschmeyer and Randall, new species.
(Figures 24, 25a.)

No literature applies to this species.

Material examined. Except for the specimen from the Honolulu market, all specimens were collected by the *Townsend Cromwell* using shrimp trawls.

Holotype: USNM 214046 (124 mm. S. L.), north coast of Oahu, 21°40′N., 158°08′W., 176–202 meters, cruise 59, station 3, 7 July 1972.

Paratypes: ANSP 130800 (1, 116), off Maui, Pailolo Channel, 21°02.3′–20°58.9′N., 156°44.4′–49.3′W., in 229–238 meters, cruise 40, station 56, 18 Nov. 1968. BPBM 4350 (1, about 134, soft), Honolulu market, J. W. Thompson, no other data. BPBM 13635 (1, 76.5), off Molokai, Penguin Bank, 21°09.7′N., 157°25′–29.8′W., in 177–188 meters, cruise 35, station 33, 7 April 1968. BPBM 17247 (2, 88.5–99.0), off Maui, 21°02.1′–20°59.0′N., 156°44.4′–44.0′W., in 238 meters, cruise 40, station 61, 18 Nov. 1968. CAS 15707 (1, 81.4), off Maui, Pailolo Channel, 21°01.2′–20°57.2′N., 156°44.1′–47.1′W., in 210 meters, cruise 40, station 47, 16 Nov. 1968. CAS 30236 (1, 88.7), Pailolo Channel, in 219 meters, no other data. CAS 30237 (2, 110–112), off Maui, 21°01.7′–20°58.8′N., 156°43.1–45.1′W., in 185–232 meters, cruise 35, station 4, 28 Mar. 1968. CAS 30238 (3, 84.8, 98.9, 117), off Maui, 21°01.7′–20°57.3′N., 156°43.1′–47.4′W., in 221 meters, cruise 40, station 51, 17 Nov. 1968. CAS 30239 (1, 118), taken with the holotype. USNM 214045 (1, 90.8), off Maui, Pailolo Channel, 21°01.6′–20°57.3′N., 156°43.0′–47.4′W., in 223 meters, cruise 40, station 54, 18 Nov. 1968. USNM 214043 (1, 87.1), off Maui, 21°02.5′–20°58.9′N., 156°44.0–49.0′W., in 229–243 meters, cruise 40, station 55, 18 Nov. 1968. USNM 214044 (2, 75.9–110), off Maui, 21°03.0′–01.2′N., 156°45.4′–50.2′W., in 199–230 meters, cruise 40, station 67, 19 Nov. 1968. USNM 214042 (1, 135), off Maui, 21°03.1′–01.4′N., 156°45.5′–50.8′W., in 198–223 meters, cruise 40, station 68, 20 Nov. 1968.

Additional material is available in the NMFS collections, but was not used in the description of the species.

Diagnosis. A species of *Scorpaena* with 9½ dorsal soft rays, 16–17 pectoral rays, and 15–17 gill rakers. Scales on sides ctenoid. Occiput with a shallow pit. Lachrymal bone with 3 spines over maxillary; suborbital ridge with 4 spines. Coronal spines absent. Color mostly red, marbled and spotted with white.

Description. Measurements and counts summarized in table 4; body shape and coloration as in figures 24, 25a.

Dorsal fin rays normally XII, 9½, third spine usually the longest. Anal fin rays III, 5½, second spine usually extending beyond third when depressed.

Figure 24. *Scorpaena pele*, USNM 214046, holotype, 124 mm. S. L., north coast of Oahu. (Drawn by Cherryl Pape.)

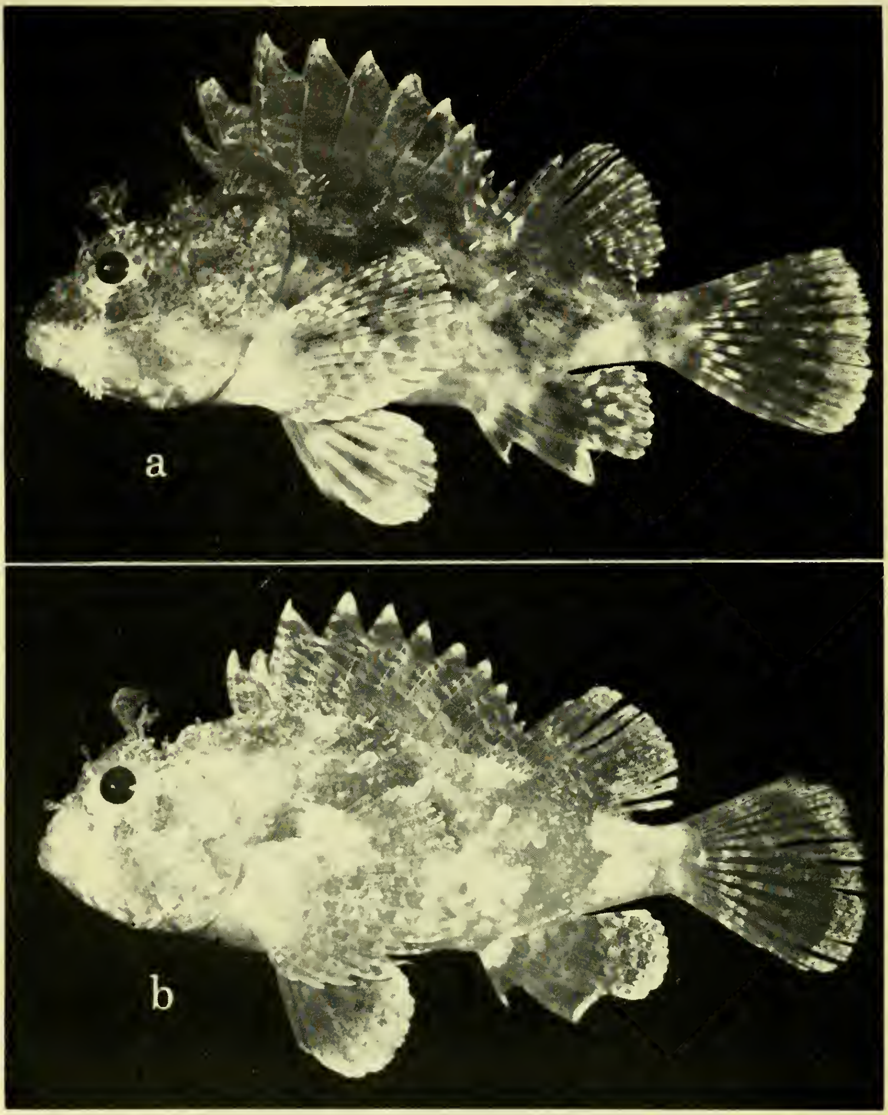


Figure 25. a: *Scorpaena pele*, CAS 30236, paratype, 88.7 mm. S. L., Pailolo Channel. b: *Scorpaena colorata*, BPBM 14130, 63.0 mm. S. L., Pailolo Channel (second dorsal spine abnormally short). (Photographs of fresh specimens.)

Pectoral fin rays 16–17, almost always 17, rays 2 through 7 or 8 branched in adults. Gill rakers, on outside of first arch including rudiments total 15–17, 4–6 on upper arch, 10–12 on lower arch, usually 5 + 11.

Head spination as in figure 24. Lachrymal bone with 3 spines over maxillary, first points forward, second near base of or on first and points forward, third points down and slightly to rear. Suborbital ridge with four spines, first on lateral face of lachrymal bone. Preopercle with supplemental and 5 preopercular spines, fifth preopercular spine sometimes tiny. Other spines include nasal, pre-, supra-, and postocular, tympanic, nuchal, parietal, upper and lower posttemporal, opercular, sphenotic (multiple), pterotic, supracleithral, and cleithral. Interorbital ridges moderate, ending at or near base of tympanic spines. Occiput with a shallow to moderate pit, usually poorly defined.

Scales on sides ctenoid; scales on belly and pectoral fin base cycloid. Head before eyes unscaled. Buried scales present behind eye and on cheek. Breast with buried scales. Vertical scale rows about 45; lateral-line scales usually 23 plus 1 on caudal fin. Vertebrae 24. Head and body with small skin appendages. Supraocular tentacle somewhat frilly distally, flattened, its length usually about one-half of orbit diameter. Lachrymal, preopercular, and preorbital spines with small skin flaps; small flaps on eye, on anterior nostril, and a few small ones at other locations on head.

Measurements are summarized in table 4. Orbit diameter about equal to snout length (orbit into snout .9–1.1); orbit into head 3.3–3.8; larger specimens tend to have proportionally smaller orbit diameters.

Color in alcohol as in figure 24. Body and head marbled and spotted with brown on a pale background. Dark spot on dorsal fin between spines 6–10, sometimes this spot reduced or absent. Large dark patches on flanks under scales (these prominent, purplish in some specimens). Smaller, scattered black spots present on body and on caudal fin and usually also on other fins. Broad lines radiate from eye, two ventral ones most noticeable. Color in life mostly red, marbled and spotted with white. All dark areas in figure 25a red in life.

Comparisons. *Scorpaena pele* is very similar to *Scorpaena colorata* in shape, live coloration, and spination. Both are upper slope species. They differ in that *S. colorata* lacks roundish black spots on the caudal fin, and usually on other fins, which are present in *S. pele*. The tooth patch on the palatine of *S. colorata* is wider and the palatine teeth are scattered, while in *S. pele* the teeth are in a narrow band of not more than two rows. The scales on the breast of *S. pele* are buried so the area appears unscaled, while they are readily apparent in *S. colorata*. *Scorpaena pele* invariably has a spine on the lateral face of the lachrymal bone, yielding a total of 4 on the "suborbital ridge"; *S. colorata* lacks a spine on the lateral face of the lachrymal bone and has 3 spines on the suborbital ridge. These two species are distinguished from other species by the characters presented in the key.

Distribution. Known only from the Hawaiian Islands; all specimens were trawled in depths from about 180–240 meters.

Table 4. *Counts and measurements for eleven type specimens of* Scorpaena pele. (*See tables 1–2 for summary of fin-ray counts; part as percent of standard length in parentheses*).

	USNM 214044	BPBM 13735	CAS 15707	CAS 30238	CAS 30236
Standard length	75.9	76.5	81.4	84.8	88.7
Dorsal rays	XII, 9½	XII, 9½	XII, 9½	XII, 9½	XII, 9½
Anal rays	III, 5½	III, 5½	III, 5½	III, 5½	III, 5½
Pectoral rays	17+17	17+17	17+17	17+17	17+17
Gill rakers (upper, lower)	4, 11	6, 11	5, 11	5, 12	5, 11
Head length	35.2(46)	36.1(46)	37.6(46)	39.7(47)	40.4(46)
Snout length	9.1(12)	9.4(12)	9.2(11)	10.8(13)	10.3(12)
Orbit diameter	10.3(14)	11.0(14)	10.6(13)	11.3(13)	10.7(12)
Interorbital width	4.0(05)	3.6(05)	4.5(06)	4.7(05)	4.7(05)
Upper jaw length	16.8(22)	17.4(23)	17.6(22)	19.0(22)	19.0(21)
Predorsal-fin length	30.1(40)	30.1(40)	31.9(39)	33.5(40)	33.6(38)
Body depth	29.6(39)	27.8(36)	30.8(38)	33.5(40)	33.7(38)
Pectoral fin length	23.7(31)	24.2(32)	25.9(32)	23.9(28)	27.0(30)
Pelvic fin length	23.0(30)	23.0(30)	23.7(29)	23.5(28)	25.8(29)
Caudal fin length	25.3(33)	23.8(31)	26.6(33)	26.7(31)	27.0(30)
Length 3rd dorsal spine	18.8(25)	18.6(24)	20.4(25)	21.0(25)	18.9*(21)
Length 11th dorsal spine	7.0(09)	6.4(08)	6.7(08)	7.4(09)	7.7(09)
Length 12th dorsal spine	13.5(18)	12.5(16)	13.0(16)	13.8(16)	14.7(17)
Length 1st anal spine	8.3(11)	8.0(10)	9.2(11)	9.6(11)	11.2(13)
Length 2nd anal spine	18.3(24)	18.4(24)	19.6(24)	18.6(22)	19.8(22)
Length 3rd anal spine	15.4(20)	14.7(19)	15.7(19)	15.4(18)	16.5(19)

* Broken at tip

Table 4. (continued)

	USNM 214044	CAS 30237	CAS 30237	CAS 30239	USNM 214046	USNM 214042
Standard length	110	110	112	118	124	135
Dorsal rays	XII, 9½	XII, 9½	XII, 9½	XII, 9½	XII, 9½	XII, 9½
Anal rays	III, 5½	III, 5½	III, 5½	III, 5½	III, 5½	III, 5½
Pectoral rays	17+17	17+17	17+17	17+17	17+17	17+17
Gill rakers (upper, lower)	5, 11	5, 11	5, 11	5, 11	5, 11	5, 11
Head length	50.7(46)	54.1(49)	53.2(48)	54.1(46)	56.2(45)	62.1(46)
Snout length	13.0(12)	13.5(12)	13.7(12)	14.3(12)	15.6(13)	15.7(12)
Orbit diameter	15.2(14)	15.4(14)	14.3(13)	16.5(14)	15.3(12)	17.9(13)
Interorbital width	5.2(05)	6.2(06)	6.2(06)	6.0(05)	6.7(05)	7.2(05)
Upper jaw length	24.6(22)	25.2(23)	25.3(23)	26.0(22)	27.9(22)	31.0(23)
Predorsal-fin length	42.6(38)	44.5(40)	45.6(41)	45.8(39)	48.0(39)	51.8(38)
Body depth	40.3(37)	43.1(39)	44.1(39)	44.5(38)	47.7(38)	50.8(38)
Pectoral fin length	31.8(29)	32.4(29)	33.3(30)	33.3(28)	35.7(29)	39.5(29)
Pelvic fin length	30.5(28)	31.0(28)	31.3(28)	31.6(27)	35.0(28)	37.5(28)
Caudal fin length	34.0(31)	34.3(31)	35.7(32)	36.7(31)	37.5(30)	42.1(31)
Length 3rd dorsal spine	24.7(22)	25.8(23)	24.3(22)	25.9(22)	28.9(23)	28.8(21)
Length 11th dorsal spine	8.6(08)	10.1(09)	8.6(08)	10.3(09)	11.3(09)	10.2(08)
Length 12th dorsal spine	17.3(16)	18.4(17)	17.3(15)	18.5(15)	19.5(16)	20.8(15)
Length 1st anal spine	11.2(10)	11.9(11)	11.2(10)	14.4(12)	14.8(12)	13.3(10)
Length 2nd anal spine	23.0(21)	23.8(22)	23.6(21)	25.2(21)	26.6(21)	25.9(19)
Length 3rd anal spine	19.4(18)	20.7(19)	19.5(17)	21.7(18)	23.2(19)	25.6(19)

Name. The specific name is based on Pele, the Hawaiian goddess of volcanoes and volcanic fires, alluding to the red coloration of the species. It is to be treated as a noun in apposition.

Scorpaena colorata (Gilbert).

(Figure 25b.)

Sebastapistes coloratus Gilbert, 1905, pp. 627–628, fig. 243 (original description; type locality Hawaiian Islands, off Molokai, *Albatross* station 3849, holotype USNM 51631, plus paratypes from *Albatross* stations 3849 and 3850); Jordan & Seale, 1906, p. 376 (listed from Hawaii); Jordan & Jordan, 1922, p. 54 (compiled); Jordan & Evermann, 1926, p. 10 (listed); Böhlke, 1953, p. 122 (location of types).

Sebastapistes bynoensis (not of Richardson): Tinker, 1944, p. 266 (compiled; figure of type of *colorata* copied from Gilbert, 1905).

Scorpaena coloratus: Gosline & Brock, 1960, pp. 285, 288, 289, 341 (in key; compiled brief description; synonymy); Gosline, 1965, p. 825 (compiled depth distribution).

Material examined. USNM 51631 (1, 57.2 mm. S. L., holotype of *Sebastapistes coloratus*), and USNM 51667 (2, 44.0–50.8, paratypes of *Sebastapistes coloratus*), south coast of Molokai, N. at 71°, W. 21.9′ from Lae-o Ka Laau Light, in 133.5–78.5 meters, coarse sand, broken shells and coral, 10-ft. Blake trawl, *Albatross* station 3849, 8 Apr. 1902. SU 8618 (1, paratype of *Sebastapistes coloratus*), south coast of Molokai, N. at 74°15′, W. 22.2′ from Lae-o Ka Laau Light, in 78.5–121 meters, coarse sand, broken shells, and coral, 10-ft. Blake trawl, *Albatross* station 3850, 8 Apr. 1902. BPBM 8808 (2, 43.8–63.3), Oahu, off Haleiwa, 21°40′N., 158°07′W., *Townsend Cromwell*, 3 Mar. 1968. BPBM 14130 (1), off Pailolo Channel, in 219 meters, *Townsend Cromwell* (no other data). BPBM 13734 (4, 61.2–70.3), CAS 15705 (8, 43.9–88.0), and CAS 15706 (3, 75–95, cleared and stained), off Oahu, Haleiwa, 21°39.4′–42.5′N., 158°07.1′W., shrimp trawl in 102 meters, *Townsend Cromwell* cruise 40, station 112, 30 Nov. 1968. CAS 15699 (1), off Molokai, 21°14.4′–15.7′N., 157°08.2′–14.5′W., shrimp trawl in 119 meters, *Townsend Cromwell* cruise 40, station 41, 13 Nov. 1968. Additional material is present in the NMFS and CAS collections.

Distinguishing features. Dorsal fin rays XII, 9½. Anal fin rays III, 5½. Pectoral fin rays usually 17 (16–18). Coronal spines absent. Shallow to moderate occipital pit. Scales on sides ctenoid; about 45 vertical scale rows. Lachrymal bone usually with 3 spines, second small and at base of first and both of these directed mostly forward, posterior spine points out and slightly back; middle spine develops when fish is about 40 mm. S. L. Suborbital ridge usually with 3 spines, first under eye, second under rear of eye, third at end of ridge. Often a dark blotch on distal part of spinous dorsal between about spines 7–9.

Scorpaena colorata closely resembles *Scorpaena pele* in live coloration and in most features, but *S. colorata* has a scaled breast, while the area before the pelvic fins is unscaled or with only a few buried scales in *S. pele* (see also the account of *S. pele*).

Distribution. *Scorpaena colorata* is known only from the Hawaiian Islands in depths of about 100–219 meters, with some from uncertain depths between 79–133 meters.

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MUSCULAR ANATOMY OF THE HIND LIMB OF THE SEA OTTER (*ENHYDRA LUTRIS*)

By

L. D. Howard

FOREWORD

In December 1973 the California Academy of Sciences published Dr. Lot D. Howard's work on the muscular anatomy of the forelimb of the sea otter, *Enhydra lutris* (Howard, 1973). This paper represented the results of several years of detailed dissection and anatomical drawing of the front limb musculature of a unique carnivore that has become specialized for life in a marine environment. As Dr. Howard noted in his introduction, one would expect a mammal that lives in the sea and uses its forelimbs for securing food from the bottom, for breaking shellfish on a rock placed on its abdomen, for elaborate grooming of fur, and for holding the young, to have a high degree of muscular specialization. This did not prove to be so. The anatomical features of the limb show a marked resemblance to those of related land mammals. Its functional specialization is basically a result of bimanual use.

Dr. Howard, prior to his retirement to Pebble Beach on the Monterey Peninsula of California, was a world-renowned hand surgeon who had spent years on the staff of Stanford University Medical School. Much of his time in his later years was devoted to watching sea otters in the ocean in front of his home as well as to the anatomical dissection of these animals. Following the completion of his manuscript on the front limb of the sea otter, Dr. Howard began work on the muscular anatomy of the hind limb. Knowing of his own fatal illness, he worked against time to try to complete the dissections and drawings which are presented in this paper and at the time of his death the work was nearly finished. Mr. Judson E. Vandevere of Monterey, California, an authority on sea otters, and Dr. and Mrs. Donald T. Abbott of Stanford University's Hopkins Marine Station at Pacific Grove contributed to the completion of the manuscript.

Robert T. Orr
Associate Director, California
Academy of Sciences.

INTRODUCTION

The following study is a presentation of the musculature of the hind limb of the sea otter. Having published the muscular anatomy of the forelimb of the sea otter (Howard, 1973) it seems only logical that a similar study of the hind limb be undertaken.

The hind limb is grossly different from the forelimb both anatomically and functionally, being used almost exclusively for swimming and showing a high degree of specialization for this purpose. The limb is relatively short and heavily muscled. The hip and knee are semi-flexed and for the most part the foot is in the plantar flexed position. Detailed studies of the use of the hind limbs in swimming have been made by Tarasoff *et al.* (1972).

The hind foot is large compared to the front foot, its length equaling that of the lower leg. Both metacarpals and phalanges are elongated and a generous skin web exists between the digits. The 5th digit is the largest and the longest, and the 1st digit the smallest. The foot becomes twice as wide when the toes are spread. In the hind foot the elongated digits and generous webbing make for individual digit mobility far in excess of that possible in the front foot.

DESCRIPTION OF THE LOWER EXTREMITY OF THE SEA OTTER

Like the upper extremity, the lower extremity is relatively short in comparison with body length and is heavily muscled in the upper and lower leg.

The foot is highly developed for aquatic propulsion and is completely covered with fur. The skin of the foot is soft and mobile with the exception of the terminal digital pads. Broad, soft webbing of skin is present between the toes extending in slightly scalloped fashion to the very tips of the digits. Unlike the forefoot or hand and in spite of the heavy fur cover, the individual digits are grossly identifiable on both volar and dorsal surfaces.

Even in the preserved specimen, the individual digital joints are highly mobile. Three phalanges are present in digits five, four, three, and two, with but two phalanges in the 'great toe' which in this case is the smallest digit. The proximal or metacarpal phalangeal joints hyperextend approximately 40° beyond the straight line. Flexion is to 110°. The middle toe joints or proximal interphalangeals extend to 55° beyond the straight line and flex to 115°. The distal joints or distal interphalangeal joints extend to 45° above the straight line and flex to 65°. For digit one, only a single interphalangeal joint is present. This single interphalangeal joint extends to approximately 45° beyond the straight line and flexes to approximately 75°

When spread, the distance between the tips of toes one and five is twice, or a little more than twice, the distance when the toes are together.

An arched and curved claw is present for each digit. Each is about equal in size, the one on digit four being perhaps slightly heavier. The distal pads cover the plantar aspect of the terminal phalanges covering approximately the distal one-third or one-fourth of the middle phalanx. A small pad also occurs at the base the 'great toe.'

Due to the extreme mobility of the small joints of the foot, when the metacarpal, phalangeal, and interphalangeal joints are flexed to their passive limits the tips of the toes actually touch the sole of the foot, curving around an ample area to permit actual grasp of objects (two or three fingers in a grip-like manner). Vandevere (pers. commun.) has seen on numerous occasions food, a tool, and a pup held against the body but never grasped by the toes.

Also because of the interdigital webs, the individual digits themselves are more highly mobile and thus the pad of the fifth can touch the pads of the fourth and the third in the manner of apposition, and can touch the pads of the second and the first in the configuration of opposition.

Thus it would appear that the foot has the potential of being rather highly prehensile in contrast to the hand, yet in spite of this the foot serves mainly for locomotion in water and to a degree for grooming. The foot appears to be more suitable than the hand as an organ for grasping food and the hand is superior to the foot as an organ for locomotion on land.

Thus the extremities present a kind of a paradox for a mammal returning to the sea. The hind legs and feet have made ready adaption for aquatic locomotion, the forefoot or hand seeming to persist in a form for ambulation on land. An amusing conclusion would be that the animal entered the sea backwards! Perhaps the forelimbs are becoming functionally obsolete as organs of locomotion in swimming.

An outstanding feature is the development of the outer side of the foot, with the fifth digit, the shortest in land mammals, becoming more massive and longer than all of the remaining digits. In seals the fifth digit has also become massive and long, but not noticeably more massive or longer than the great toe. When sea otters are swimming on their backs, this development of their fifth digit gives maximum skulling surface and the largest excursion of motion. In underwater swimming, accomplished by undulations of the body in the AP diameter, the trailing feet can take on the general configuration of the flukes of a whale.

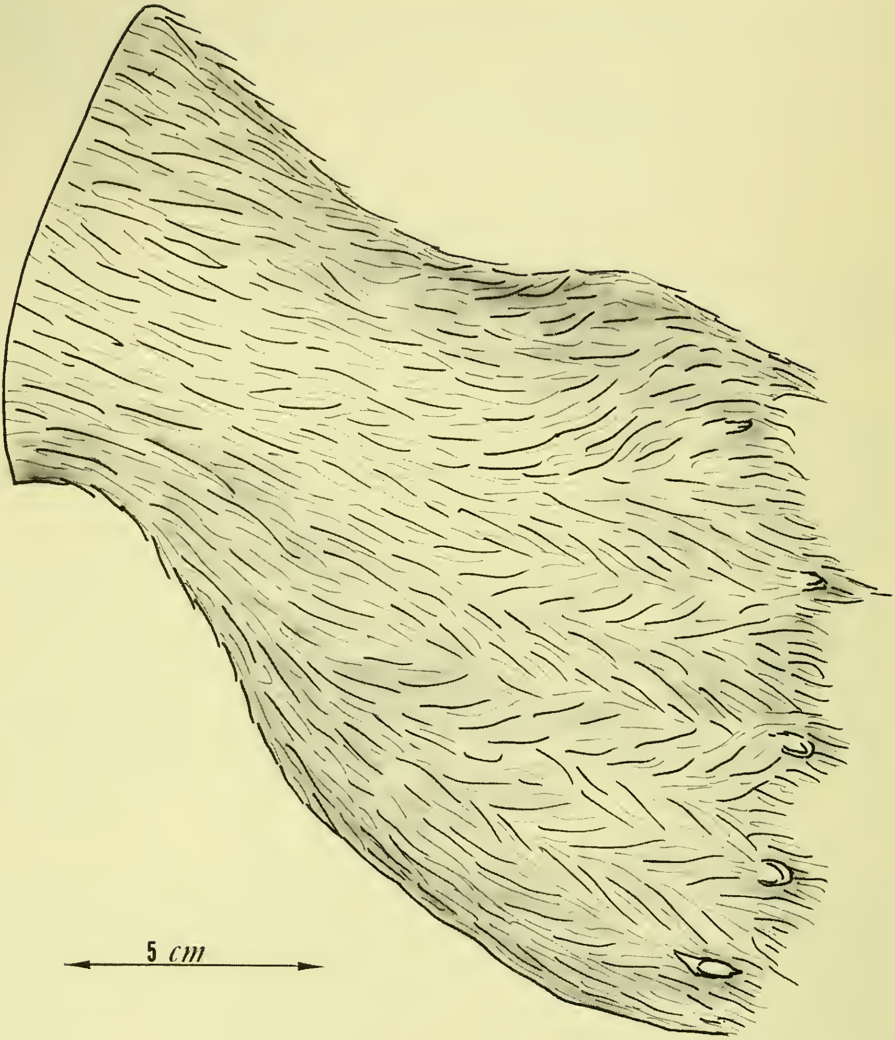

Figure 1. Dorsal view of right hind foot. Note elongation of the digits on the lateral side of the foot so that the fifth digit becomes the longest. Also note the tendency of the digits to angulate slightly medially.

The claws terminate the distal phalanges of each digit. Unlike the forefoot, the terminal phalanges are not hyperextended but lie in line with the proximal and middle phalanges.

Skin webbing between the digits is extensive and the entire dorsal surface of the foot is covered with hair.

MUSCLES OF THE HINDLIMB OF THE SEA OTTER
ALPHABETICAL LISTING

Muscle	No.	Muscle	No.
Abductor digiti quinti	40	Interossei (interosseus)	46
Abductor hallucis	43	Lumbricales	48
Adductor digiti quinti	41	Obturator externus	21
Adductor femoris	5s = superficial 5d = deep	Obturator internus	23
		Opponens digiti quinti	42
Adductor hallucis	44	Panniculus carnosis	A
Adductor longus	5-A	Pectineus	6
Biceps femoris	12	Peroneus brevis	30
Caudofemoralis	11	Peroneus digiti quinti	29
Calcaneometatarsalis	39	Peroneus longus	28
Extensor digitorum brevis	47	Plantaris	31
Extensor digitorum longus	27	Popliteus	32
Extensor hallucis proprius (longus)	26	Presemimembranosus	17
Flexor digitorum brevis	37	Piriformis	19
Flexor digitorum longus	36	Quadratus plantae	38
Flexor hallucis longus	35	Rectus femoris	7
Gastrocnemius	24	Sartorius	1
Gemelli (gemellus)	20	Semimembranosus	4
Gluteus maximus	9	Semitendinosus	3
Gluteus medius	16	Tenuissimus	13
Gluteus minimus	18	Tibialis anterior	25
Gracilis	2	Tibialis posterior	34
Iliocapsularis (quadratus femoris)	22	Vastus medialis	14
Iliopsoas	8	Vastus lateralis	10

DESCRIPTIONS OF MUSCLES

A. **Panniculus carnosis.**

This voluntary muscle for moving the skin is well developed in the area of the hind limb of the sea otter. The skin and subcutaneous tissues are very mobile over the underlying deep fascia. The panniculus carnosis muscle is a broad thin layer of rather coarse longitudinal muscle fibers closely attached to the undersurface of the skin, so closely that rather meticulous sharp dissection is required to separate them.

ORIGIN. For the hind limb, this muscle layer is a continuation of that present in the trunk area. The fibers paralleling the middorsal line cover most of the lateral aspect of the hind limb and wrap about the knee to reach the medial surface of the limb to some degree in this area.

INSERTION. Insertion of this muscle is in the deep layers of the skin as far posteriorly as the skin web between the tail and the ankle.

ACTION. This muscle serves to voluntarily mobilize the skin over the hind limb from the trunk to the heel area.

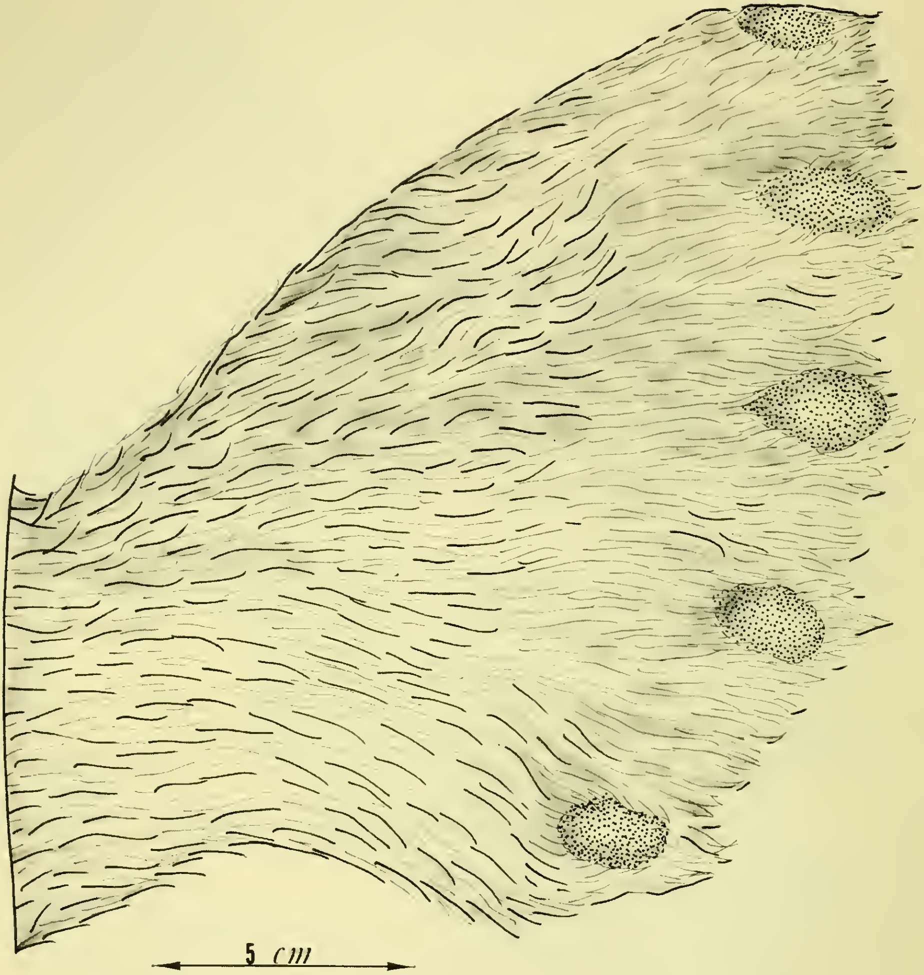

Figure 2. The plantar view of the right hind foot. Note the relatively small pads overlying the terminal phalanges of each digit. A smaller pad at the metatarsophalangeal joint of digit 1 is covered with hair and therefore is out of view. The pads have a rough texture similar to the pads of the forefoot. Hair coverage on the plantar surface of the foot is extensive.

1. Sartorius.

This muscle is fleshy, somewhat flat, and superficial in position, overlying the anterior aspect of the hind limb connecting the pelvis to the knee area.

Origin. The muscle arises by fleshy and short tendinous fibers from the iliac crest. It is the most superficial muscle overlying in part the origins of the glutei musculature. The muscle passes distally from its origin over the anterior thigh, narrowing somewhat and shifting slightly medial.

Insertion. The insertion is along the full length of the patella tendon with some short tendinous fibers entering the medial side of the tibial tubercle.

Action. This muscle assists in extension of the knee through its patellar tendon attachment and also assists in flexion of the hip.

2. Gracilis.

This broad, flat, superficial muscle is on the medial aspect of the lower limb and connects the pelvis with the tibia.

Origin. The muscular fibers of origin come from the full width of the pubis in the area of the symphysis. From its origin, the muscle maintains a constant width and courses like a muscular strap toward the upper tibia.

Insertion. The insertion is by fleshy and short tendinous fibers into the tibial crest beginning at and extending distal to the tibial tubercle. The insertion overlies the insertion of the semitendinosus (3).

Action. This muscle serves to adduct the lower limb and assists in flexion of the knee and internal rotation of the extremity.

3. Semitendinosus.

This muscle is a flat, somewhat triangular superficial muscle joining the caudal area of the axial skeleton to the tibia. This muscle participates with the biceps femoris (12) to form a sort of muscular web between the caudal area and the knee.

Origin. This muscle arises as fleshy and short tendinous fibers from the spinous processes and associated fascia of caudal vertebrae 1–7. The more superior area of origin overlies the origin of the caudofemoralis (11) at the caudal 1–2 level. The muscle now crosses toward the medial side of the tibia and while so doing underlies and gives off a group of muscle fibers to the biceps femoris (12).

Insertion. The muscle narrows as it approaches the tibia and terminates as a short flat tendon which inserts on the crest of the tibia partly under the insertion of the gracilis (2).

Action. This muscle assists in flexion of the knee and internal rotation of the lower limb.

4. Semimembranosus.

This is a somewhat flat muscle connecting the pelvis with the upper tibia.

Origin. Muscular fibers arise superficially along the ischial tuberosity overlying and almost in common with a portion of the superficial division of the adductor femoris (5). The muscle then extends obliquely toward the knee underlying the gracilis (2) and paralleling the adductor femoris (5).

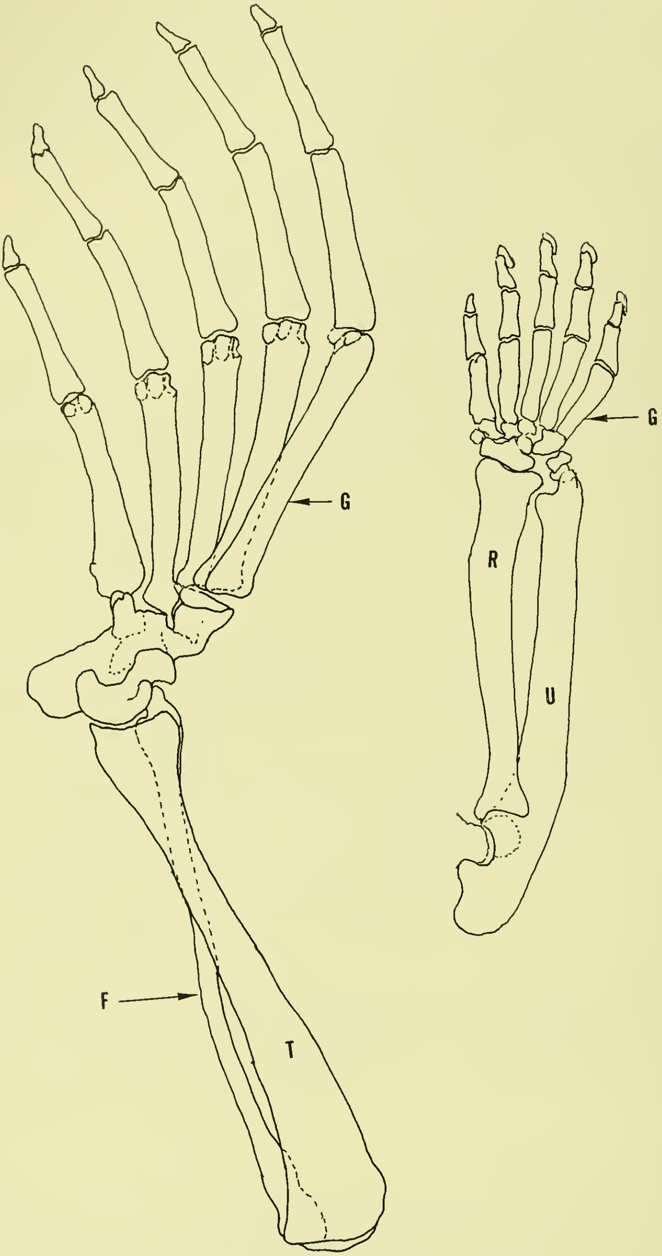

Figure 3. Tracing from an x-ray of the fore limb and hind limb of the same animal to show relationship of length of foot to length of limb and also relative length of digits compared one to the other. Key: F, fibula; G, digit 5; R, radius; T, tibia; U, ulna.

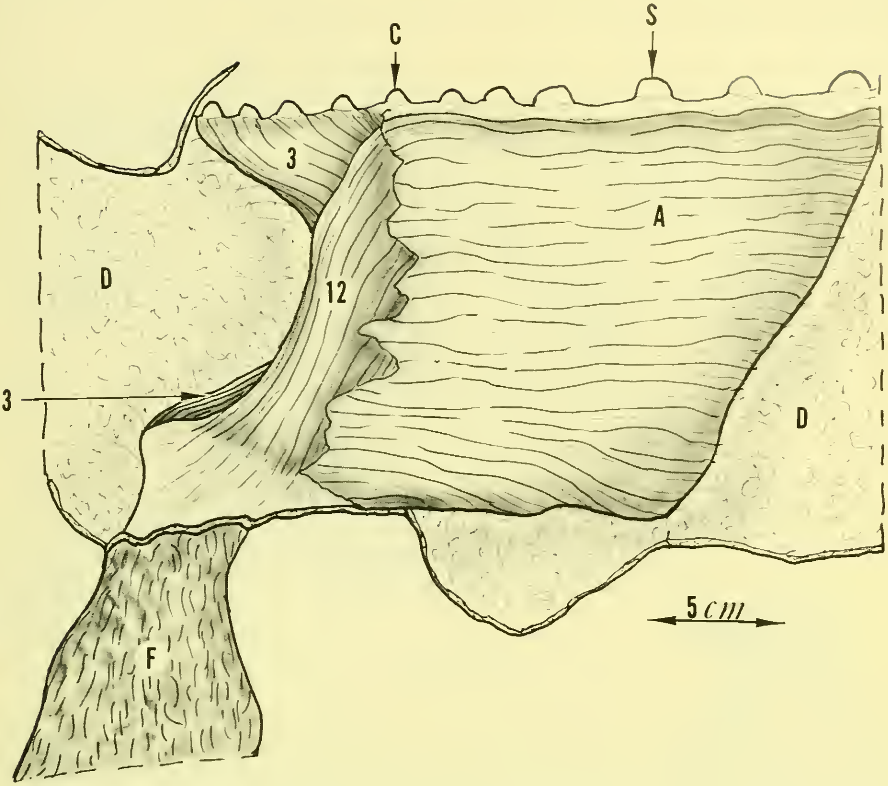

Figure 4. Lateral view of right lower extremity and caudal area. The skin has been carefully dissected from the panniculus carnosis muscle and reflected to show this most superficial muscle (A). The rather coarse parallel muscle fibers terminate in the deep layer of the skin in an irregular manner along the web-like fold of skin between the tail and the heel. Key: C, spinous process of the first caudal vertebra; D, reflected skin and subcutaneous tissue; F, foot; S, spinous process of the first sacral vertebra; A, panniculus carnosis; 3, semitendinosis; 12, biceps femoris; 13, tenuissimus.

Insertion. Nearing its insertion, the muscle narrows to form a short flat tendon which passes under the medial collateral ligament of the knee and inserts on the tibia just medial to the tuberosity at the level of the junction of the insertion of the gracilis (2) and sartorius (1).

Action. This muscle serves as a flexor of the knee and an internal rotator of the lower limb.

5. Adductor femoris.

The adductor femoris is a large muscle joining the pelvis with the femur. It is divided into two: the superficial and deep portions.

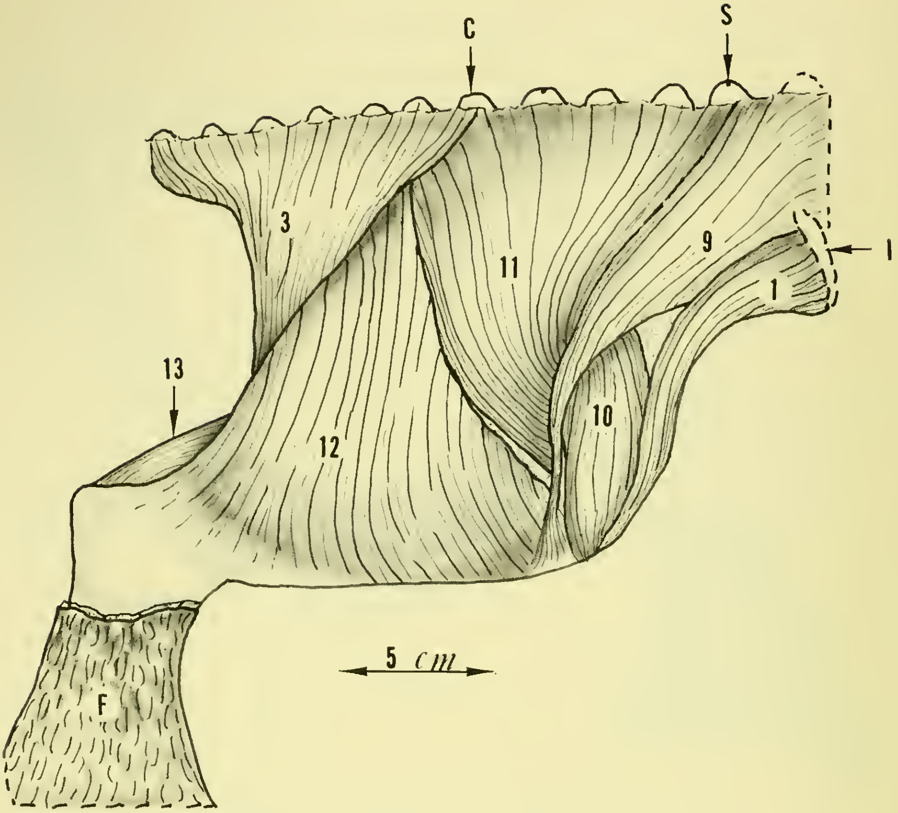

Figure 5. Lateral view of right lower extremity and hip area. The panniculus carnosis muscle (A) has been removed to show the disposition of the superficial musculature beneath. Key: C, spinous process of first caudal vertebra; F, foot; I, iliac crest; S, spinous process of first sacral vertebra; 1, sartorius; 3, semitendinosus; 9, gluteus maximus; 10, vastus lateralis; 11, caudofemoralis; 12, biceps femoris; 13, tenuissimus.

Superficial portion.

Origin. The superficial portion arises from the most distal area of the external surface of the pelvis adjacent to the origin of the semimembranosus and in close association with the deep portion of the adductor femoris. From the semitriangular area of origin the muscle broadens and flattens as it approaches the knee area where it underlies the broad sartorius muscle (1).

Insertion. The insertion by muscular and short tendinous fibers is over a fairly broad area about the knee. The more distal fibers insert into the medial epicondyle area of the femur and the remainder insert into the deep fascia on the medial side of the knee joint.

Action. Adduction of the femur.

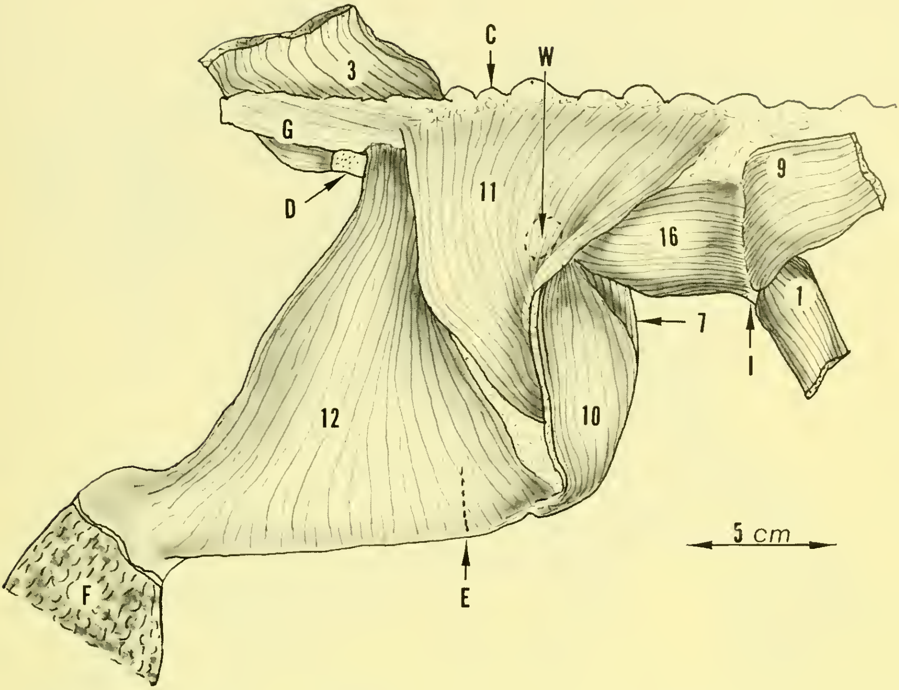

FIGURE 6. Lateral view of right lower extremity and hip area. The sartorius (1) and the gluteus maximus (9) have been reflected superiorly from their origins, and the semitendinosus (3) has been reflected dorsally. Origins of the biceps femoris (12) and the caudofemoralis (11) are more clearly visualized. Seen in the deeper layer of muscle are the gluteus medius (16) and the rectus femoris (7). Key: C, spinous process of the first caudal vertebra; D, ischial tuberosity; E, knee joint level; F, foot; G, caudal musculature; I, iliac crest; W, femur (greater trochanter); 1, sartorius (reflected); 3, semitendinosus (reflected); 7, rectus femoris; 9, gluteus maximus (reflected); 10, vastus lateralis; 11, caudofemoralis; 12, biceps femoris; 16, gluteus medius.

DEEP PORTION.

ORIGIN. The deep portion of this muscle arises from the external surface of the ischium and pubis immediately proximal to and almost in common with the superficial portion. The greater area of the crescent shaped origin is from the pubic bone, where it borders the gracilis muscle (2) origin medially and the origin of the adductor longus (5A) superiorly. From its origin, the muscle parallels the superficial portion as it passes toward the femur.

INSERTION. Distally, the muscle spreads fan-like to insert by tendinous fibers into the posteromedial aspect of the femur. The more distal portion underlies the insertion of the superficial portion of the adductor femoris in

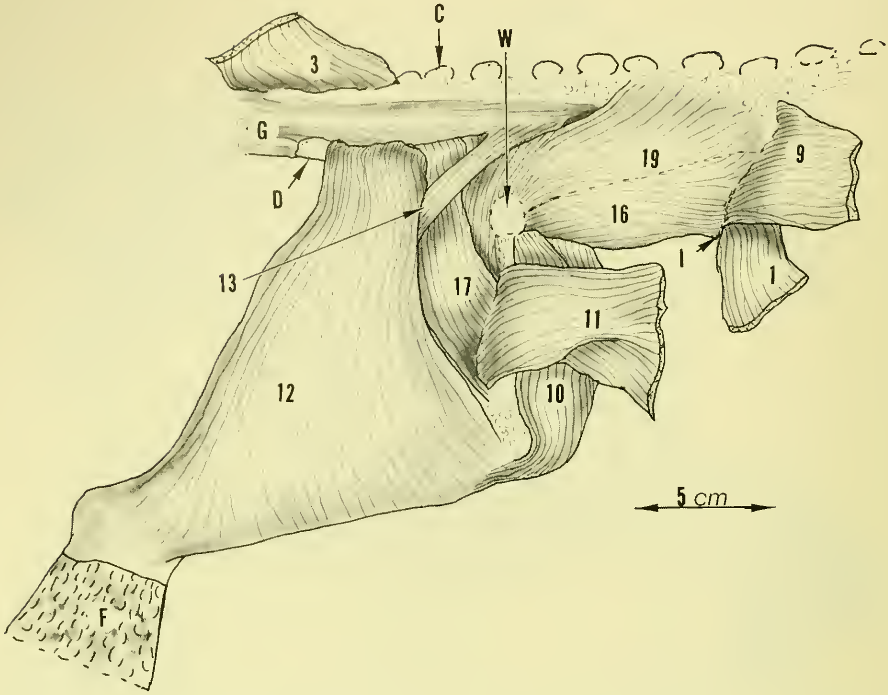

Figure 7. Lateral view of the right lower extremity and hip area, similar to figure 6 but with the caudofemoralis (11) detached at its origin and reflected anteriorly. The deeper muscles are thus exposed, and the area of origin of the biceps femoris (12) and gluteus medius (16) are clearly seen. Key: C, spinous process of first caudal vertebra; D, ischial tuberosity; F, foot; G, caudal musculature; I, iliac crest; W, femur (greater trochanter); 1, sartorius (reflected); 3, semitendinosus (reflected); 9, gluteus maximus (reflected); 10, vastus lateralis; 11, caudofemoralis (reflected); 12, biceps femoris; 13, tenuissimus; 16, gluteus medius; 17, presemimembranosus; 19, piriformis.

the area of the medial epicondyle of the femur. Insertion extends proximally along the medial ridge to the level of the lesser trochanter.

Action. The muscle is an adductor of the femur.

5A. Adductor longus.[1]

This muscle is the most superior of the adductor group and is smaller than the others.

Origin. The origin of this muscle is by short tendinous and muscular fibers from the external surface of the superior ramus of the pubis. At the symphysis the origin is adjacent to the gracilis muscle (2) and superiorly

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[1] There is some indication in Dr. Howard's notes that he intended to renumber this muscle as '15.' Editor.

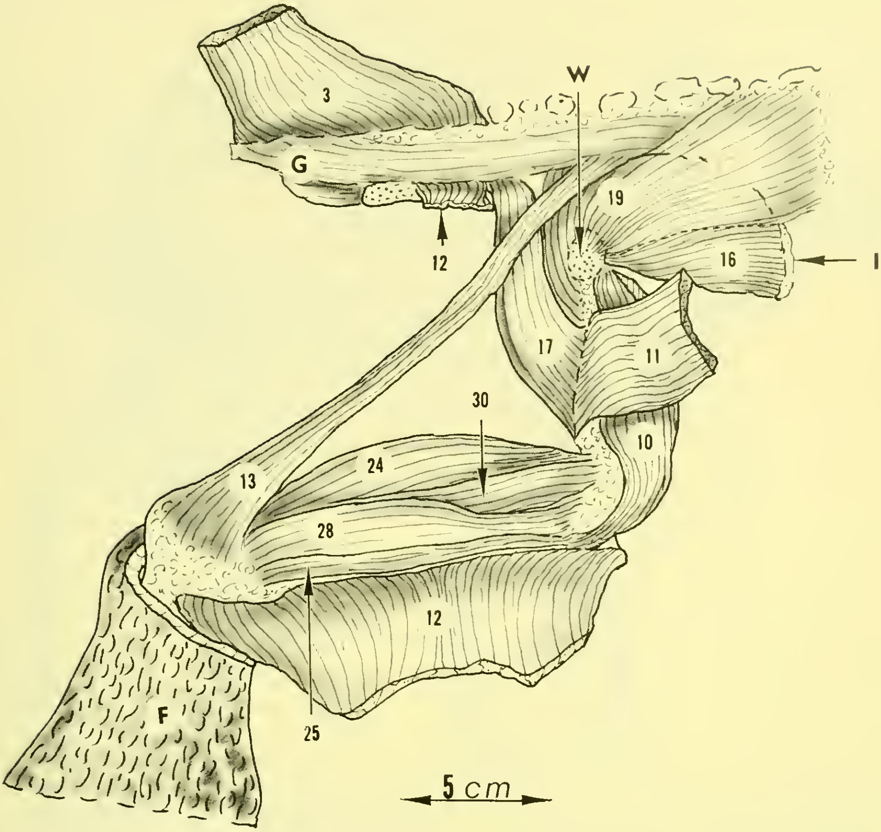

Figure 8. Lateral view of right lower extremity and hip area. The large biceps femoris (12) has been detached from its origin leaving a short stump and reflected anteriorly at its insertion. As a result, the musculature of the lower leg is exposed and the tenuissimus (13) and presemimembranosus (17) are seen from their origin to their insertion. Key: F, foot; G, caudal musculature; I, iliac crest; W, femur (greater trochanter); 3, semitendinosus; 10, vastus lateralis; 11, caudofemoralis (reflected); 12, biceps femoris (reflected from the tibia and also the stub from the pelvis); 13, tenuissimus; 16, gluteus medius; 17, presemimembranosus; 19, piriformis; 24, gastrocnemius; 25, tibialis anterior; 28, peroneus longus; 30, peroneus brevis.

the origin extends to that of the pectineus (6). On the pubis, the origin of the deep portion of the adductor femoris (5) is immediately adjacent distally.

Insertion. This muscle parallels the other adductors to a long insertion the full length of the medial ridge of the femur adjacent and anterior to the deep portion of the adductor femoris (5) and just posterior to the pectineus (6), thus inserting between these two muscles.

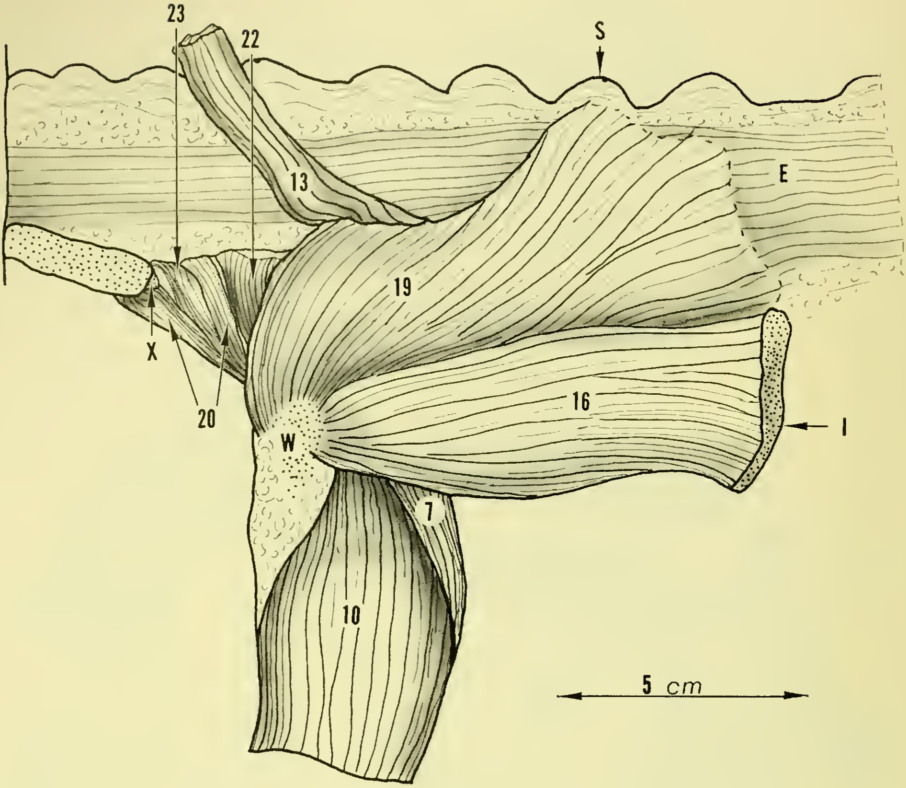

Figure 9. An enlarged dorsolateral view of the right hip area. Superficial muscles have been removed to disclose the deeper musculature about the hip joint and the relationship of these muscles to one another. Key: E, spinal musculature and fascia; I, iliac crest; S, spinous process of first sacral vertebra; W, femur (greater trochanter); X, ischial spine; 7, rectus femoris; 10, vastus lateralis; 13, tenuissimus (reflected); 16, gluteus medius; 19, piriformis; 20, gemelli; 22, iliocapsularis; 23, obturator internus.

Action. Adduction and internal rotation of the femur would result from contraction of this muscle.

6. Pectineus.

This is a smaller muscle, as far as total mass is concerned, but is clearly associated with the adductor group connecting the pelvis to the femur.

Origin. The muscle arises in an elliptical configuration from the full width of the anterior surface of the pelvic bone directly opposite the acetabulum and just proximal to the adductor longus (5A).

Insertion. From its origin, the muscle fans out paralleling the adductors

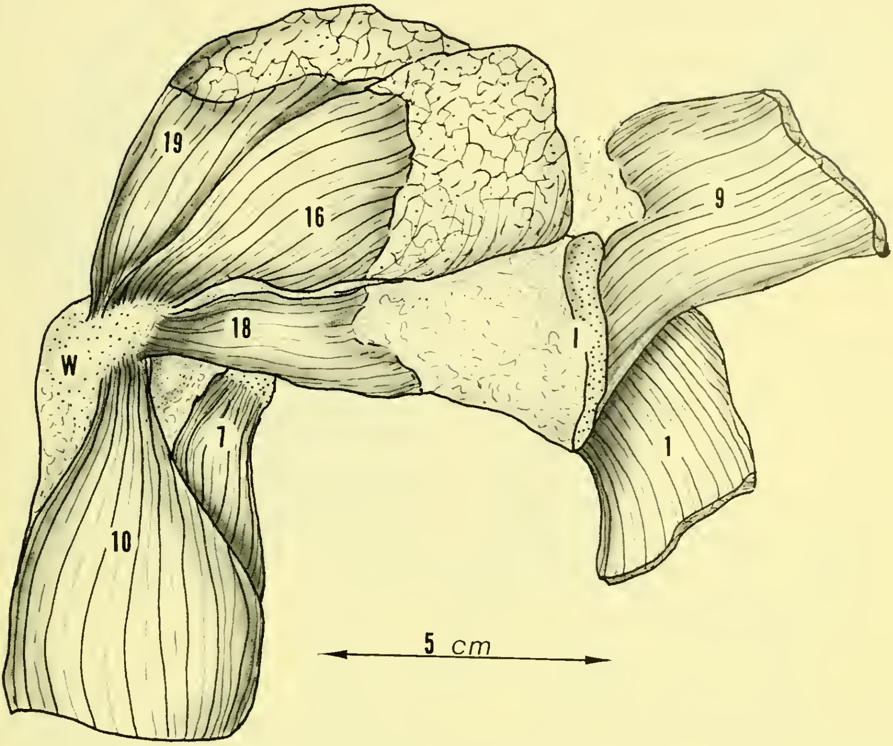

FIGURE 10. An enlarged and localized lateral view of the right hip area. The sartorius (1) and gluteus maximus (9) have been reflected from the iliac crest. The gluteus medius (16) has been peeled off the wing of the ilium and, with the piriformis (19), rolled upward to disclose the gluteus minimus (18). Also visualized are the origins of the rectus femoris (7) and vastus lateralis (10). Key: I, iliac crest and wing of ilium; W, femur (greater trochanter); 1, sartorius (reflected); 7, rectus femoris; 9, gluteus maximus (reflected); 10, vastus lateralis; 16, gluteus medius (reflected); 18, gluteus minimus; 19, piriformis (reflected).

to insert along the full length of the anterior ridge of the femur just anterior to the adductor longus (5A).

ACTION. This muscle would give adduction and internal rotation to the femur.

7. Rectus femoris.

This muscle is round in cross-section proximally and laterally compressed distally. It is a large fusiform muscle overlying the anterior surface of the femur joining the pelvis to the tibia.

ORIGIN. A short strong tendon of origin arises from the pelvic bone

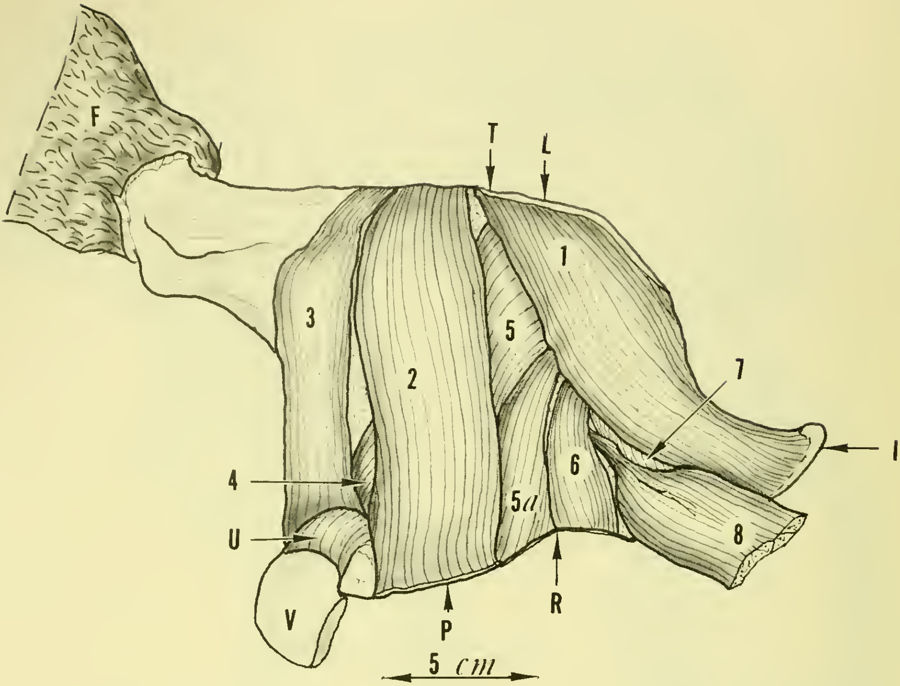

Figure 11. Medial view of the right lower extremity. The limb has been abducted approximately 90° so that the pelvic area presents an anterior view. With the skin and subcutaneous tissues removed, the superficial musculature is shown. Key: F, foot; I, iliac crest; L, patellar ligament; P, symphysis pubis; R, pelvic rim; T, tibial tuberosity; U, perineal muscles; V, penis; 1, sartorius; 2, gracilis; 3, semitendinosus; 4, semimembranosus; 5, adductor femoris; 5A, adductor longus; 6, pectineus; 7, rectus femoris; 8, iliopsoas.

(ilium) just above the acetabulum in the anterolateral area. At the site of origin, the bone has two shallow crater-like depressions joined by a slight ridge of bone. From its tendinous origin the muscle enlarges in a spindle-like form passing distally along the anterior femur overlying and being bordered by the vastus medialis (14) and vastus lateralis (10).

Insertion. Tendinous fibers of insertion begin developing in the distal one-third of the muscle, particularly on the medial side. A strong tendon is present at the insertion into the proximal end of the patella. Laterally, the tendon of insertion of the vastus lateralis (10) joins in to make a common insertion. Medially, the vastus medialis (14) with fleshy fibers underlies the rectus femoris tendon but inserts into the patella to the medial side of the rectus femoris tendon. The strong patellar tendon then continues the insertion of all three muscles to the tibial tubercle.

Action. Strong extension of the knee.

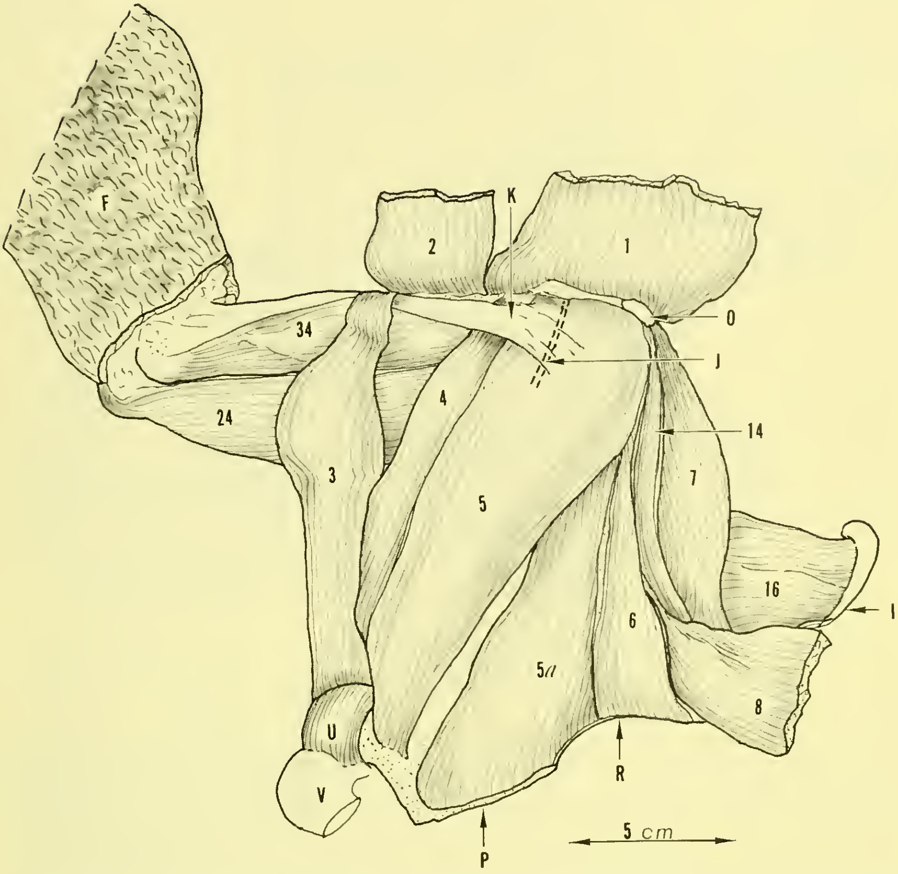

Figure 12. Medial view of abducted right lower leg. The sartorius (1) and the gracilis (2) have been reflected at their insertions to show relationship of the underlying deeper musculature. The medial collateral ligament of the knee takes its origin from the femur in the area of insertion of the superficial portion of the adductor femoris (5). Key: F, foot; J, tibial plateau; K, medial collateral ligament of the knee; O, patella; P, symphysis pubis; R, pelvic rim; U, perineal muscle; V, penis; 1, sartorius (reflected); 2, gracilis (reflected); 3, semitendinosus; 4, semimembranosus; 5, adductor femoris; 5A, adductor longus; 6, pectineus; 7, rectus femoris; 8, iliopsoas; 14, vastus medialis; 16, gluteus medius; 24, gastrocnemius; 34, tibialis posterior.

8. **Iliopsoas.**

This is a large heavy muscle connecting the lumbar spine and ilium with the femur.

Origin. Superior portion of this large muscle arises from the volar surfaces of the transverse processes of the last three lumbar vertebrae and adjacent fascia. As the muscle forms and passes caudally into the pelvis, an additional

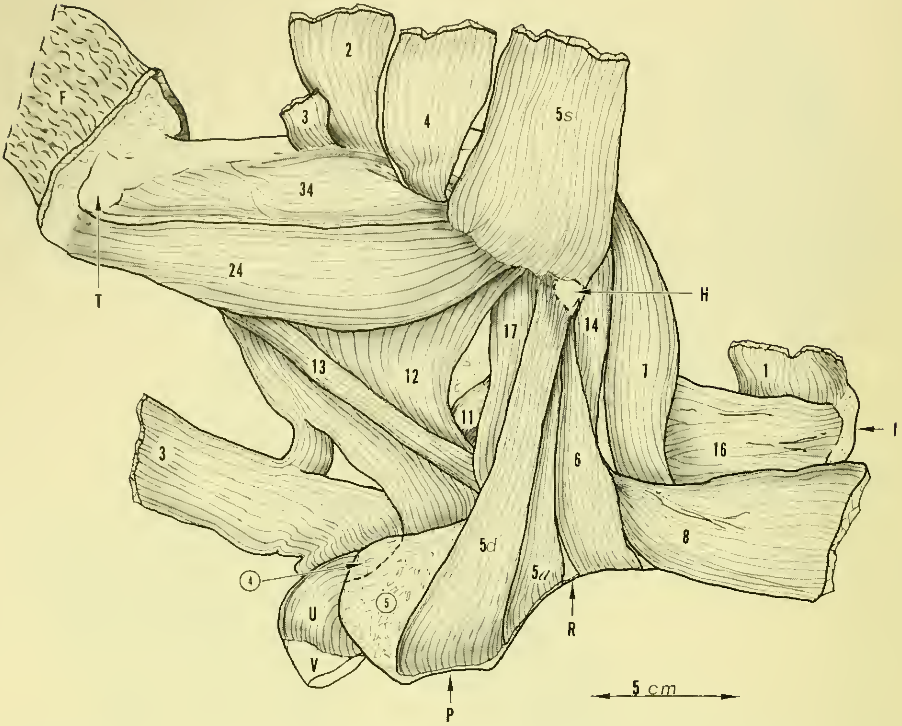

FIGURE 13. Medial view of abducted right lower extremity, similar to figure 12. The semimembranosus (4) and the superficial portion of the adductor femoris (5) have now been removed at their origin from the pubis and reflected at their insertions. Further detail of the adductor muscles is made visible, and other deep muscles shown in relationship to one another. Note the contribution of muscle fibers from the semitendinosus (3) to the biceps femoris (12). That portion of the sartorius (1) which arises from the iliac crest is shown reflected at that site. Key: F, foot; H, femur (medial epicondyle); P, symphysis pubis; R, pelvic rim; T, tibia (medial malleolus); U, perineal muscles; V, penis; 1, sartorius (reflected); 2, gracilis (reflected); 3, semitendinosus, origin and reflected muscle; 4, semimembranosus, origin and reflected muscle; 5, adductor femoris (origin of superficial portion); 5S, adductor femoris (superficial portion reflected); 5D, adductor femoris (deep portion); 5A, adductor longus; 6, pectineus; 7, rectus femoris; 8, iliopsoas; 11, caudofemoralis; 12, biceps femoris; 13, tenuissimus; 14, vastus medialis; 16, gluteus medius; 17, presemimembranosus; 24, gastrocnemius; 34, tibialis posterior.

area of origin develops from the anterior surface of the ilium immediately adjacent to the sacroiliac joint.

INSERTION. The muscle becomes elliptical in transverse section and tapers into a heavy tendon which dips deeply along the side of the vastus medialis (14) to insert on the medial side of the lesser trochanter of the femur.

ACTION. Flexion and external rotation of the femur.

9. Gluteus maximus.

This is a flat triangular muscle lying over the extensor surface of the hip area connecting the pelvis with the femur and lateral fascia of the tibia.

Origin. This muscle arises as a broad thin tendon from the outer side of the iliac crest. The origin is more or less fused with the tendon of origin of the gluteus medius (16). The anterior one-half of the origin underlies the origin of the muscle sartorius (1). The posterior one-half arises from the lumbar fascia overlying the spinal musculature in the area of the last lumbar vertebra. The muscle is superficial in position and from its origin triangulates toward the greater trochanter of the femur.

Insertion. Near the upper femur, a short flat tendon develops from the greater portion of the muscle and inserts into the distal end of the greater trochanter, more or less in common with the proximal end of the caudofemoralis (11) insertion. Some of the more lateral fibers remain superficial and appear to insert into the deep fascia on the lateral aspect of the hip with continuation toward the knee. This portion may represent a tensor fascia lata muscle, although such a muscle is not specifically present in the sea otter.

10. Vastus lateralis.

This is the larger of the two vasti muscles which join the femur with the tibia through the patella and patella ligament.

Origin. Fleshy fibers take origin from the proximal and lateral one-half of the femur. The origin begins on the anterior surface of the greater trochanter adjacent to the insertion of the gluteus minimus (18) and medius (16). The muscle then passes distally toward the knee joint where it joins with the rectus femoris (7).

Insertion. The more lateral muscle fibers continue along the patella laterally and insert distal to but in the same plane as the tendon of the rectus femoris (7). The more medial fibers, which join in part with the rectus femoris (7), also form a strong short flat tendon which inserts into the lateral one-half of the proximal pole of the patella just under the rectus femoris (7) tendon.

Action. Extension of the knee through the patella and patella tendon.

11. Caudofemoralis.

This heavy superficial triangular muscle on the lateral aspect of the hip area connects the spine to the femur.

Origin. The muscle arises from the spinous processes and deep fascia over the spinal muscles from the level of the last lumbar vertebra, the sacrum, and the first two caudal vertebrae. Inferiorly, the origin overlies two-thirds of the origin of the biceps femoris (12) and also the origin of the tenuissimus (13). Superiorly, the origin borders out of the gluteus maximus (9).

Insertion. From its origin, the muscle triangulates somewhat and, passing over the greater trochanter, spreads to its insertion along the lateral femoral ridge of the inferior border of the greater trochanter to the upper border of the lateral femoral condyle.

Action. Abduction and external rotation of the femur.

12. **Biceps femoris.**

This is a very heavy and strong triangular muscle appearing superficially as the most prominent muscle on the lateral aspect of the lower limb. The muscle connects the pelvis to the tibia.

Origin. The origin is by muscular tendinous fibers arising from a double bony exostosis-like protuberance along the posterior margin of the ischium just above the ischial tuberosity.

Insertion. From its origin, the muscle spreads out fan-like to encompass the full length of the lower leg. Terminally, a thin flat tendon forms which inserts along the full length of the tibial crest laterally. Proximally, the insertion begins on the midlateral area of the tibia just below the joint surface. Distally, the tendinous fibers spread out into the deep fascia covering the entire lateral aspect of the ankle.

Action. This muscle acts as a flexor of the knee and external rotator of the lower limb.

13. **Tenuissimus.**

This is a long, uniformly thin and flat strap-type muscle bridging the sacrum to the ankle.

Origin. This muscle arises as mostly muscular fibers from the transverse process of the third sacral vertebra and adjacent spinal muscle fascia. From here, the muscle courses diagonally toward the ankle, overlying the presemimembranosus (17) and underlying the caudofemoralis (11) and the biceps femoris (12).

Insertion. At the ankle, the muscle inserts into a fascia-like structure on the lateral aspect which has attachments to the lateral malleolus and to the calcaneus.

Action. Action of this muscle would be to flex the knee and to plantar flex the ankle.

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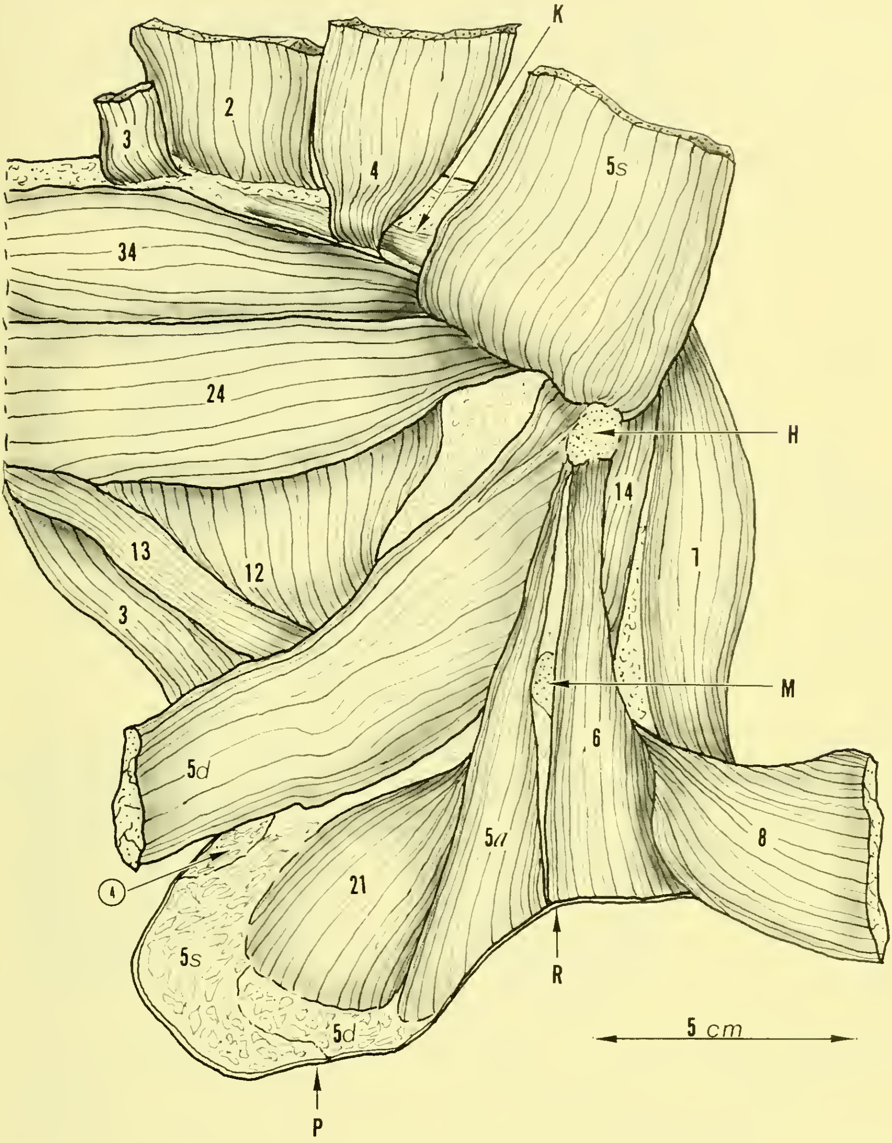
Figure 14. Medial view of abducted right lower extremity, similar to figure 13, but in addition to the other reflected muscles, the deep portion of the adductor femoris (5D) has been removed from its origin and reflected distally. The relationship between the adductor longus (5A) and the pectineus (6) is now seen, and also the origin of the obturator



externus (21) is made visible. Key: H, femur (medial epicondyle); K, medial collateral ligament of knee; M, femur (lesser trochanter); P, symphysis pubis; R, pelvis rim; 2, gracilis (reflected); 3, semitendinosus (reflected); 4, semimembranosus (origin and reflected muscle); 5A, adductor longus; 5S, adductor femoris (superficial portion, origin and reflected muscle); 5D, adductor femoris (deep portion, origin and reflected muscle); 6, pectineus; 7, rectus femoris; 8, iliopsoas; 12, biceps femoris; 13, tenuissimus; 14, vastus medialis; 21, obturator externus; 24, gastrocnemius; 34, tibialis posterior.

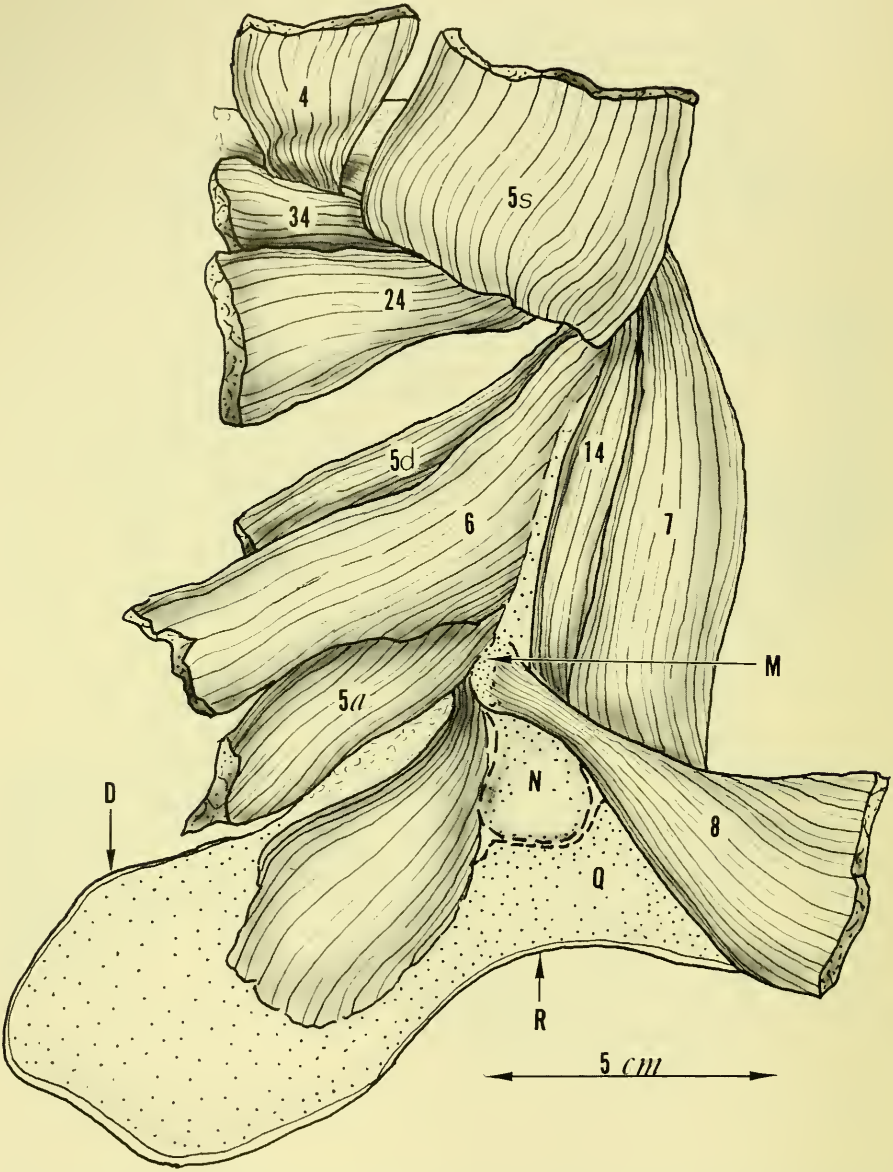


FIGURE 15. Medial view of abducted right lower extremity, similar to figures 13 and 14, but in addition the adductor longus (5A) and the pectineus (6) have been detached from their origins on the pelvis and reflected distally. By so doing, the head of the femur and the hip joint are exposed. Also, the insertion of the iliopsoas (8) can be seen as well as the relationship of the adjacent muscle. Key: D, ischial tuberosity; M, femur (lesser tuberosity); N, head of femur; Q, pelvis; R, pelvic rim; 4, semimembranosus; 5A, adductor

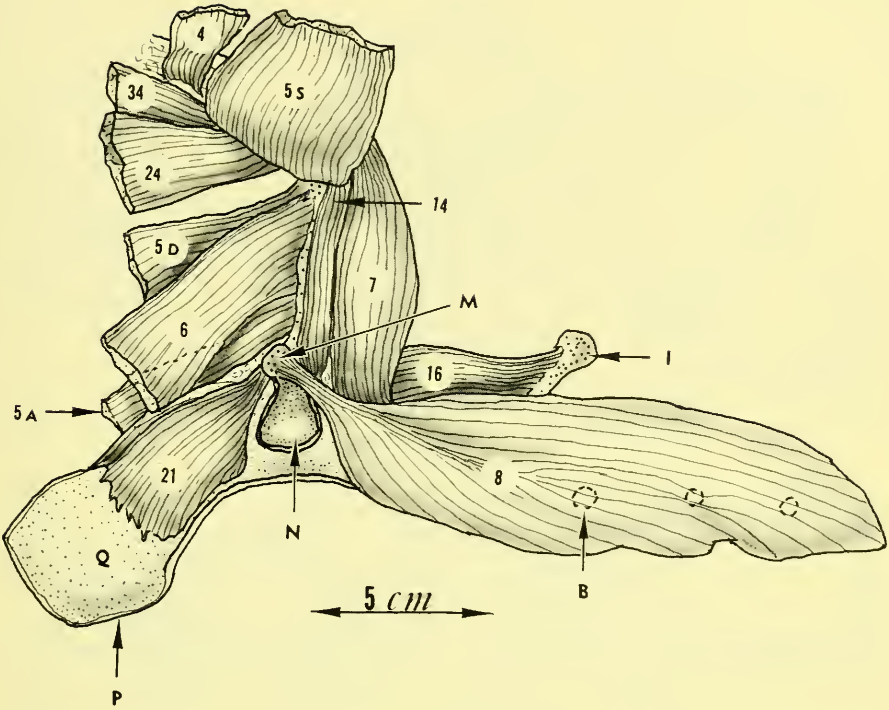


Figure 16. Medial view of abducted right lower extremity and ventral view of pelvis. The origin and insertion of the iliopsoas (8) muscle is shown. All of the deep muscles can be identified. Key: B, transverse process, last lumbar vertebra; I, iliac crest; M, femur (lesser trochanter); N, head of femur; P, symphysis pubis; Q, pelvis; 4, semimembranosus (reflected); 5A, adductor longus (reflected); 5S, adductor femoris (superficial portion, reflected); 5D, adductor femoris (deep portion, reflected); 6, pectineus (reflected); 7, rectus femoris; 8, iliopsoas; 14, vastus medialis; 16, gluteus medius; 21, obturator externus; 24, gastrocnemius; 34, tibialis posterior.

14. Vastus medialis.

This smaller of the two vasti muscles joins the femur to the tibia as a component of the extensor mechanism of the knee.

Origin. Fleshy fibers arise from the medial one-half of the anterior surface of the femur. Proximally, the origin tapers to a point on the base of

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longus (reflected); 5S, adductor femoris (superficial portion, reflected); 5D, adductor femoris (deep portion, reflected); 6, pectineus (reflected); 7, rectus femoris; 8, iliopsoas; 14, vastus medialis; 24, gastrocnemius; 34, tibialis posterior.

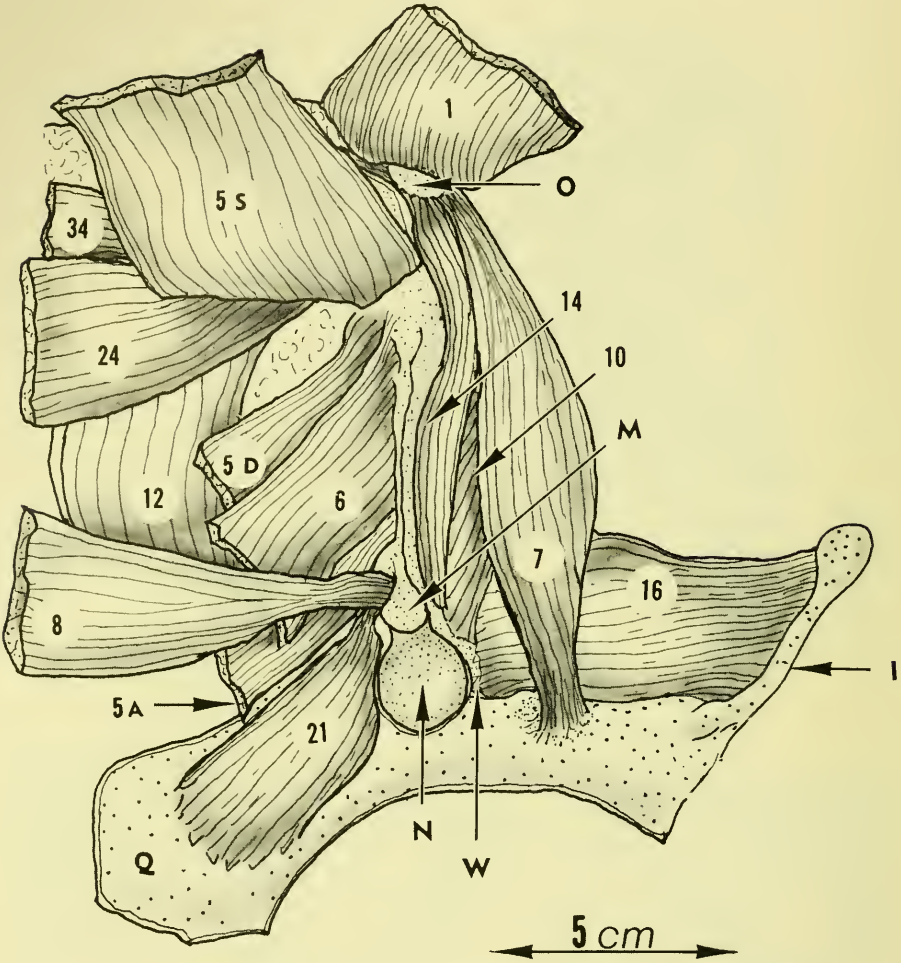

Figure 17. Medial view of abducted right lower extremity, similar to figure 16. The iliopsoas (8) has been detached from its origin on the lumbar vertebra and ilium and reflected posteriorly. Doing so uncovers the origin of the rectus femoris (7) and, with the rectus femoris displaced anteriorly a bit, the proximal origin of the vastus medialis (14) and vastus lateralis (10) can be seen. Also, the gluteus medius (16) can be seen going toward its insertion on the greater trochanter. Key: I, iliac crest; M, femur (lesser trochanter); N, head of femur; O, patella; Q, pelvis; W, femur (greater trochanter); 1, sartorius (reflected); 5A, adductor longus (reflected); 5S, adductor femoris (superficial portion, reflected); 5D, adductor femoris (deep portion, reflected); 6, pectineus (reflected); 7, rectus femoris (displaced); 8, iliopsoas (reflected); 10, vastus lateralis; 12, biceps femoris; 14, vastus medialis; 16, gluteus medius; 21, obturator externus; 24, gastrocnemius; 34, tibialis posterior.

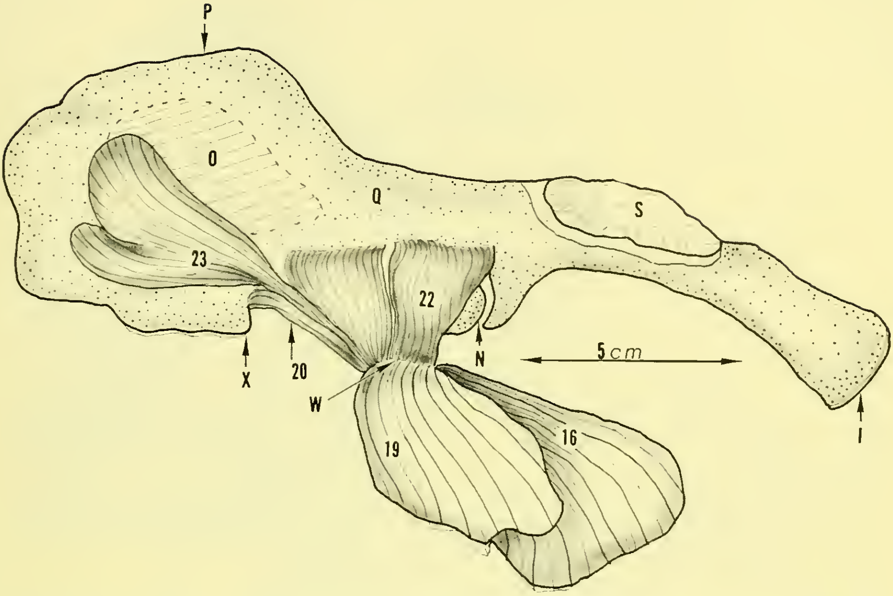

FIGURE 18. Medial view of right pelvis after disarticulation through the sacroiliac joint. The femur is viewed end-on from its proximal end, and the hip joint is visible. The gluteus medius (16) and piriformis (19) are reflected outward, and the origins and insertions of the short hip muscles can be seen. Key: I, iliac crest; N, head of femur; O, obturator foramen; P, symphysis pubis; Q, pelvis; S, sacroiliac joint; W, femur (greater trochanter); X, ischial spine; 16, gluteus medius; 19, piriformis; 20, gemelli; 22, iliocapsularis; 23, obturator internus.

the neck of the femur. Distally, the origin extends to just proximal to the articular surface, at which point it underlies the rectus femoris (7).

INSERTION. A short tendon forms distally and inserts into the medial one-half of the proximal end of the patella. This tendon partially underlies that of the vastus lateralis (10), which in turn underlies in part the rectus femoris (7) tendon.

ACTION. The action of this muscle is to extend the knee through the patella and its patellar tendon.

15. There is some indication in Dr. Howard's notes that muscle 5A—the adductor longus—should be numbered '15.' Editor.

16. **Gluteus medius.**

This large pyramidal-shaped muscle of coarse fibers connects the wing of the ilium to the greater trochanter of the femur.

ORIGIN. The muscle arises as fleshy fibers from most of the lateral surface

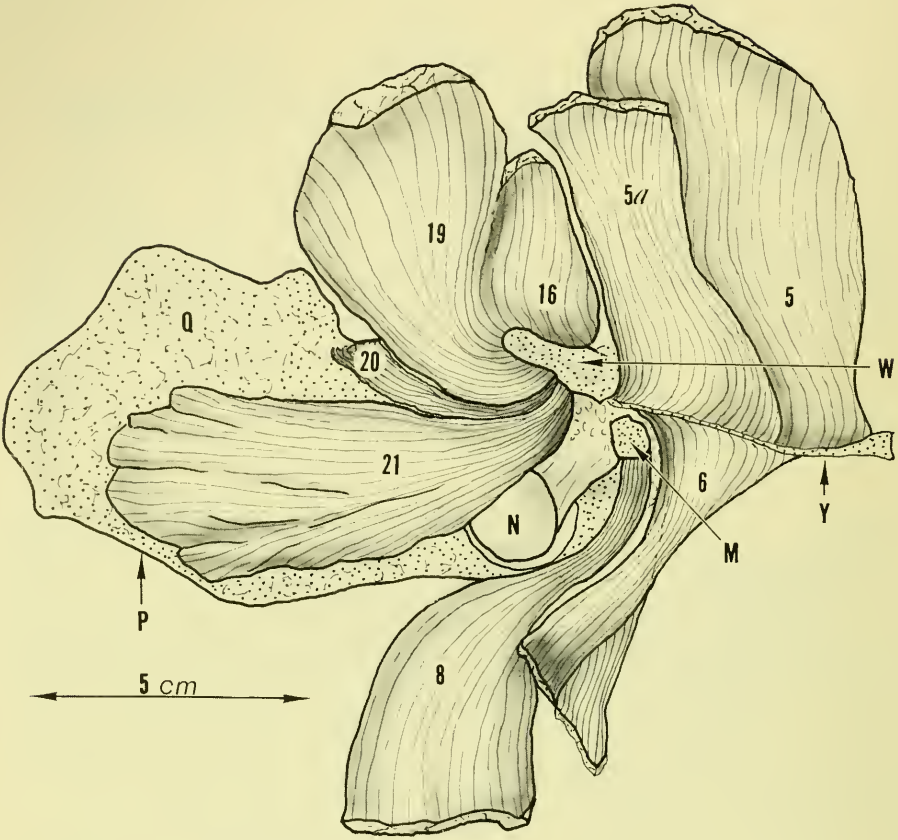

FIGURE 19. Lateral view of right pelvis with hip flexed and internally rotated so that the femur presents a posterior view showing both greater and lesser trochanters. Visible also are the head and neck of the femur and the hip joint. The obturator externus (21) is seen throughout its course. The other muscles have been reflected to disclose their insertions. Key: M, femur (lesser trochanter); N, head of femur; P, symphysis pubis; Q, pelvis; W, femur (greater trochanter); Y, femur (posterior ridge); 5, adductor femoris; 5A, adductor longus; 6, pectineus; 8, iliopsoas; 16, gluteus medius; 19, piriformis; 20, gemelli; 21, obturator externus.

of the wing of the ilium from the crest area to the lower border of the sacroiliac joint dorsally. The origin is practically inseparable from that of the gluteus minimus (18), which is immediately anterior and inferior on the iliac wing surface. Posteriorly, the muscle is practically inseparable from

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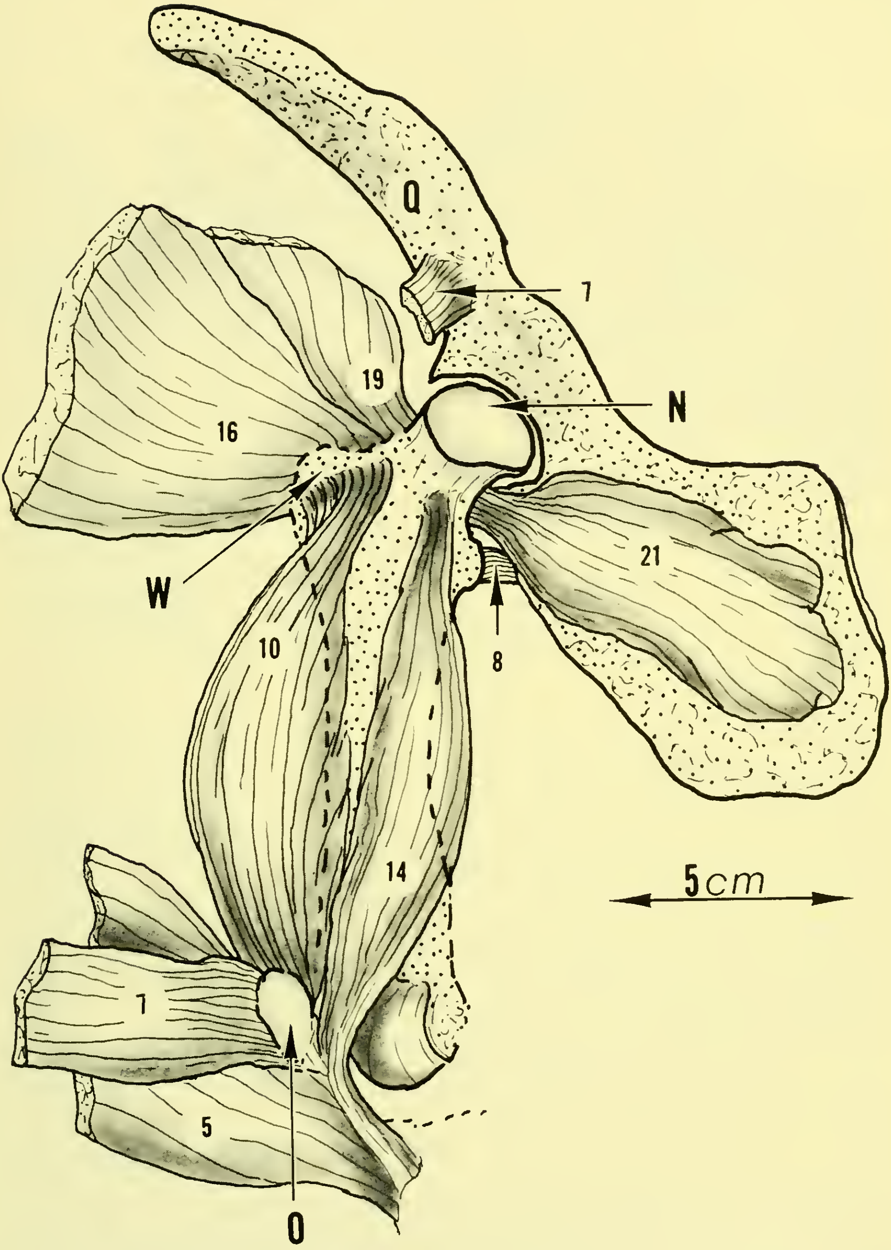
FIGURE 20. Anterior view of right femur and pelvis. The hip joint is exposed. The distal end of the femur is seen. The patella has been reflected laterally between the vastus



medialis (14) and the vastus lateralis (10), thus exposing its articular surface. Key: N, head of femur; O, patella; Q, pelvis; W, femur (greater trochanter); 5, adductor femoris; 7, rectus femoris; 8, iliopsoas; 10, vastus lateralis; 14, vastus medialis; 16, gluteus medius; 19, piriformis; 21, obturator externus.

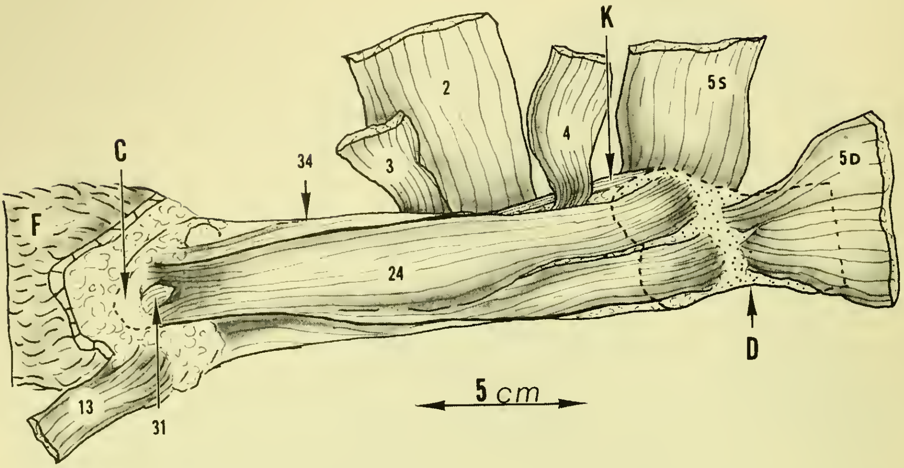


Figure 21. Posterior view of right knee and lower leg to show origin and insertion of the large superficial gastrocnemius (24) muscle. Note muscle insertions on the medial side of the tibia and their relation to the medial collateral ligament of the knee. Key: C, calcaneus; D, femur (distal end); F, foot; K, medial collateral ligament of knee; 2, gracilis (reflected); 3, semitendinosus (reflected); 4, semimembranosus (reflected); 5S, adductor femoris (superficial portion, reflected); 5D, adductor femoris (deep portion, reflected); 13, tenuissimus (reflected); 24, gastrocnemius; 31, plantaris; 34, tibialis posterior.

the piriformis (19), which has the bulk of its origin from the axial skeleton, thus marking the division between the two.

Insertion. The gluteus medius terminates in a short heavy tendon inserting on the outer anterior and superior aspect of the greater trochanter of the femur.

Action. This muscle abducts and extends the femur.

17. **Presemimembranosus.**

A rather thin, flat, roughly triangular muscle connecting the first caudal vertebra with the femur.

Origin. This muscle arises by a short strong tendon from the superior border of the transverse process of the first caudal vertebra. The muscle passes immediately over the dorsum of the ilium just above the tuberosity directed toward the femur and lies beneath the tenuissimus (13) and the caudofemoralis (11).

Insertion. The muscle spreads out for a linear insertion on the femur (lateral ridge area) immediately posterior to the caudofemoralis (11). The insertion extends from a short distance below the greater trochanter to the distal femur, swinging somewhat medially at the epicondyle level.

Action. The action of this muscle is to extend the femur.

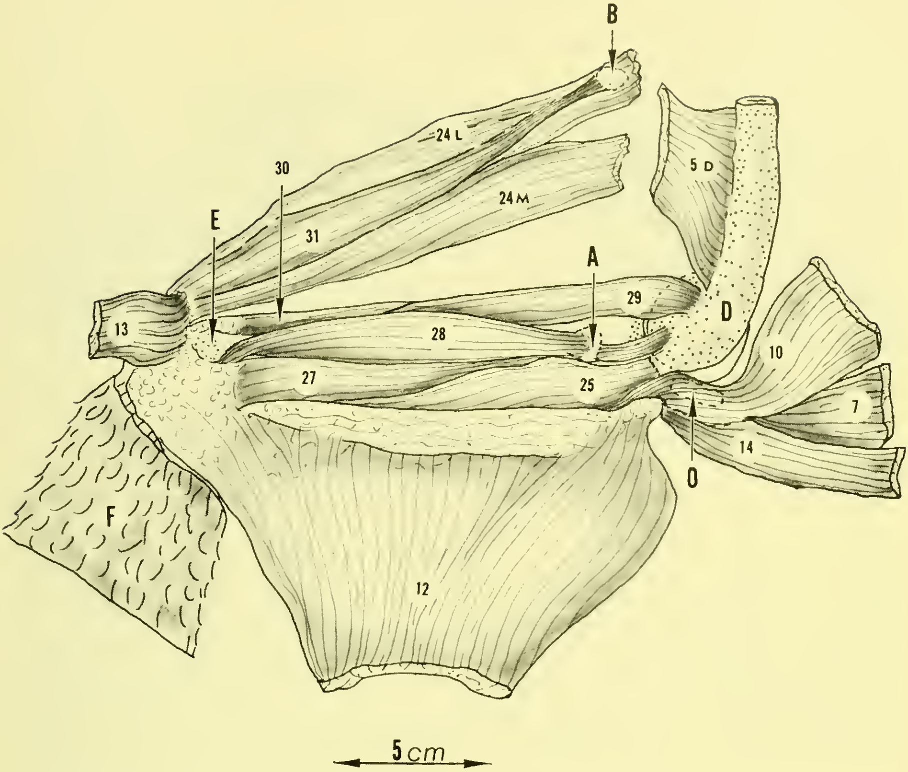


Figure 22. Lateral view of right knee and lower leg. The biceps femoris (12) has been reflected anteriorly to show the lower leg musculature. Both heads of the gastrocnemius (24) have been detached at their origins and the muscle reflected posteriorly and rotated somewhat to show the undersurface. Thus, the plantaris muscle (31) is exposed. Note the relationship of other lower leg muscles in this view. Key: A, fibula (head); B, sesamoid; D, femur (distal end); E, fibula (lateral malleolus); F, foot; O, patella; 5D, adductor femoris (deep portion, reflected); 7, rectus femoris (reflected); 10, vastus lateralis (reflected); 12, biceps femoris (reflected); 13, tenuissimus (reflected); 14, vastus medialis (reflected); 24L, gastrocnemius, lateral head (reflected); 24M, gastrocnemius, medial head (reflected); 25, tibialis anterior; 27, extensor digitorum longus; 28, peroneus longus; 29, peroneus digiti quinti; 30, peroneus brevis; 31, plantaris.

18. **Gluteus minimus.**

This is the lesser of the three glutei muscles and lies in close relation to the gluteus medius (16) in both origin and insertion.

Origin. Muscular fibers arise from the inferior anterior aspect of the outer surface of the iliac wing, practically inseparable from the gluteus medius (16) and in close proximity to the origin of the rectus femoris (7). Toward its

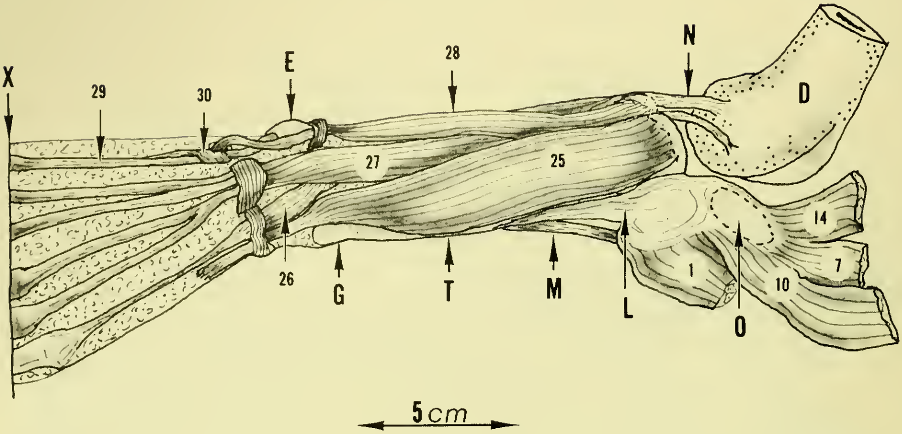


Figure 23. Anterolateral view of right lower extremity to show relationship of the more superficial extensor muscles. The distal femur and knee joint are shown. The medial collateral ligament has been detached from the femur. The extensor musculature of the knee has been reflected anteriorly and rotated to show the undersurface of the patella and the patellar tendon. Note the transverse ligaments at ankle level; these serve as pulleys to prevent the extensor muscles from bowstringing when the foot is dorsiflexed. Key: D, femur (distal end); E, fibula (lateral malleolus); G, tibia (medial malleolus); L, patellar tendon; M, medial collateral ligament of knee; N, lateral collateral ligament of knee; O, patella; T, tibial crest; X, metatarsophalangeal joint level; 1, sartorius (reflected); 7, rectus femoris (reflected); 10, vastus lateralis (reflected); 14, vastus medialis (reflected); 25, tibialis anterior; 26, extensor hallucis longus (proprius); 27, extensor digitorum longus; 28, peroneus longus; 29, peroneus digiti quinti; 30, peroneus brevis.

insertion, the muscle becomes a little more individualized as its short strong tendon of insertion develops.

Insertion. Insertion by the tendon is on the outer surface of the greater trochanter, just distal and anterior to the gluteus medius (16) tendon with which it is closely associated.

Action. Abduction and internal rotation of the femur.

19. **Piriformis.**

This large strong muscle of the buttock connects the axial skeleton to the femur.

Origin. Tendinous and fleshy fibers arise from the fascia overlying the spinal musculature adjacent to the wing of the ilium and from the last lumbar and first sacral vertebrae. A few deeper fleshy fibers arise from the outer surface of the ilium adjacent to the sacroiliac joint. On surface viewing, it appears inseparable from the gluteus medius (16). The muscle mass curves superiorly around the greater trochanter.

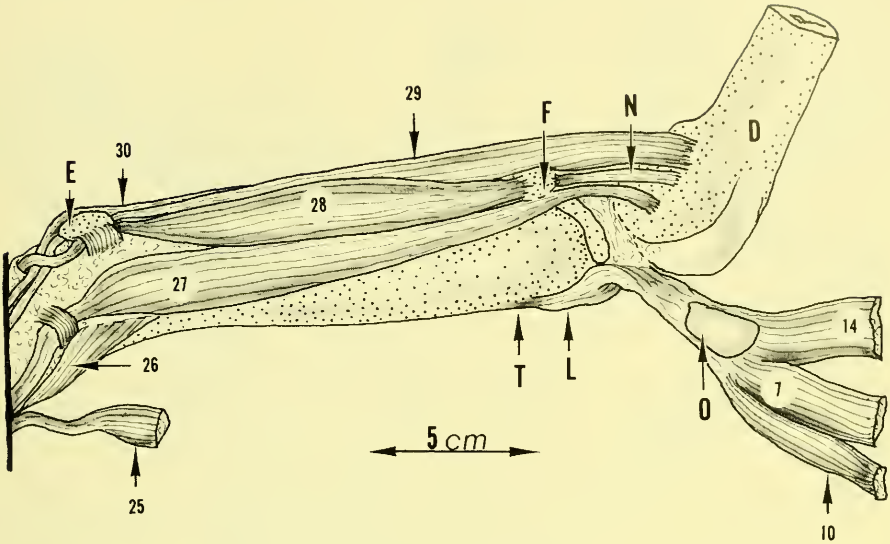


FIGURE 24. Lateral view of right lower leg including knee and ankle area. The tibialis anterior (25) has been removed from its origin and the distal portion reflected. The origin of the extensor digitorum longus (27) is now disclosed. As in figure 23, the patella and its tendon are again shown, reflected in a manner to disclose the undersurface. Key: D, femur (distal end); E, fibula (lateral malleolus); F, fibula (head); L, patellar tendon; N, lateral collateral ligament of knee; O, patella; T, tibial tuberosity; 7, rectus femoris (reflected); 10, vastus lateralis (reflected); 14, vastus medialis (reflected); 25, tibialis anterior (reflected); 26, extensor hallucis longus (proprius); 27, extensor digitorum longus; 28, peroneus longus; 29, peroneus digiti quinti; 30, peroneus brevis.

INSERTION. The short heavy tendon inserts on the outer posterior aspect of the greater trochanter appearing as a continuation of the tendon of the gluteus medius (16).

ACTION. Abduction and distention of the femur.

20. **Gemelli.**

These two small short muscles designated as superior and inferior join the pelvis to the femur, lying one on either side of the obturator internus tendon (23).

ORIGIN. Both muscles arise from the rim of the sciatic notch; the inferior one between the obturator internus (23) and sciatic spine, and the superior one adjacent to the obturator internus (23) to the border of the acetabulum.

INSERTION. The two gemelli join with the obturator internus (23) to form a common tendon which inserts on the medial surface of the greater trochanter as described for the obturator internus (23).

ACTION. The same action as the obturator internus (23).

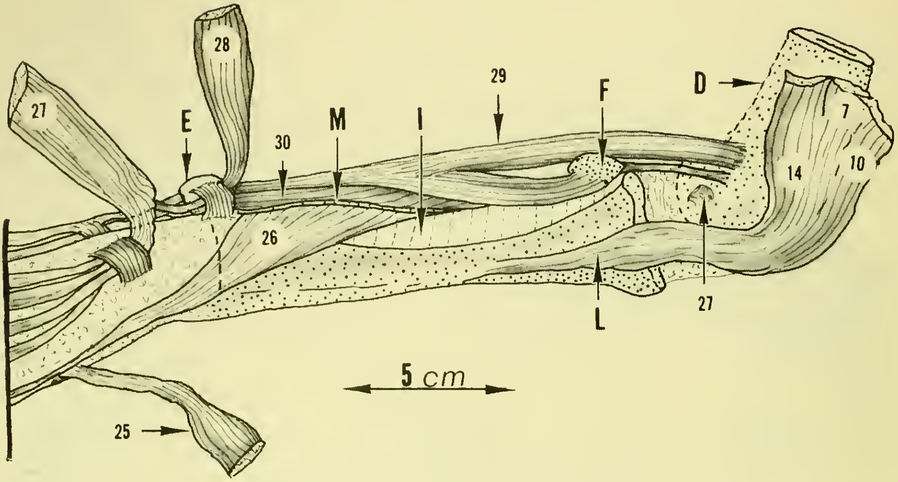


FIGURE 25. Anterolateral view of the right lower leg including knee and ankle areas. The tibialis anterior (25), the extensor digitorum longus (27), and the peroneus longus (28) have been reflected. The double origin of the peroneus digiti quinti (29) is visible. The origin of the extensor hallucis longus (proprius) (26) from the intermuscular septum is also seen. Key: D, femur (distal end); E, fibula (lateral malleolus); F, fibula (head); I, interosseus membrane; L, patellar tendon; M, intermuscular septum; 7, rectus femoris; 10, vastus lateralis; 14, vastus medialis; 25, tibialis anterior; 26, extensor hallucis longus (proprius); 27, extensor digitorum longus (reflected muscle and stump of origin); 28, peroneus longus; 29, peroneus digiti quinti; 30, peroneus brevis.

21. **Obturator externus.**

Lying deep to the adductor musculature, this strong pear-shaped muscle connects the distal pelvis with the greater trochanter of the femur.

ORIGIN. Fleshy fibers arise from the entire outer surface of the obturator membrane, which covers the obturator foramen, and from the adjacent bony rim of the ischium and pubis.

INSERTION. The converging fibers form a strong tendon which inserts into the posteromedial aspect of the greater trochanter just inferior to the combined tendons of the obturator internus (23) and gemelli (20).

ACTION. External rotation of the femur.

22. **Iliocapsularis.**

This is a small, flat, triangular muscle arising from the acetabular rim and inserting on the greater trochanter.

ORIGIN. Fleshy fibers arise from the posterior rim of the acetabulum starting immediately adjacent to the superior gemelli (20). The muscle overlies the hip joint capsule as it triangulates toward the greater trochanter.

INSERTION. A short tendon is formed and the insertion is into the medial

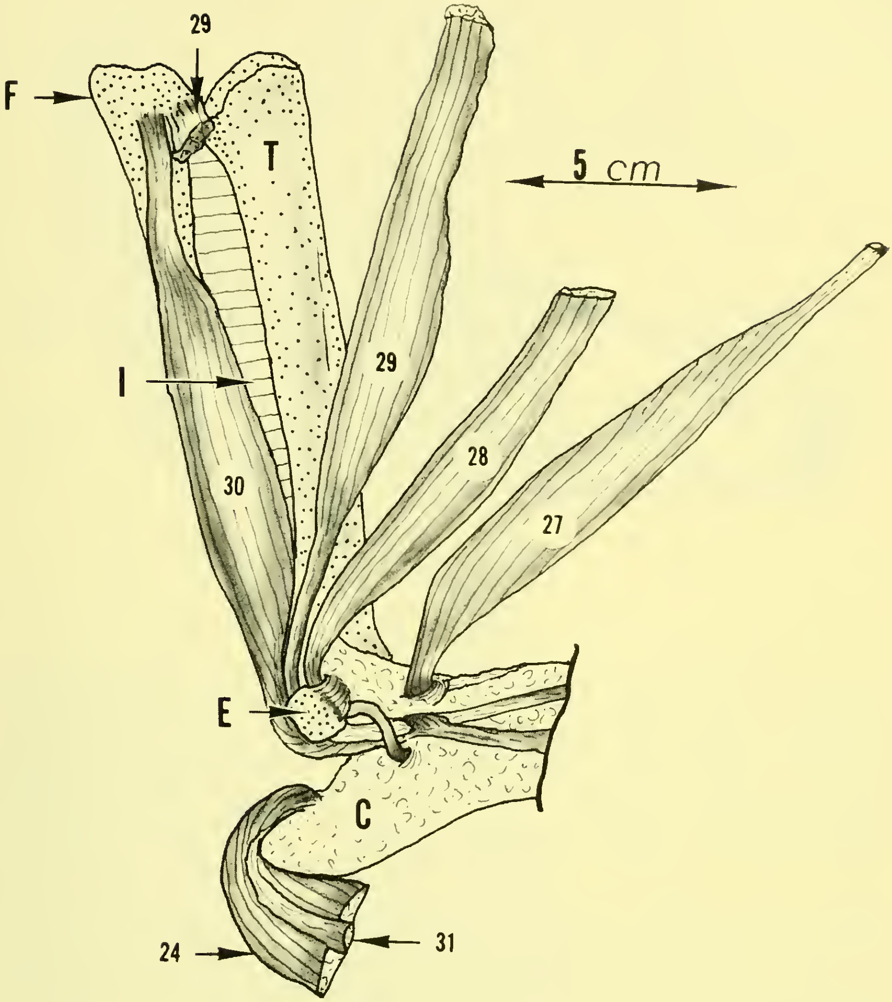


Figure 26. Lateral view of right lower leg and ankle. The peroneus digiti quinti (29), peroneus longus (28), and extensor digitorum longus (27) have been detached at their origins and reflected anteriorly to disclose the origin of the peroneus brevis (30). Note how, in the ankle area, the peroneus brevis (30) invests the peroneus digiti quinti (29) in a sling-like manner. Key: C, calcaneus; E, fibula (lateral malleolus); F, fibula (head); I, interosseus membranes; T, tibia; 24, gastrocnemius (reflected); 27, extensor digitorum longus; 28, peroneus longus; 29, peroneus digiti quinti (origin from fibula with muscle belly reflected); 30, peroneus brevis; 31, plantaris (reflected).

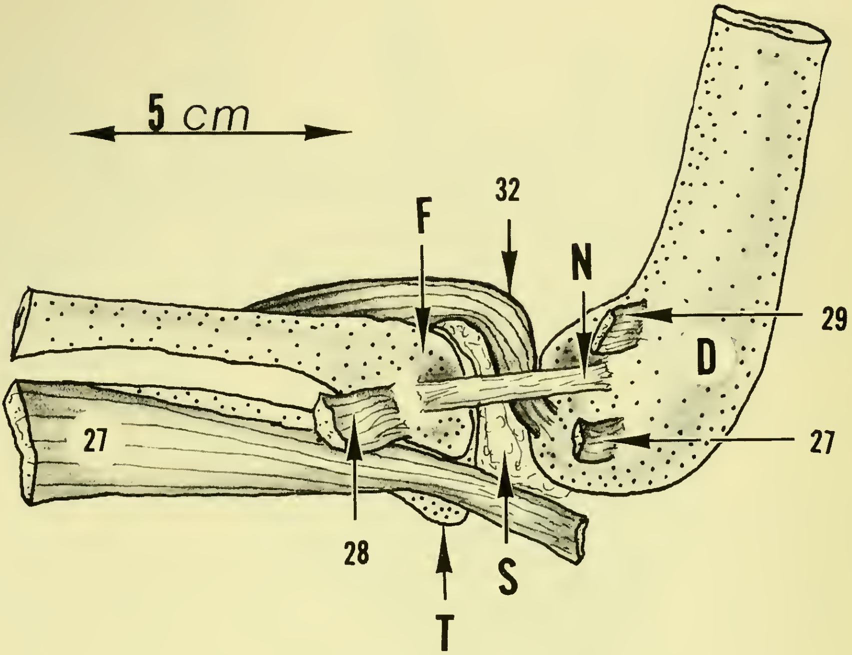


FIGURE 27. Lateral view of right knee following removal of the overlying musculature. The tendon of origin of the popliteus muscle (32) is seen. The extensor digitorum longus (27) has been divided near its origin and the distal portion reflected anteriorly. The stumps of origin of adjacent muscles are identified. A lateral semilunar cartilage is interposed between the joint surfaces. Key: D, femur (distal end); F, fibula (head); N, collateral ligament (lateral); S, semilunar cartilage; T, tibia; 27, extensor digitorum longus; 28, peroneus longus; 29, peroneus digiti quinti; 32, popliteus.

surface of the greater trochanter adjacent and anterior to the obturator (23) and gemelli (20) common tendon.

ACTION. This small muscle probably serves to stabilize the hip joint to some degree.

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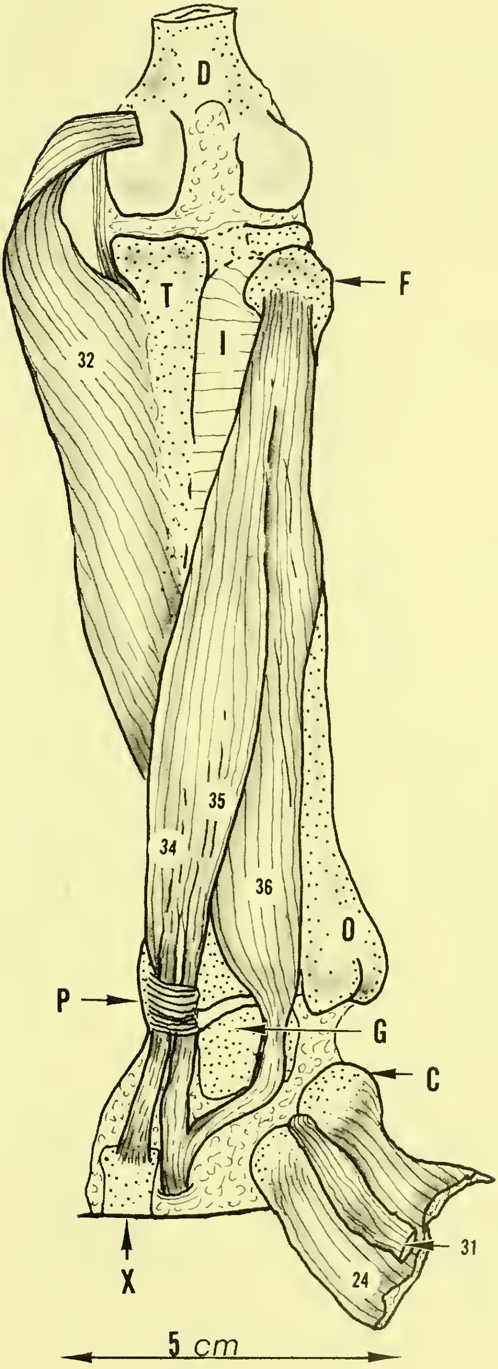
FIGURE 28. Posterior view of right lower leg with knee and ankle areas included. The foot is in plantar flexion. The popliteus muscle (32) has been detached at its tendinous origin and reflected medially. The origins, dispositions, and relationships of the tibialis posterior (34), flexor hallucis longus (35), and flexor digitorum longus (36) are shown. Note tendon arrangement at ankle. Key: C, calcaneus; D, femur (distal end); F, fibula (head); G, talus; I, interosseus membrane; O, fibula (lateral malleolus); P, tibia (medial malleolus); T, tibia; X, metatarsal 1 (base); 24, gastrocnemius (reflected); 31, plantaris (reflected); 32, popliteus; 34, tibialis posterior; 35, flexor hallucis longus; 36, flexor digitorum longus.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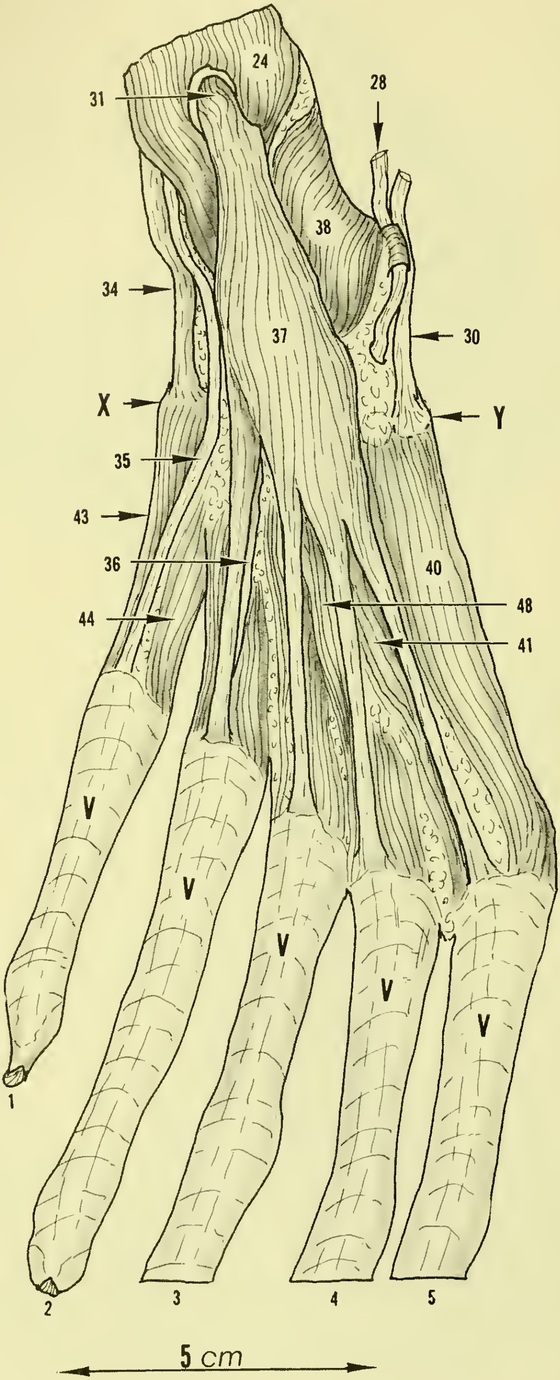
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23. Obturator internus.

This is a rather small flat muscle arising from the inner surface of the pelvis and extending to the femur.

Origin. This muscle arises by fleshy fibers from the distal and inferior surface of the obturator membrane and from along the ischium in the region of the spine and extends anteriorly along the pubic ramus. A heart-shaped indentation seems to separate the ischial from the pubic origin. The muscle tapers abruptly to pass over the rim of the sciatic notch where it is flanked by the superior and inferior gemelli (20).

Insertion. A common tendon is formed with the gemelli which then inserts into the medial surface of the greater trochanter beneath the insertion of the piriformis (19) and between the insertion of the iliocapsularis (22) and the obturator externus (21).

Action. Abduction of the femur and also external rotation of the femur.

24. Gastrocnemius.

This large calf muscle arises by two heads on the distal femur and inserts on the calcaneus. The muscle covers much of the posterior aspect of the lower leg.

Origin. The medial head arises by heavy tendinous fibers from the posterior aspect of the distal femur just proximal to the medial condyle. The lateral head arises from a comparable position just proximal to the lateral condyle. The more medial fibers are fleshy and take origin from a slightly depressed area in the bone. The lateral tendinous fibers arise from a bony ridge along the posterior margin of the epicondyle. The sesamoid bone is in the tendon near its origin. The two heads meet about midway down the lower leg and at this point the tendon of insertion begins forming on the outer surface.

Insertion. Distally, the tendon inserts at the tip of the calcaneus, separating slightly to let the plantaris (31) tendon pass through the groove in

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Figure 29. Sole of right foot with skin and subcutaneous tissue removed to show superficial musculature and tendon insertion in the proximal area. Also note fibrous flexor tendon sheaths of the digits. The plantaris (31), surrounded by the insertion of the gastrocnemius (24), emerges from a groove in the calcaneus to assist in formation of the flexor digitorum brevis (37). Key: V, fibrous flexor tendon sheath of digits; X, base of metacarpal 1; Y, base of metacarpal 5; 24, gastrocnemius; 28, peroneus longus; 30, peroneus brevis; 31, plantaris; 34, tibialis posterior; 35, flexor hallucis longus; 36, flexor digitorum longus; 37, flexor digitorum brevis; 38, quadratus plantae; 40, abductor digiti quinti; 41, adductor digiti quinti; 43, abductor hallucis; 44, adductor hallucis; 48, lumbricales.

this bone. Muscular fibers continue a short distance down the medial side of the calcaneus.

Action. Contraction of this muscle gives strong plantar flexion of the foot.

25. Tibialis anterior.

The most anterior of the anterolateral muscle group is this large roughly pyramidal-shaped muscle connecting the tibia to the foot.

Origin. Fleshy fibers arise from the lateral surface of the proximal one-third of the tibia, plus a small area from the adjacent interosseus membrane. Some posterior fibers of origin span over the tendon of origin of the extensor digitorum longus (27). The muscle then tapers and passes distally in close approximation to the tibia. In the upper two-thirds, the muscle is immediately anterior to the extensor digitorum longus (27), and in the lower one-third to the extensor hallucis proprius (26). At the ankle, a strong tendon has formed which, passing under the restraining transverse tarsal ligament, deviates medially to the base of the first metatarsal.

Insertion. The tendon inserts into the base of the first metatarsal, attaching to a lateral bony prominence.

Action. The action is dorsoflexion of the foot and inversion of the foot.

26. Extensor hallucis proprius (longus).

This is a relatively small muscle, somewhat triangular in shape and deep in origin, connecting the lower leg with digit 1.

Origin. The muscle arises by fleshy fibers from the lower one-half of the anterior surface of the intermuscular septum and from the anterior surface of the fibula in the same area, with a few fibers arising from the very margin of the adjacent intermuscular septum. The fleshy fibers of origin triangulate as they progress toward the medial side of the ankle. The muscle continues distally in front of the ankle to about the tarsal and metatarsal junction where a thin tendon is formed. This tendon, passing under the transverse ligament of the ankle, proceeds directly along the first metatarsal.

Insertion. On reaching the metatarsal phalangeal joint level, the tendon spreads slightly making some fascial attachments, but continues down the dorsum of the proximal phalanx to insert at the dorsum of the base of the terminal phalanx.

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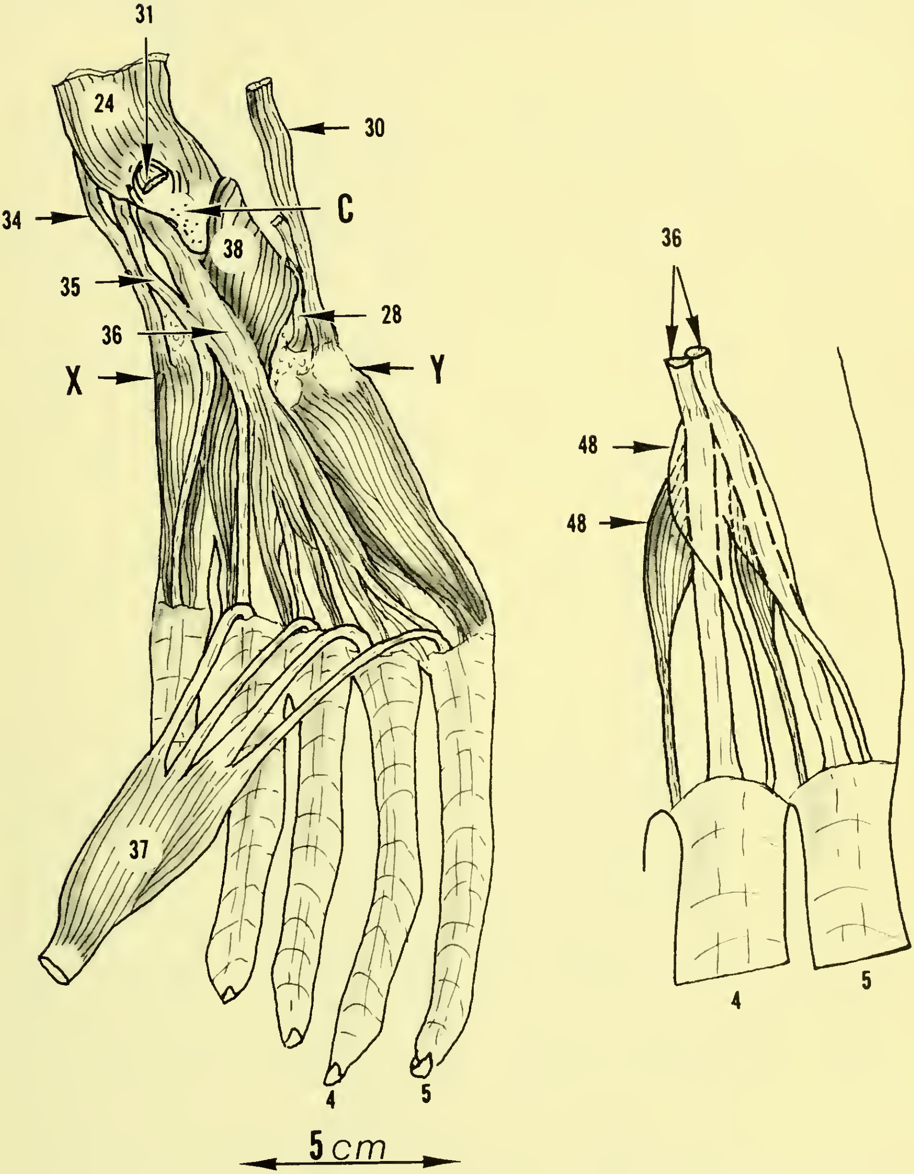
Figure 30. Sole of right foot, identical with figure 29 except plantaris (31) has been transected at the calcaneus permitting the flexor digitorum brevis (37) to be reflected distally exposing the flexor digitorum longus (36) and lumbricale (48) musculature. The sketch at the right is a diagrammatic enlarged view of the flexor digitorum longus (36) for



digits 4 and 5 to show the two superficial lumbrical muscles (48) (unshaded) which arise from these tendons and pass to the ulnar side of each digit respectively. Key: C, calcaneus; X, metatarsal 1 (base); Y, metatarsal 5 (base); 24, gastrocnemius; 28, peroneus longus; 30, peroneus brevis; 31, plantaris; 34, tibialis posterior; 35, flexor hallucis longus; 36, flexor digitorum longus; 37, flexor digitorum brevis (reflected); 38, quadratus plantae; 48, lumbricales.

ACTION. Action of this tendon is to extend both the proximal and distal joints of the first digit.

27. Extensor digitorum longus.

This is a spindle-shaped muscle in the lateral aspect of the lower leg, which connects the femur to the digits.

ORIGIN. Origin of this muscle is by long, strong, rounded tendons from the lateral aspect of the distal femur adjacent to the articular surface of the knee. Crossing the knee joint, the tendon lies in the groove of the upper tibia and under the muscular fibers of origin of the tibialis anterior (25). The spindle-shaped muscle belly then forms and courses the length of the lower leg between the tibialis anterior (25) and the peroneus digiti quinti (29), and overlying the extensor hallucis proprius (26). Just above the ankle, the tendon of insertion develops and passes under the transverse ankle ligament where it divides promptly into four separate tendons which pass directly toward digits 2, 3, 4, and 5.

INSERTION. On reaching the metatarsal phalangeal joint level, the tendon enters the extensor aponeurosis of the respective digit. The tendon fibers continue distally in the aponeurosis and most of them insert into the base of the middle phalanx, but some may continue to the distal joint (see details of extensor aponeurosis).

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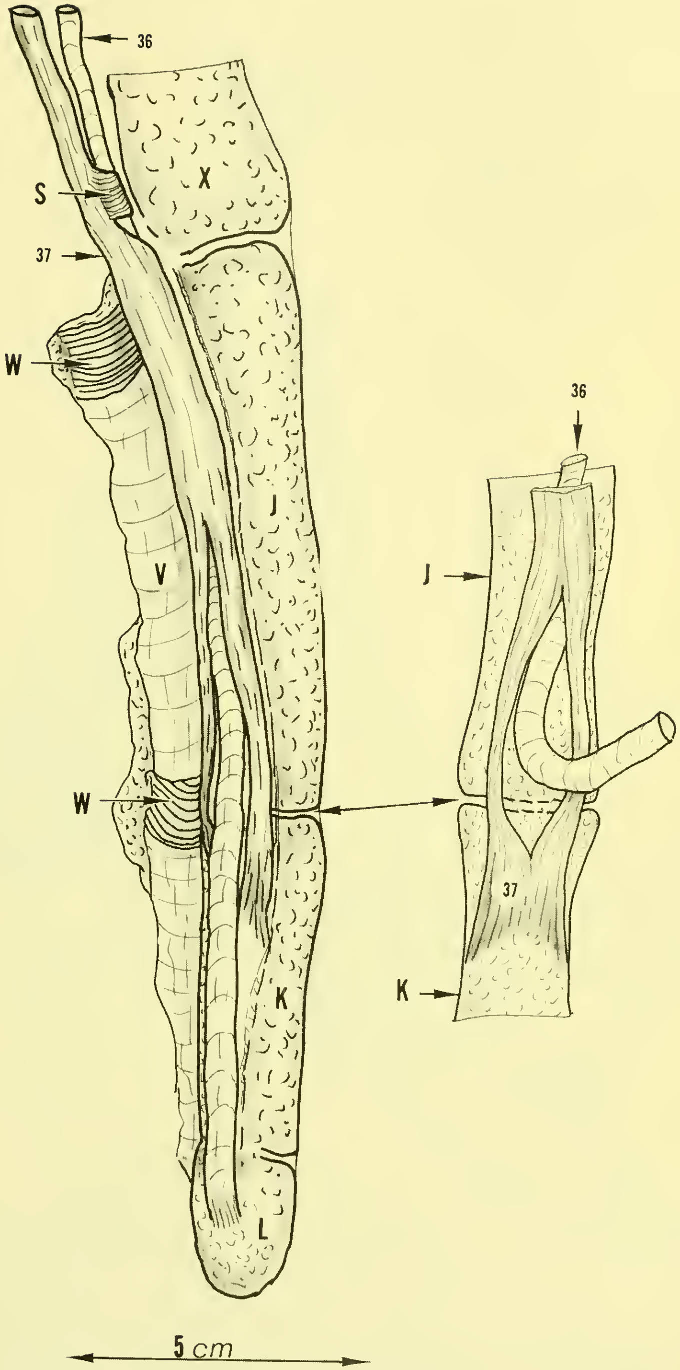
FIGURE 31. Anterolateral view of the fifth digit with the fibrous flexor tendon sheath (V) reflected to show relationship and insertions of flexor digitorum longus (36) and flexor digitorum brevis (37). This is the pattern for digits 2 to 5. Note the concentration of transverse connective tissue fiber strands (W) in flexor tendon sheath (V) to form a pulley mechanism for the flexor tendons. Also note the sling-type structure (S) from flexor digitorum brevis (37) surrounding flexor digitorum longus (36) at metatarsal head level. Digit 1, of course, is without a flexor digitorum brevis tendon. The diagrammatic sketch to the right represents an anterior view at proximal interphalangeal joint level showing the manner of insertion of flexor digitorum brevis (37) at the base of the middle phalanx. Key: J, proximal phalanx; K, middle phalanx; L, distal phalanx; S, sling-like structure of brevis surrounding longus; V, flexor tendon sheath; W, flexor tendon sheath pulleys; X, metatarsal; 36, flexor digitorum longus; 37, flexor digitorum brevis.

FIGURE 32. Sole of right foot with flexor digitorum brevis (37) and flexor digitorum longus (36) reflected to include the lumbricales (48), thus exposing the deep layer of intrinsic muscles and the ventral joint level of the tarsus. Key: C, calcaneus; S, sesamoid (base of metatarsal 5); T, capsule of tarsus; X, base of metatarsal 5; Y, base of metatarsal 1; 24, gastrocnemius; 28, peroneus longus; 30, peroneus brevis (reflected); 31, plantaris; 34, tibialis posterior; 35, flexor hallucis longus (reflected); 36, flexor digitorum longus (reflected); 37, flexor digitorum brevis (reflected); 38, quadratus plantae (reflected); 40, abductor digiti quinti; 41, adductor digiti quinti; 42, opponens digiti quinti; 43, abductor hallucis; 44, adductor hallucis; 46, interossei; 48, lumbricales.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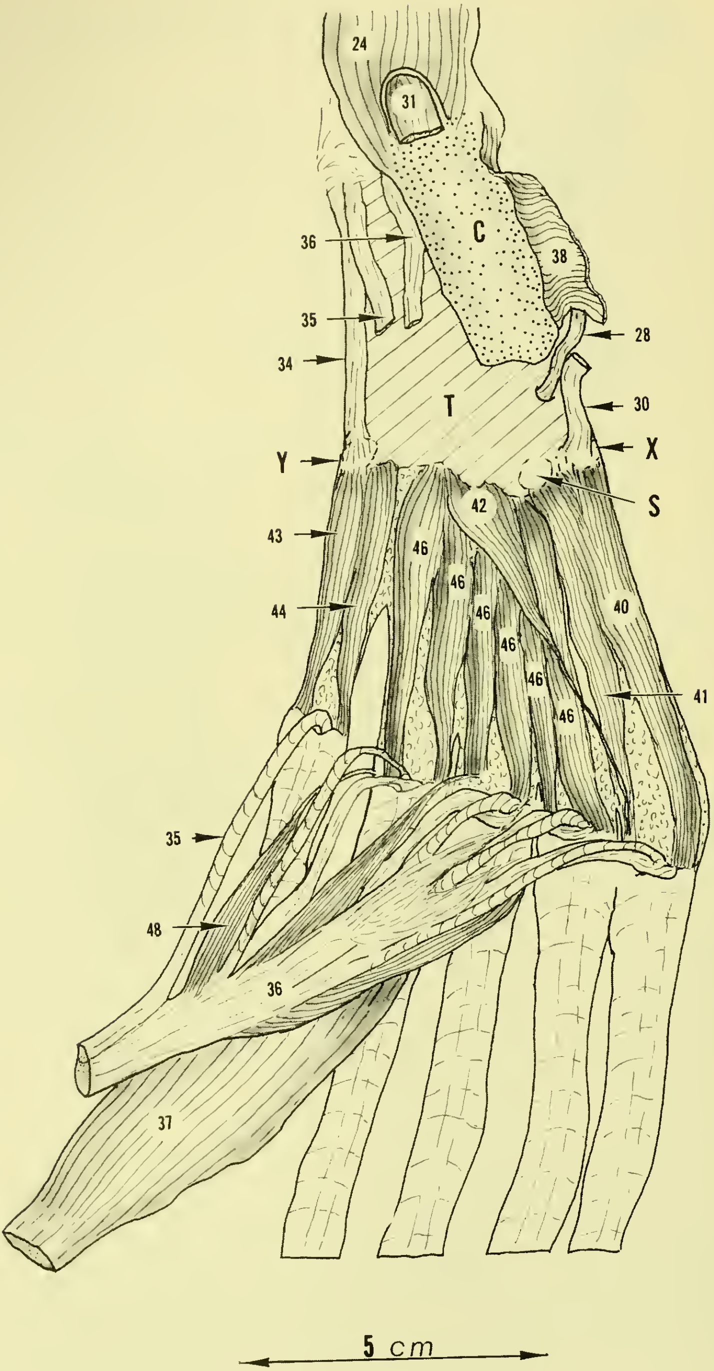
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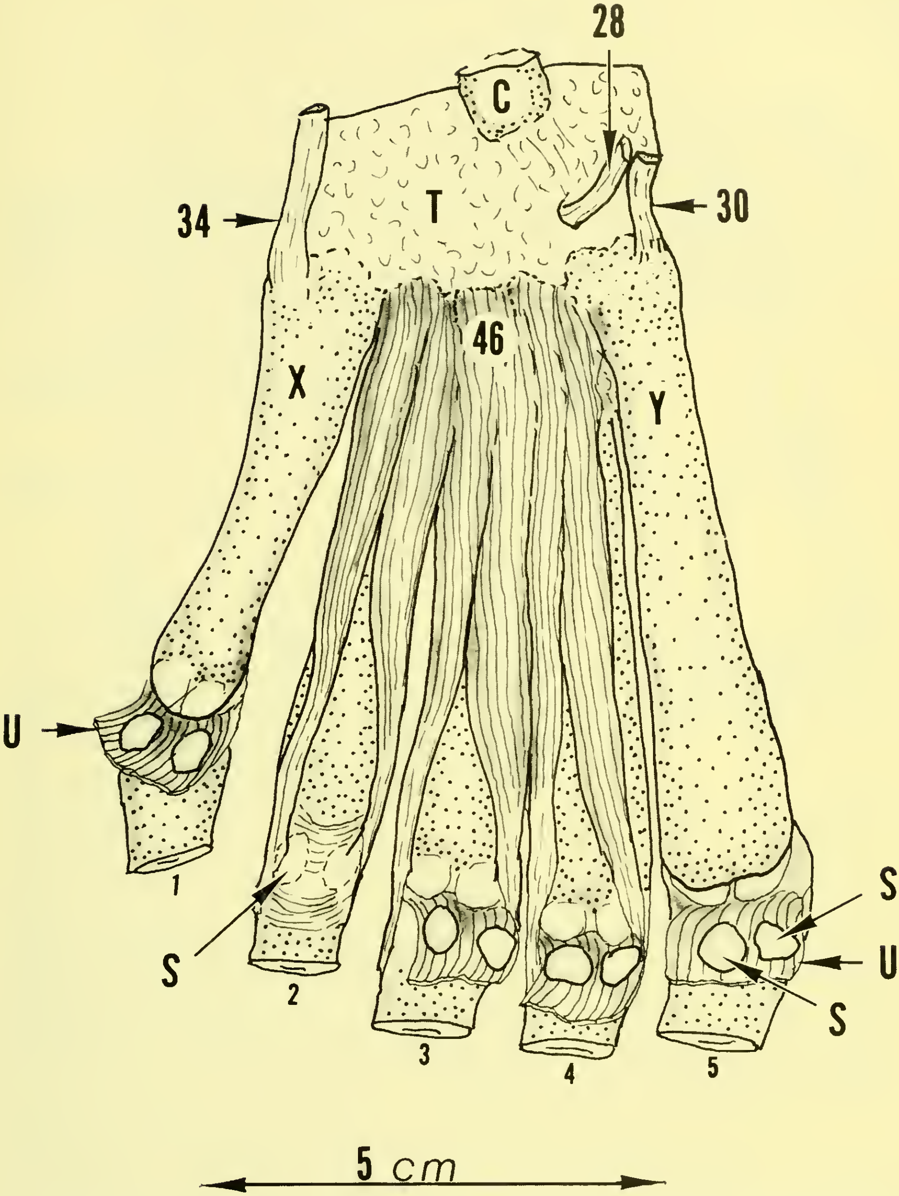

Figure 33. Plantar view of metatarsal area of right foot. All small muscles have been removed, except the interossei (46). The plantar joint capsules of the metacarpophalangeal joints, except for digit 2, have been detached from the metacarpal and reflected distally, thus exposing the joints and revealing the two sesamoid bones in the capsule. For digit 2, the plantar joint capsule remains in place. Key: C, calcaneus; S, sesamoid bone; T, plantar capsule of tarsus; U, plantar joint capsule of metatarsophalangeal joint, reflected; X, metatarsal 1; Y, metatarsal 5; 28, peroneus longus; 30, peroneus brevis; 34, tibialis posterior; 46, interossei.

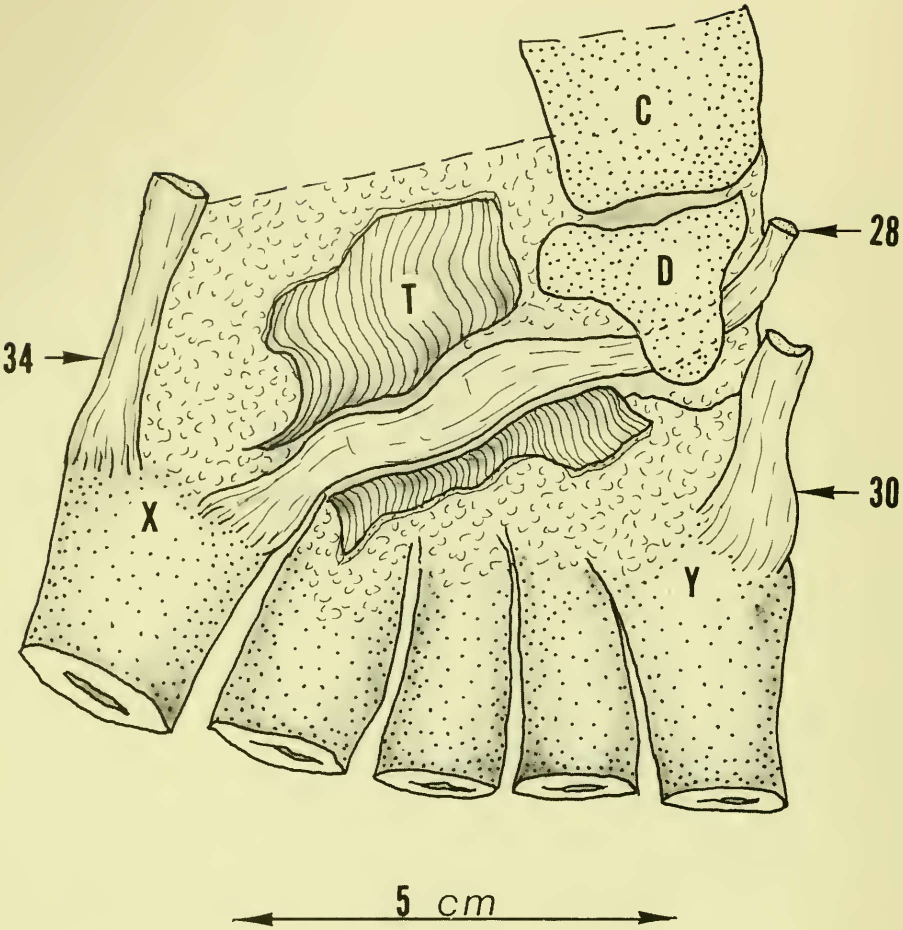

Figure 34. Plantar view of metatarsotarsal area. All small intrinsic muscles have been removed. The plantar joint capsule has been incised and reflected proximally to reveal the course of the peroneus longus (28) tendon as it passes in a groove in the cuboid to cross the foot and insert at the base of the first metatarsal. Key: C, calcaneus; D, cuboid; T, capsule of tarsus (reflected); X, base of metatarsal 1; Y, base of metatarsal 5; 28, peroneus longus; 30, peroneus brevis; 34, tibialis posterior.

Action. The extensor action through the aponeurosis is to extend the proximal or metatarsal phalangeal joint, and also the middle and distal joints providing the metatarsal phalangeal joint is not in hyperextension.

28. **Peroneus longus.**

This spindle-type muscle connects the upper tibia with the foot.

Origin. The muscle arises with mostly tendinous fibers from the anterior,

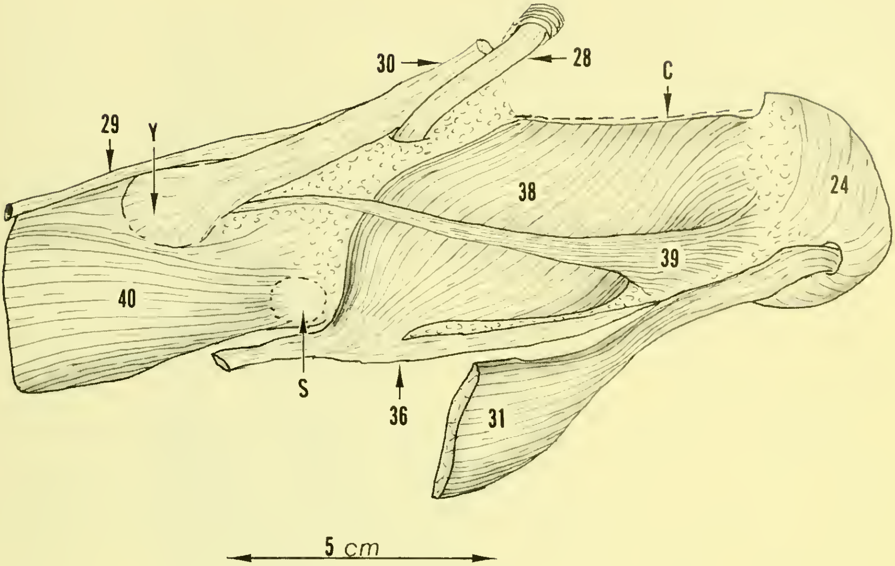

Figure 35. Posterolateral aspect of left ankle in an enlarged view to show the diminutive calcaneometatarsalis muscle (39), which was not visualized on the right side. Note also the quadratus plantae (38) joining into the flexor digitorum longus (36). Key: C, margin of calcaneus; S, sesamoid; Y, base of metatarsal 5; 24, gastrocnemius; 28, peroneus longus; 29, peroneus digiti quinti; 30, peroneus brevis; 31, plantaris (reflected); 36, flexor digitorum longus; 38, quadratus plantae; 39, calcaneometatarsalis; 40, abductor digiti quinti.

lateral, and inferior surfaces of the head of the fibula. Passing distally down the lower leg in the lateral position, the muscle lies between the extensor digitorum longus (27) and the peroneus digiti quinti (29). At the ankle, a strong round tendon develops which passes over the anterior surface of the lateral malleolus, under strong restraining ligament, and at this point the tendon overlies the peroneus digiti quinti (29) tendon and the peroneus brevis (30) tendon. Passing through a groove (perineal groove of the cuboid), the tendon dives deeply into the sole of the foot.

Insertion. The tendon lies in its own sheet as it crosses the foot, buried deep in the plantar fibrous capsule of the tarsal area. Its actual insertion is into the base of the first metatarsal on the ventral aspect.

Action. The action of this muscle is to plantar flex and pronate the foot.

29. **Peroneus digiti quinti.**

This is a strong fleshy muscle of double origin, which joins the femur and fibula to the fifth digit.

Origin. Origin of this muscle is by two heads; the larger and most posterior head arises by fleshy fibers from the lateral side of the distal femur and immediately posterior to the lateral collateral knee ligament and from a very slight bony prominence at the site. The lesser and more anterior head arises from the anterolateral surface of the very proximal portion of the fibular shaft and immediately adjacent to the peroneus longus (28) origin. Two muscle bellies join at about the junction of the upper and middle thirds of the fibula and continue distally between the peroneus brevis (30) and longus (28) muscles. Near the lateral malleolus, an ovoid strong tendon forms which then passes posteriorly and deep in the groove behind the malleolus to continue along the lateral side of the ankle passing under the peroneus longus (28) tendon. The tendon of the peroneus brevis (30) lies immediately posterior and, near its insertion at the base of metatarsal 5, a fibrous-type investment sheath arises and surrounds the tendon of the peroneus digiti quinti as the restraining ligament.

INSERTION. The peroneus digiti quinti tendon continues distally along the lateral border of the fifth metatarsal to the proximal joint level, then on distally to enter the extensor aponeurosis of this digit. The tendon continues to stay well to the lateral side, and at middle joint level it inserts into the base of the middle phalanx.

ACTION. In view of the location of this tendon, it would serve as an extensor of the metatarsal phalangeal joint of the fifth digit when working with the extensor digitorum longus (27), but when working independently it would

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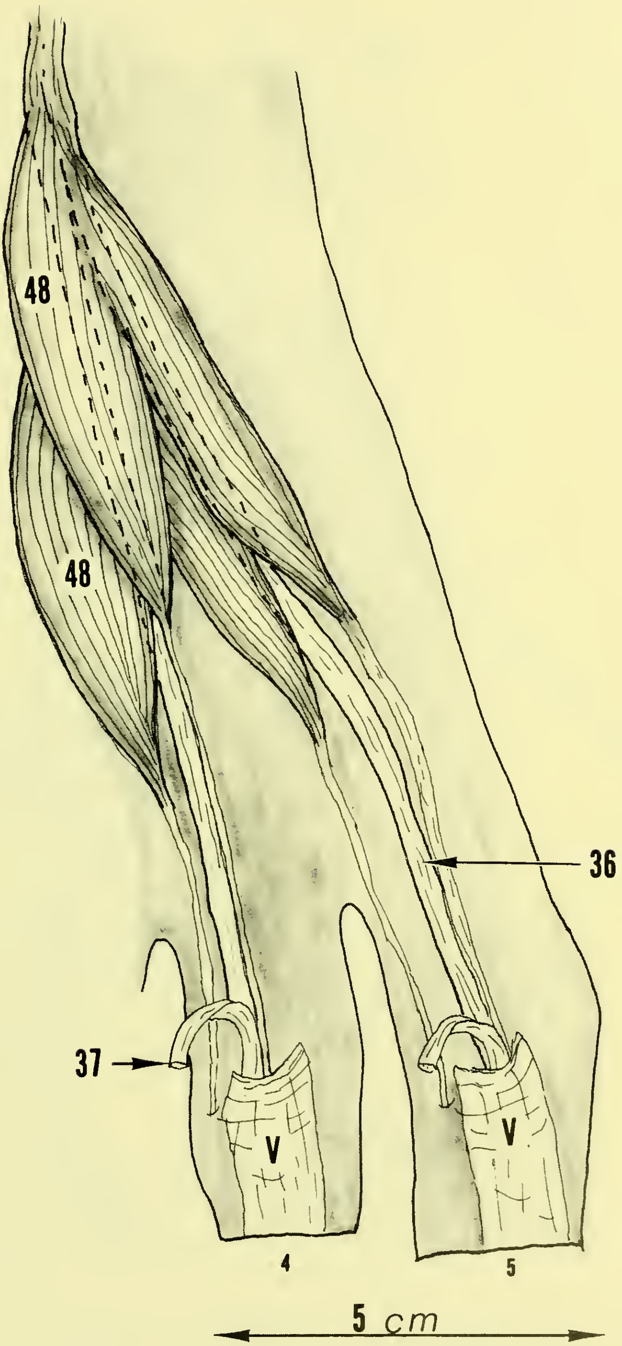
FIGURE 36. Semidiagrammatic plantar view of fourth and fifth digits of right foot to show origin and insertion of the two superficial lumbrical muscles (48). The flexor digitorum brevis (37) tendons are reflected just prior to their entering the flexor tendon sheath. Note the small tendons of the more superficial lumbrical muscles (48) joining the flexor digitorum brevis (37) tendon on the lateral side at this site. Key: V, flexor tendon sheath (muscles); 36, flexor digitorum longus; 37, flexor digitorum brevis; 48, lumbricales (both deep and superficial).

FIGURE 37. Dorsal view of left foot. All skin and subcutaneous tissue have been removed, including the interdigital webbing. Visible is the distribution pattern of the toe extensors, and the extensor aponeuroses over the dorsum of digits 2, 3, 4, and 5. The proximal end of the aponeurosis forms the tendinous hood about the metatarsophalangeal joint. Key: A, extensor aponeurosis; H, extensor hood; J, metatarsophalangeal joint level; K, proximal interphalangeal joint level; L, distal interphalangeal joint level; X, metatarsal 1; Y, metatarsal 5; 25, tibialis anterior; 26, extensor hallucis longus (proprius); 27, extensor digitorum longus; 29, peroneus digiti quinti; 47, extensor digitorum brevis.

FIGURE 38. Anterior or dorsal view of left foot. The extensor digitorum longus (27) tendons have been reflected distally to show the origin of the extensor digitorum brevis musculature (47). Note that the extensor digitorum brevis (47) has good representation for digits 2, 3, and 4. The token representation to digits 1 and 5 has tiny tendons which appear to join into the extensor digitorum longus (27) for each digit. Key: 25, tibialis anterior; 26, extensor hallucis longus (proprius); 27, extensor digitorum longus (reflected); 29, peroneus digiti quinti; 47, extensor digitorum brevis.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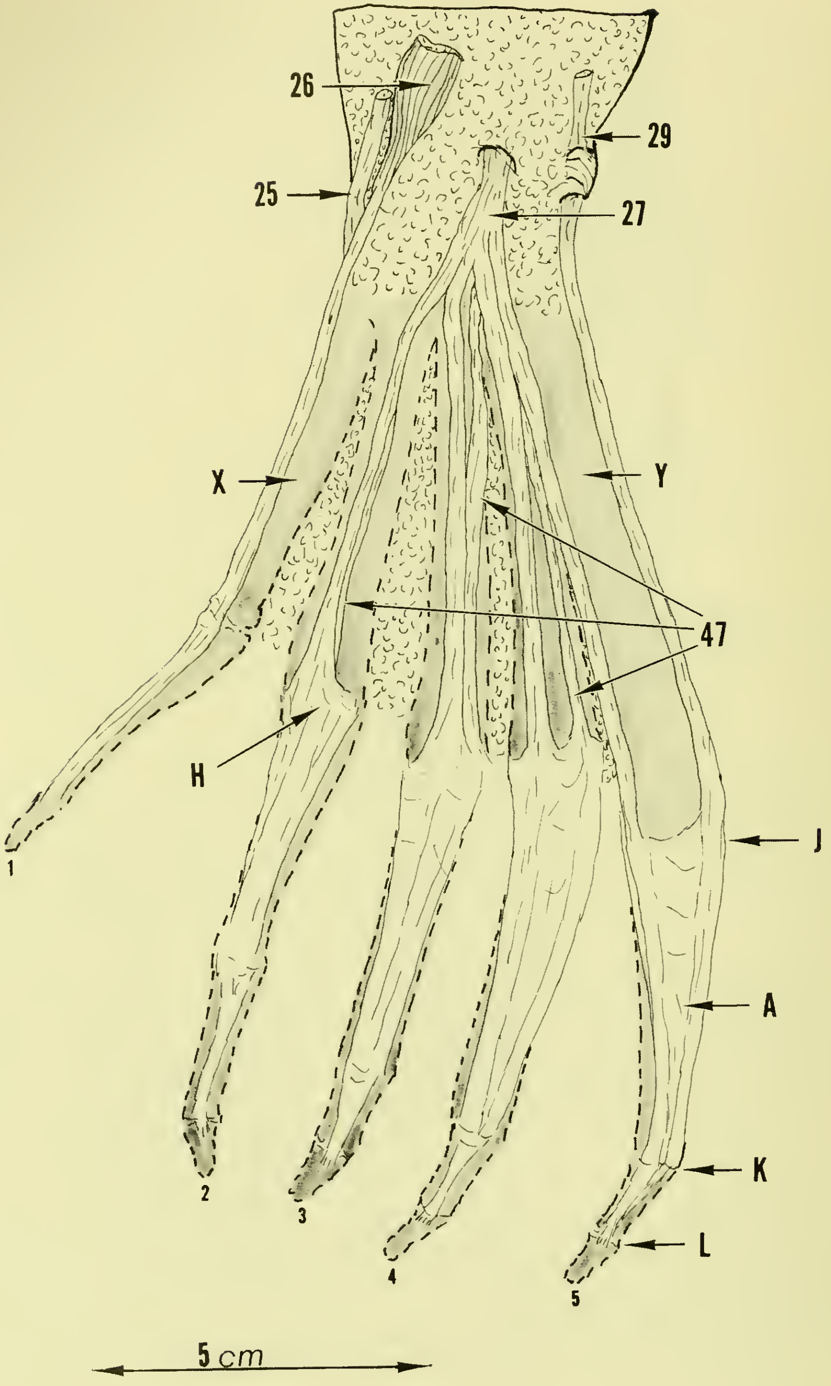
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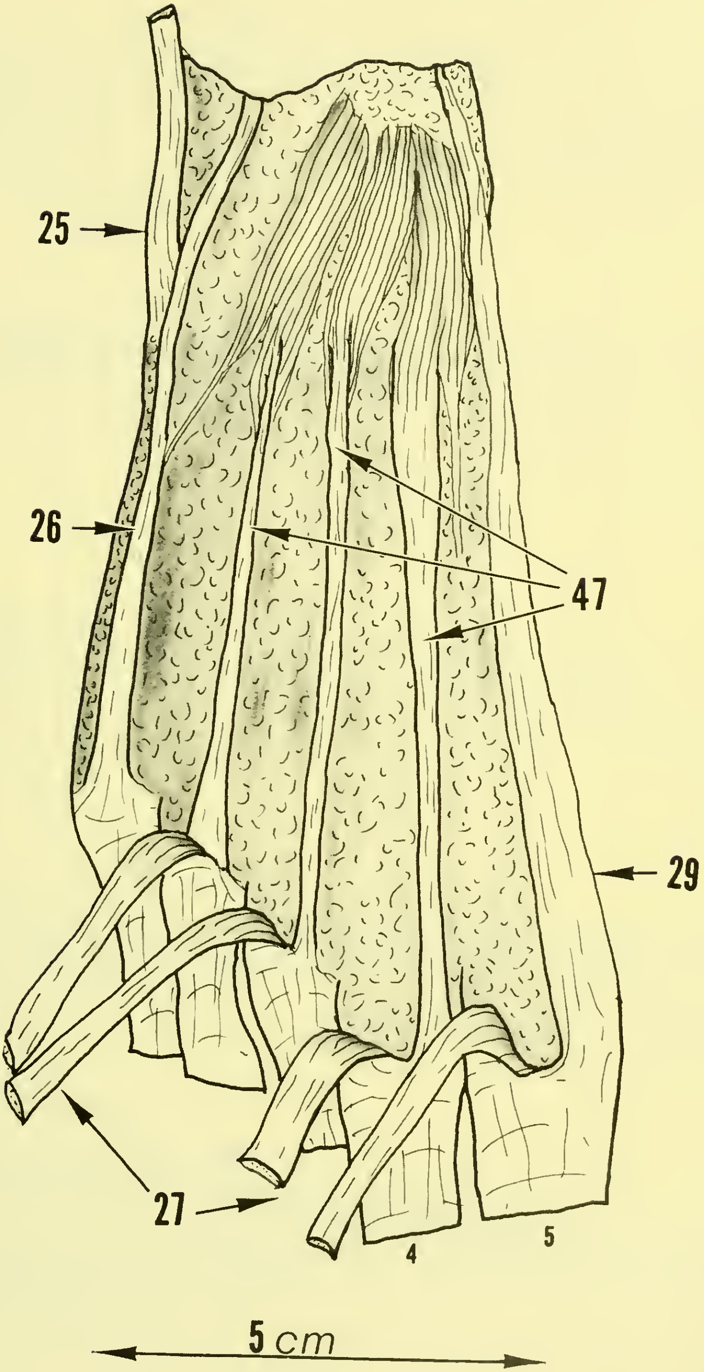
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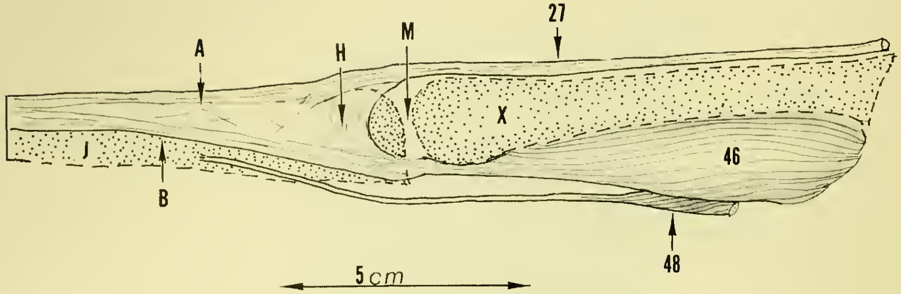

FIGURE 39. An enlarged medial view of the second digit of the right foot to show the usual relationship of long extensor (27), interossei (46), and lumbrical (48) tendons. Note the tendinous hood about the metatarsophalangeal joint, and the extensor aponeurosis, which continues distally. The tendon of the interosseus (46) forms the lateral band of the aponeurosis. The small lumbrical (48) tendon inserts into the proximal phalanx. Key: A, extensor aponeurosis; B, lateral band of extensor aponeurosis; H, extensor hood; J, proximal phalanx; M, metatarsophalangeal joint; X, metatarsal; 27, extensor digitorum longus; 46, interossei; 48, lumbricales.

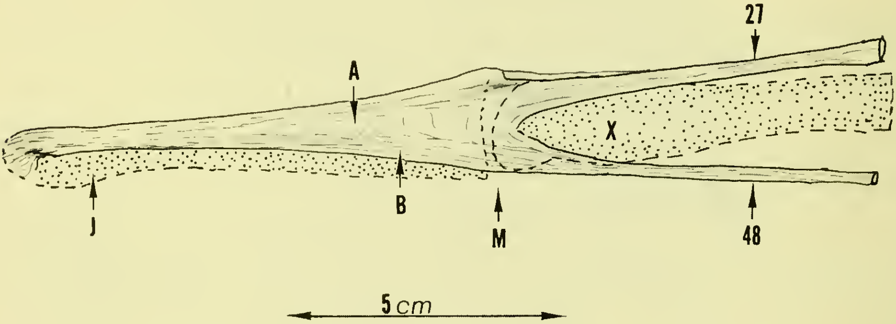

FIGURE 40. Medial view of the fifth digit of the right foot. Note that there is no interosseus muscle for this digit, and that the lumbrical (48) tendon, instead of inserting into the proximal phalanx, joins the extensor (27) aponeurosis to form the lateral band on the medial side. Key: A, extensor aponeurosis; B, lateral band of extensor aponeurosis; J, proximal phalanx; M, metatarsophalangeal joint; X, metatarsal 5; 27, extensor digitorum longus; 48, lumbricales.

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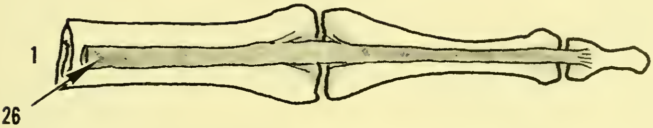
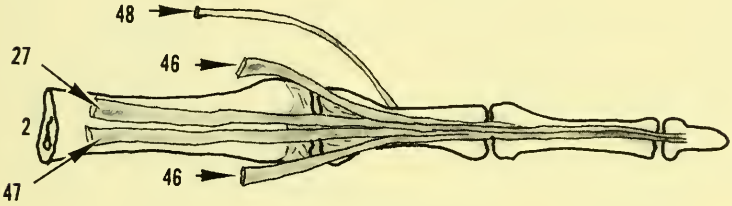
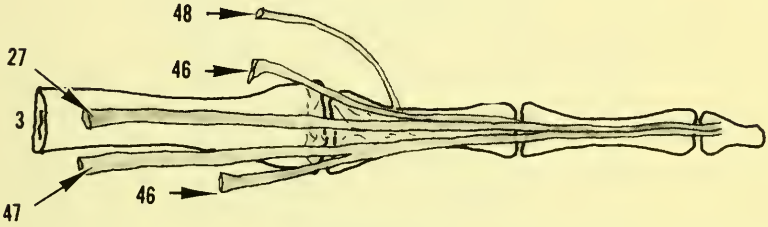
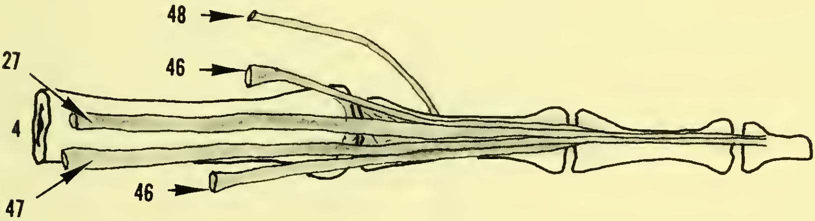
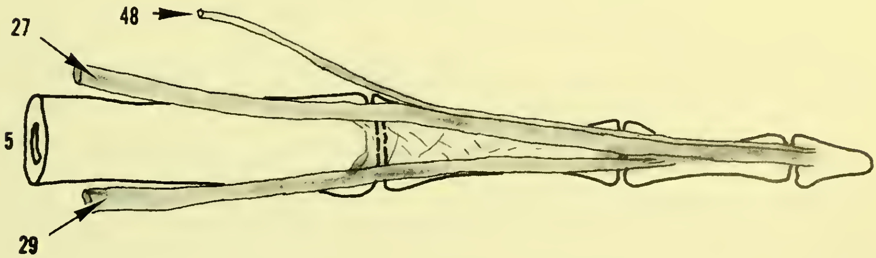
FIGURE 41. Diagrammatic representation of the extensor mechanism of the digits of the right foot. Note that only for digits 2, 3, and 4 are interossei (46) and extensor digitorum brevis (47) present. For digit 5, the peroneus digiti quinti (29) serves as an extensor digitorum brevis, and the lumbrical (48) joins the extensor aponeurosis instead of inserting directly into the proximal phalanx. Digit 1 shows the simple arrangement of a single extensor tendon made possible by the presence of only two joints. Key: 26, extensor hallucis longus (proprius); 27, extensor digitorum longus; 29, peroneus digiti quinti; 46, interossei; 47, extensor digitorum brevis; 48, lumbricales.


1
26


48
27
46
2
47
46


48
27
46
3
47
46


48
27
46
4
47
46


48
27
5
29

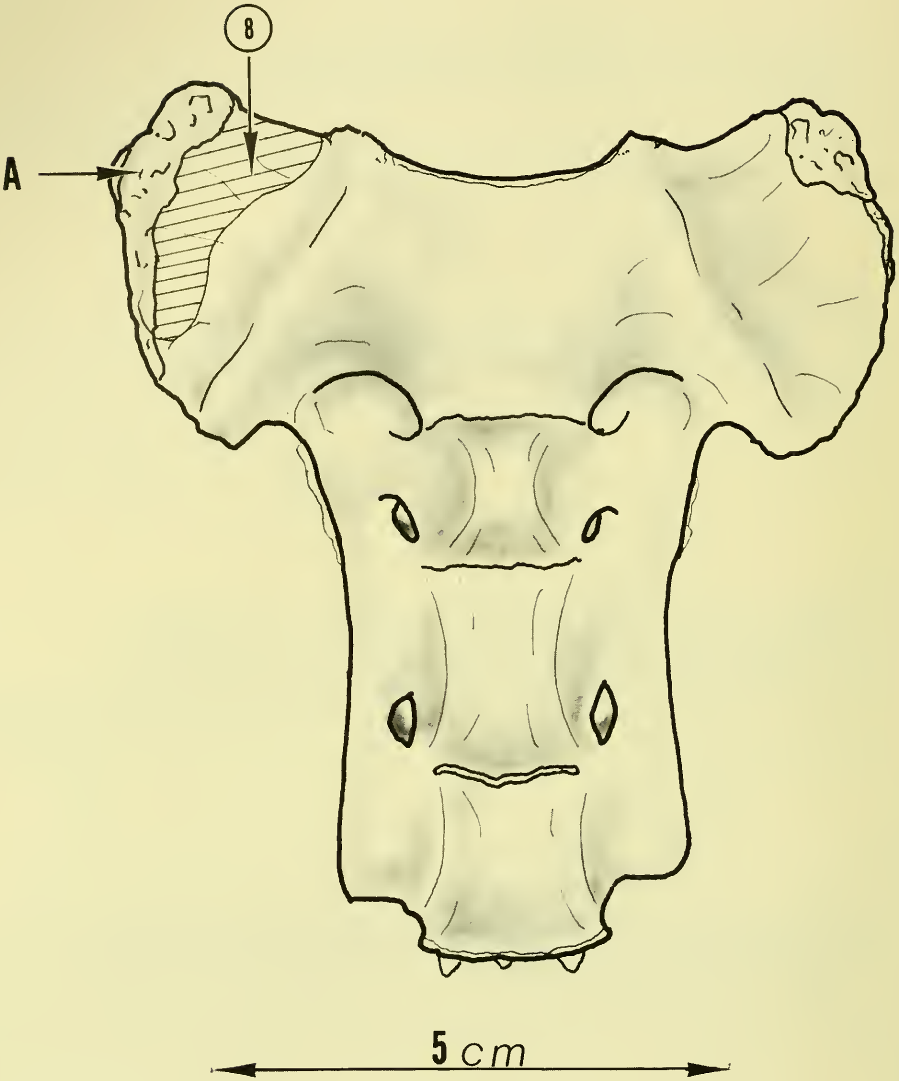


FIGURE 42. Anterior view of the sacrum. Key: A, sacroiliac joint; 8, iliopsoas (origin).

serve to abduct digit 5 at the metatarsal phalangeal joint level. Actually, the action would be mostly abduction from the adduction position, since abduction *per se* of this joint is practically nil past the straight line with the metatarsal.

30. **Peroneus brevis.**

This is the most posterior of the peroneal group connecting the fibula with the foot.

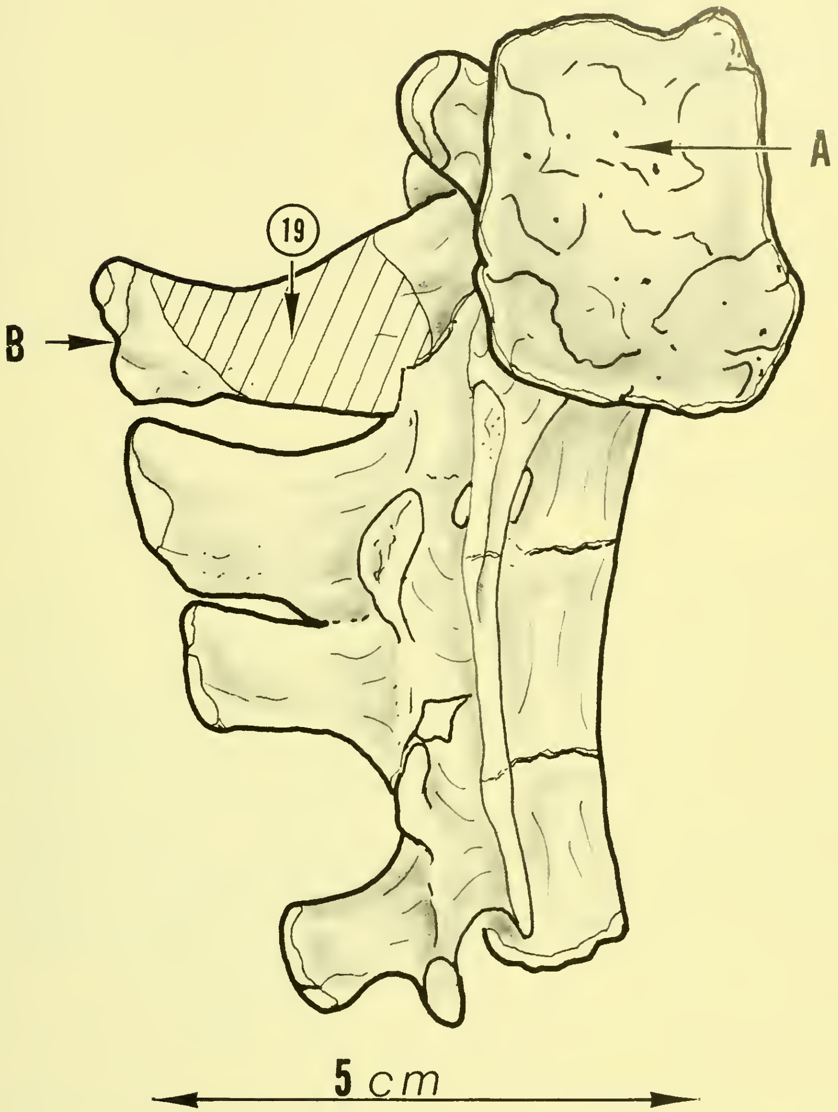


Figure 43. Right lateral view of sacrum. Key: A, sacroiliac joint; B, spinous process of first sacral vertebra; 19, piriformis (origin).

Origin. The muscle arises from the distal two-thirds of the shaft of the fibula from the lateral, posterior, and anterior surfaces and from the posterior side of the interosseus membrane in this area. The origin is by fleshy fibers for the most part. Superiorly and posteriorly, the origin is in close association

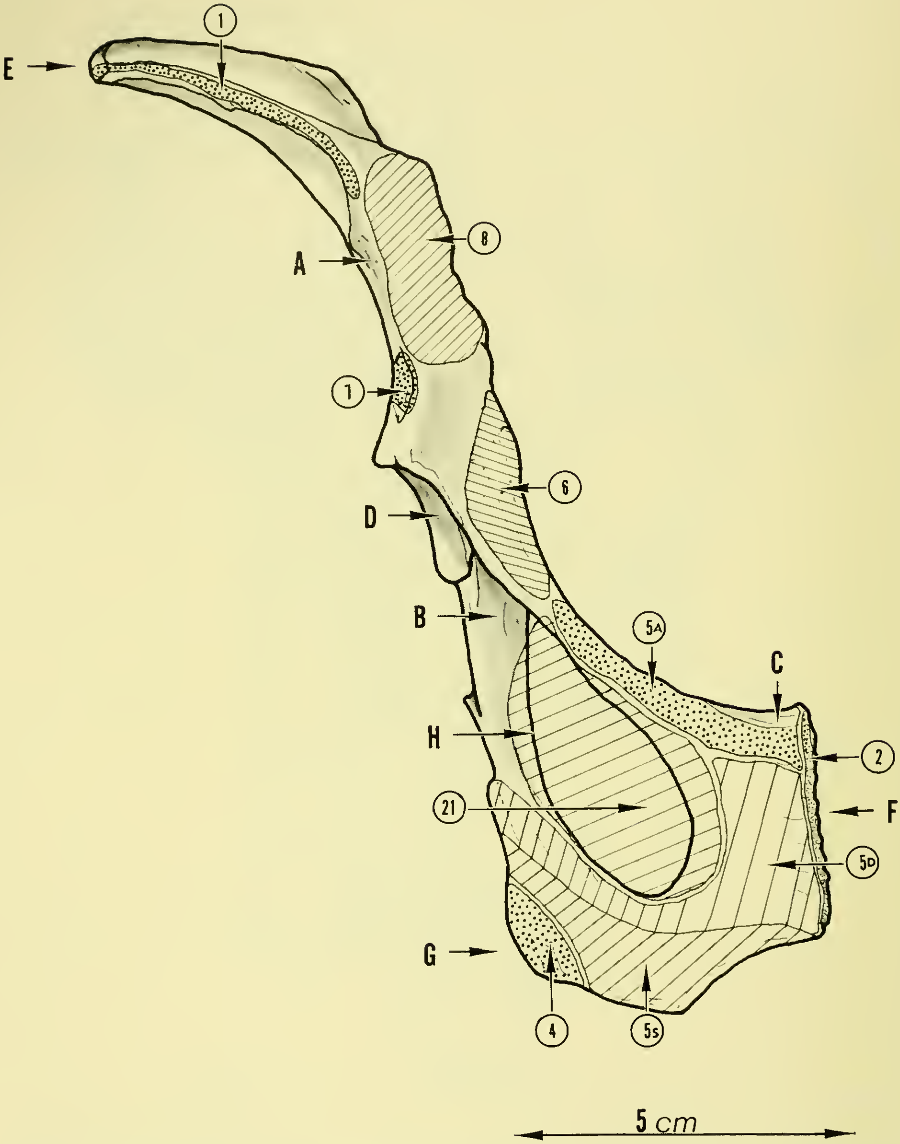


FIGURE 44. Anterior view of right pelvis. Key: A, ilium; B, ischium; C, pubis; D, acetabulum; E, iliac crest; F, symphysis pubis; G, ischial tuberosity; H, obturator foramen; 1, sartorius (origin); 2, gracilis (origin); 4, semimembranosus (origin); 5A, adductor longus (origin); 5D, adductor femoris (deep portion—origin); 5S, adductor femoris (superficial portion—origin); 6, pectineus (origin); 7, rectus femoris (origin); 8, iliopsoas (origin); 21, obturator externus (origin).

with the flexor digitorum longus (36). The muscle then courses distally along the side and posterior to the peroneus digiti quinti (29). Near the ankle, a heavy tendon forms which rounds the lateral malleolus posterior to, but in a common sheath with, the tendon of the peroneus digiti quinti (29). A few muscle fibers on the posterior surface of the tendon continue with the tendon around the lateral malleolus.

Insertion. It continues distally along the lateral side of the ankle under the peroneus longus (28) tendon to the base of metatarsal 5. Near its insertion, the fibrous sheath-like structure envelops the more anterior peroneus digiti quinti (29) tendon for a short distance.

Action. Eversion and plantar flexion of the foot.

31. **Plantaris.**

This muscle bears a close association with the lateral head of the gastrocnemius (24) and, for most of its distance in the muscular area, it is inseparable from this lateral head.

Origin. Distinct tendinous fibers arise in conjunction with the origin of the lateral head. These fibers are the most lateral ones, and from the origin to midway to the ankle distinct separation of the lateral head does not occur. At midpoint, however, the muscle becomes separate and moves medially to the midline. A tendon of insertion begins to form at this point. By the time the calcaneus is reached, a distinct, somewhat flattened tendon has formed which lies directly under the tendon of the gastrocnemius (24).

Insertion. The tendon now enters a groove at the posterior end of the calcaneus as the gastrocnemius (24) tendon is inserting to either side. Passing through the tendon of the gastrocnemius (24), the plantaris tendon reaches the sole of the foot where it enters into the flexor digitorum brevis (37) mechanism.

Action. This tendon would serve to plantar flex the foot and to also flex the digits through the flexor digitorum brevis (37) complex.

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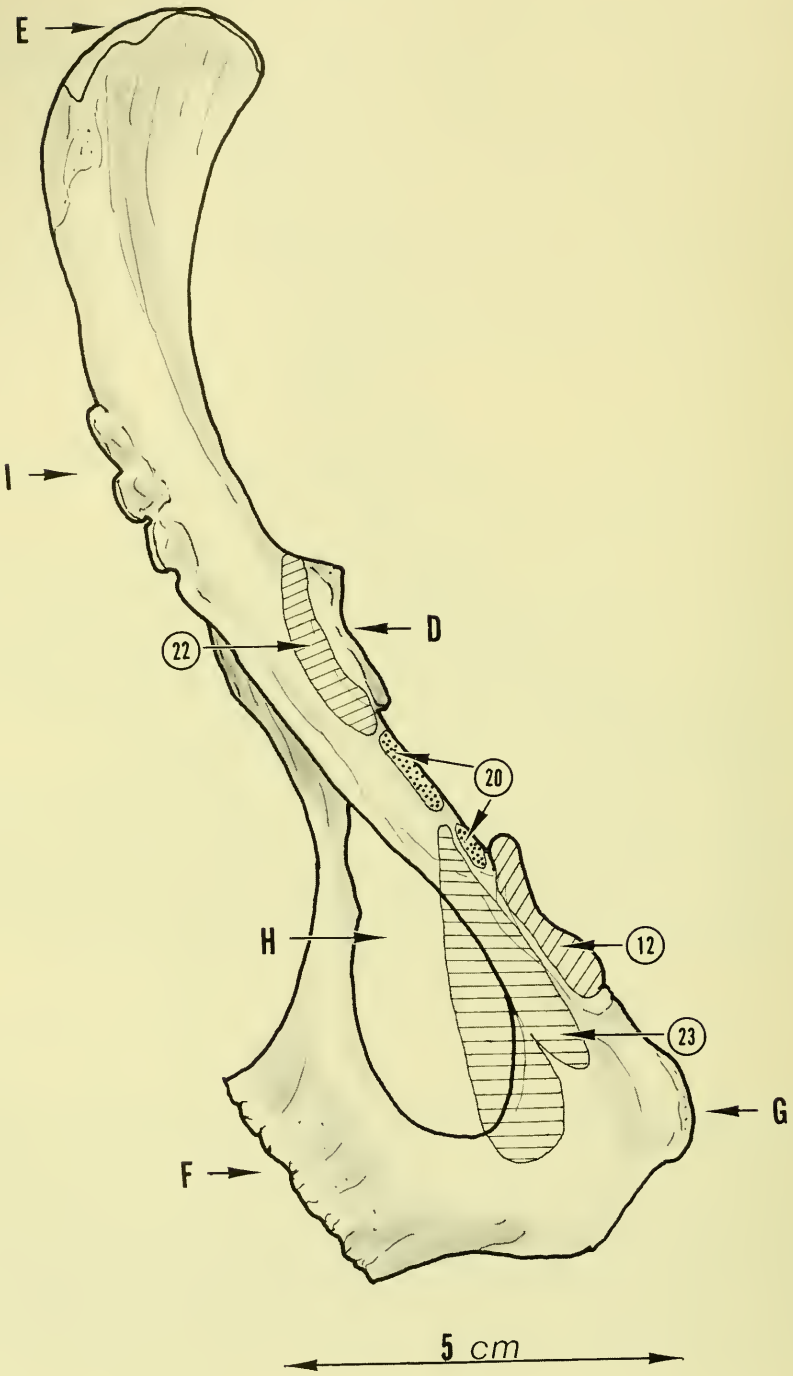
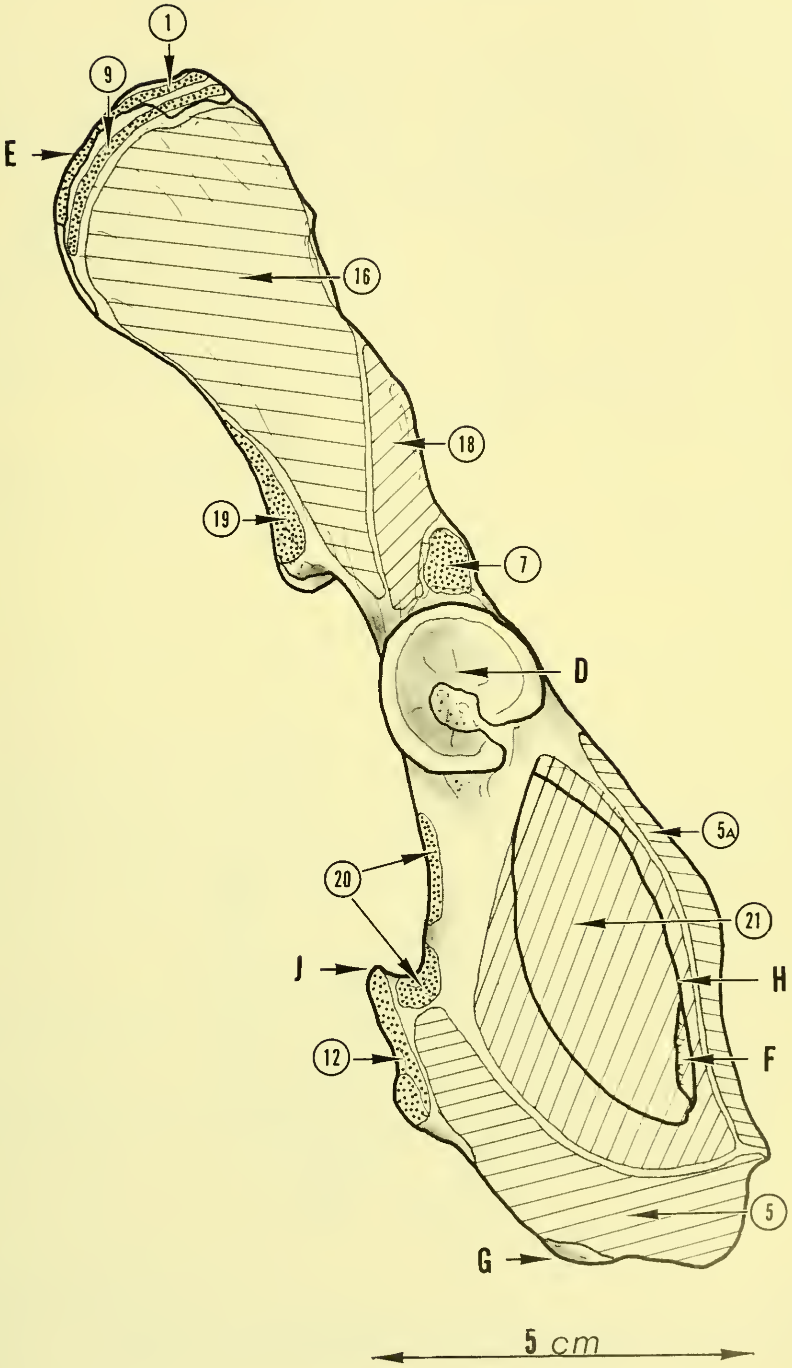
Figure 45. Posterior view of right pelvis. Key: D, acetabulum; E, iliac crest; F, symphysis pubis; G, ischial tuberosity; H, obturator foramen; I, sacroiliac joint; 12, biceps femoris (origin); 20, gemelli (origin); 22, iliocapsularis (origin); 23, obturator internus (origin).

Figure 46. Lateral view of right pelvis. Key: D, acetabulum; E, iliac crest; F, symphysis pubis; G, ischial tuberosity; H, obturator foramen; J, ischial spine; 1, sartorius (origin); 5, adductor femoris (origin); 5A, adductor longus (origin); 7, rectus femoris (origin); 9, gluteus maximus (origin); 12, biceps femoris (origin); 16, gluteus medius (origin); 18, gluteus minimus (origin); 19, piriformis (origin); 20, gemelli (origin); 21, obturator externus (origin).


E
I
D
㉒
⑳
H
⑫
㉓
G
F
5 cm



①
⑨
E
⑯
⑱
⑲
⑦
D
5A
⑳
㉑
J
H
⑫
F
⑤
G
5 cm

32. **Popliteus.**

This is a large posterior muscle of the lower leg connecting the femur with the tibia. The muscle lies beneath the medial head of the gastrocnemius (24).

ORIGIN. The origin of this muscle is by a very strong tendon in the lateral aspect of the distal femur, adjacent to the lateral condylar articular surface and distal to the tendon of origin of the extensor digitorum longus (27). The tendon lies transverse to the axis of the femur; it passes posteriorly under the lateral collateral ligament of the knee and over the lateral semilunar cartilage and joint capsule. Reaching the posterior aspect of the knee, the tendon spreads rapidly into a large triangular-shaped muscle which immediately starts its insertion into the posteromedial aspect of the upper tibia. The lateral side of the muscle parallels and overlaps somewhat the tibialis posterior (34) and the flexor hallucis longus (35).

INSERTION. Muscular fibers insert on the medial side of the posterior aspect of the tibia, starting at joint level and passing diagonally medially from the mid-upper tibia to a point distally and medially a distance one-fourth from the distal end of the tibia.

ACTION. This would be a strong medial rotator of the tibia and a flexor of the knee.

33. Dr. Howard's notes state "Not found" after the number '33.' Editor.

THE ORIGIN OF THE DEEP POSTERIOR MUSCULATURE

The tibialis posterior (34), the flexor hallucis longus (35), and the flexor digitorum longus (36) form a more or less common combined origin from the full length of the posterior aspect of the fibula, the interosseus membrane, and the distal posterior surface of the tibia. Intercommunicating fibers exist for all three muscles.

The fibers of origin of the tibialis posterior (34) rise mainly from the head of the fibula, interosseus membrane, and lower tibia.

The fibers of origin of the flexor hallucis longus (35) come mainly from the posterior surface of the head of the fibula, medial to and overlying those of the tibialis posterior (34).

The fibers of origin of the flexor digitorum longus (36) arise mainly from the posterior aspect of the fibula for its full length and the adjacent interosseus membrane.

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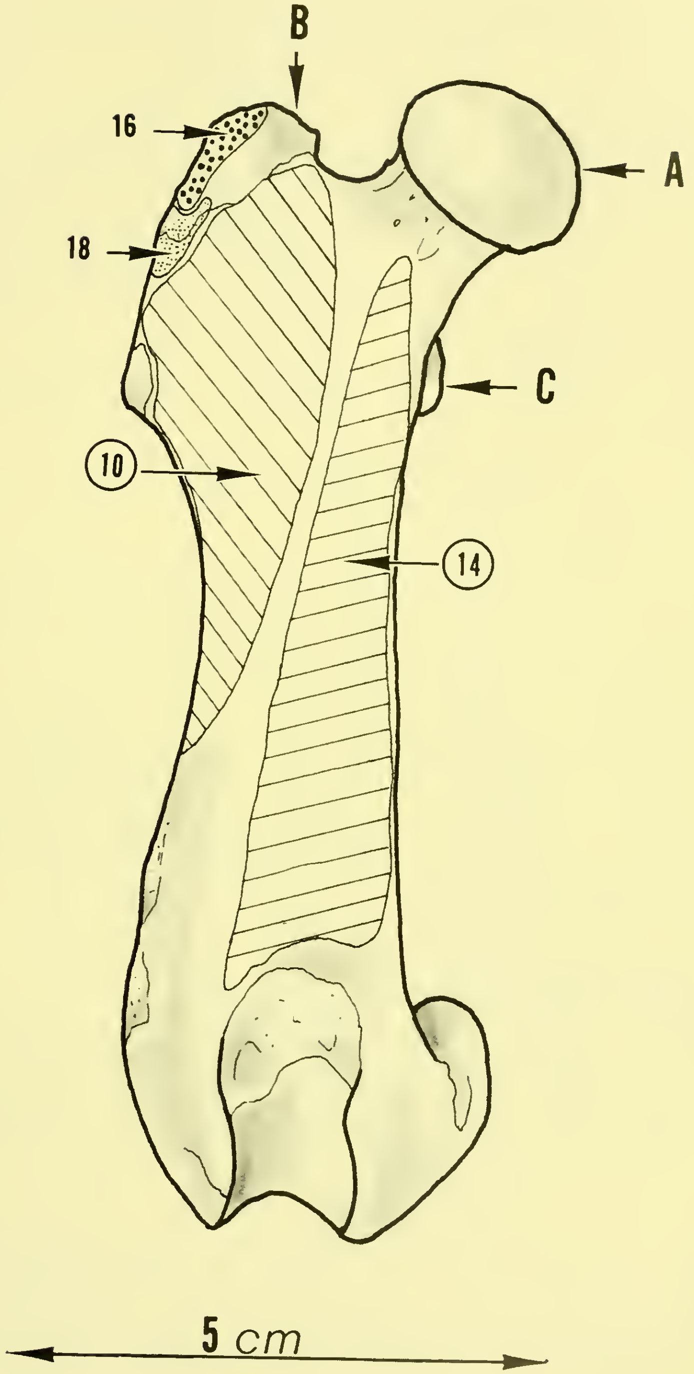
FIGURE 47. Anterior view of the right femur. Key: A, head of femur; B, greater trochanter of femur; C, lesser trochanter of femur; 10, vastus lateralis (origin); 14, vastus medialis (origin); 16, gluteus medius; 18, gluteus minimus.


B
16
A
18
C
10
14
5 cm

The fiber interdigitation of these muscles is mainly in the upper two-thirds. The tendon of each develops in the lower one-third.

34. Tibialis posterior.

This is a deep muscle in the posterior aspect of the lower leg connecting the leg to the foot.

Origin. Muscular fibers are mainly from the head of the fibula and lower end of the tibia and interosseus membrane. Near the ankle, a tendon forms that is most medial and close along that of the flexor hallucis longus (35). The tendon passes around the medial malleolus with a sheath in common with the flexor hallucis longus (35).

Insertion. The tendon flattens somewhat as it passes distally to the base of the first metatarsal, inserting into the plantar aspect of the proximal end of this bone.

Action. The action is plantar flexion of the ankle and foot.

35. Flexor hallucis longus.

This is a slender muscle passing from the lower leg to the first toe.

Origin. The origin is mainly by muscular fibers from the head of the fibula on the medial side of the posterior aspect. The origin is closely associated with the tibialis posterior (34) until the tendon starts to form. The tendon parallels that of the tibialis posterior (34) and passes around the medial malleolus in the same sheath. Just distal to the talus, the tendon joins with the flexor digitorum longus (36), but shortly thereafter again becomes a separate tendon passing down the line of metatarsal 1 to enter the fibrous flexor tendon sheath at the metatarsal phalangeal joint level. At this point distally, the tendon passes within the sheath to its insertion on the ventral lip of the distal phalanx adjacent to the articular surface.

Action. Flexion of the proximal and distal joints of digit 1.

36. Flexor digitorum longus.

This is a deep posterior muscle connecting the lower leg to the digits.

Origin. The origin is mainly by muscular fibers from the posteromedial aspect of the fibula for its full length and adjacent interosseus membrane. The muscle broadens distally and abruptly narrows into a tendon at ankle joint level. The tendon then passes through the groove in the posterior talus

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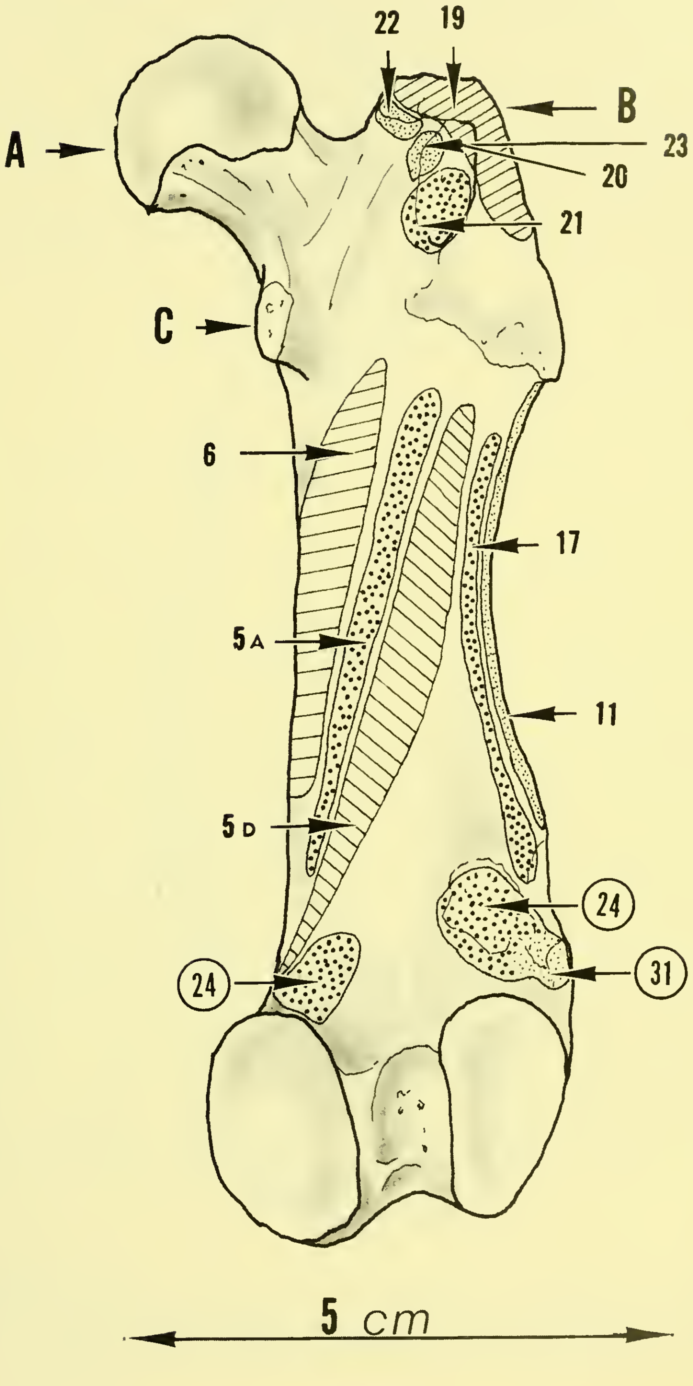
Figure 48. Posterior view of right femur. Key: A, head of femur; B, greater trochanter; C, lesser trochanter; 5A, adductor longus; 5D, adductor femoris (deep portion); 6, pectineus; 11, caudofemoralis; 17, presemimembranosus; 19, piriformis; 20, gemelli; 21, obturator externus; 22, iliocapsularis; 23, obturator internus; 24, gastrocnemius (medial and lateral heads—origins); 31, plantaris (portion of origin).


22
19
B
A
23
20
21
C
6
17
5A
11
5D
24
31
24
5 cm

to join the tendon of the flexor hallucis longus (35) as both emerge into the sole of the foot at the distal medial side end of the calcaneus. Here, interdigitation of fibers occurs for a short distance. The flexor hallucis longus (35) then again separates and passes down the line of the first metatarsal to the proximal or metatarsal interphalangeal joint level. The remaining tendon (flexor digitorum longus) continues into the sole of the foot, underlying the flexor digitorum brevis (37). From the area of interdigitation with the flexor hallucis longus (35) to just beyond the calcaneal-cuboid articulation, the long digital flexors join from the lateral side by the musculotendinous fibers of the short, flat, and broad quadratus plantae (38).

37. Flexor digitorum brevis.

This muscle develops the connection with the plantaris (31) tendon as it appears in the sole of the foot.

ORIGIN. As the plantaris tendon (31) enters the sole of the foot from the groove in the calcaneus, it expands into a musculotendinous structure (flexor digitorum brevis) (37). This structure is superficial and occupies or covers much of the proximal foot in a manner similar to a plantar fascia. Distally at about the half-way point of the sole, the musculotendinous mass separates into four slightly flattened tendons which proceed fan-like to the metacarpal head areas of digits 2, 3, 4, and 5. At this point, each tendon directly overlies the flexor digitorum longus (36) tendon, and together they enter the flexor tendon sheath which extends for the full length of the digit. This flexor tendon sheath is a fibrous connective tissue tunnel with transverse reinforcements (termed pulleys) at proximal and middle joint levels. The pulleys and sheath act to prevent bowstringing of the flexor tendons as the digits are flexed. At proximal joint level, the flexor digitorum brevis forms a sling-like structure which completely surrounds the profundus tendon for a short distance and holds the two tendons in close proximity. Just within the flexor tendon sheath, the tendon splits and assumes a more dorsal position, which permits the flexor digitorum longus (36) to become superficial. Continuing on either side of the flexor digitorum longus (36), the flexor brevis now passes with the longus under the distal flexor tendon sheath pulley at proximal interphalangeal joint level. Each half of the tendon then broadens. The two halves join together deep to the flexor digitorum longus, forming a flat tendon which inserts into the ventral lip of the middle phalanx at proximal interphalangeal joint level. Vincula are present as the tendon approaches its insertion.

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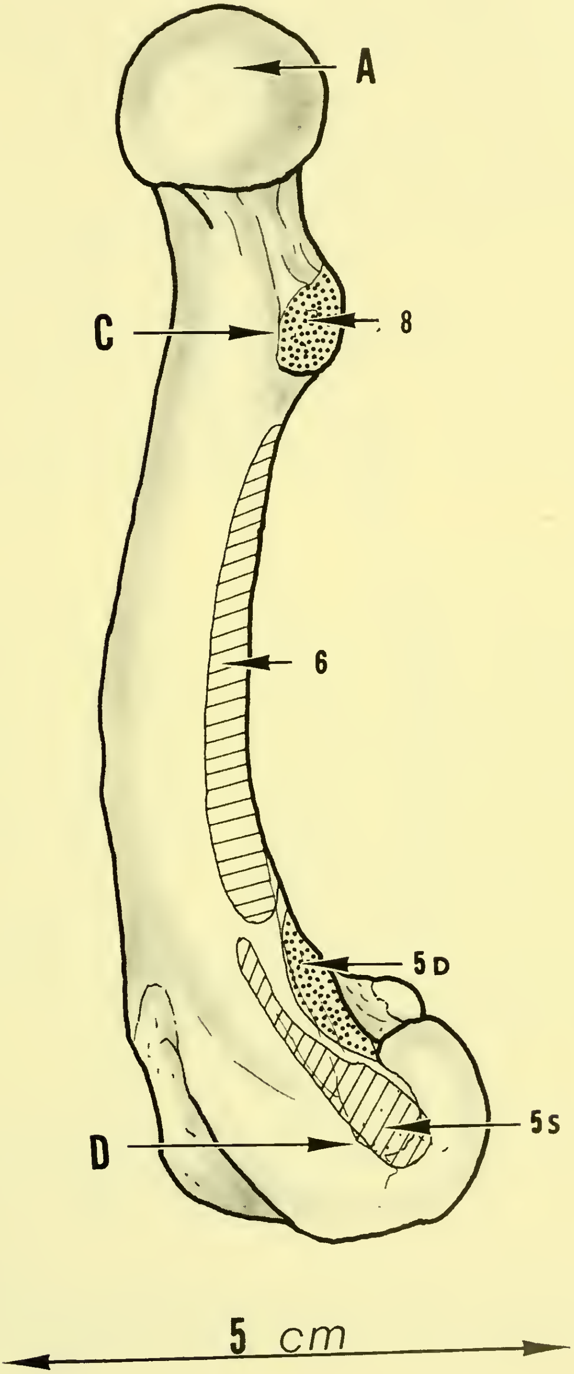
FIGURE 49. Medial view of right femur. Key: A, head of femur; C, lesser trochanter of femur; D, medial epicondyle of femur; 5S, adductor femoris (superficial portion); 5D, adductor femoris (deep portion); 6, pectineus; 8, iliopsoas.


A
C
8
6
5D
5S
D
5 cm

ACTION. The tendon of the flexor digitorum brevis can serve to flex independently the proximal interphalangeal joint, but can flex the metatarsal phalangeal joint as well.

38. **Quadratus plantae.**

This is a short, broad, flat muscle joining the calcaneus to the flexor digitorum longus (36) tendons.

ORIGIN. This muscle arises from the lateral aspect of the calcaneus for its full length. The muscle triangulates somewhat, passing distally and covering most of the plantar surface of the distal one-half of the calcaneus on its plantar aspect. Mostly fleshy fibers then join the flexor digitorum longus tendon (36) just opposite where the flexor hallucis longus (35) tendon also joins, and just proximal to the point of division of the flexor digitorum longus (36) into the separate tendons which pass to digits 2, 3, 4, and 5.

ACTION. The exact function of this muscle is not clear, but it probably aids in holding the long digital flexors laterally during the time that they are contracting.

39. **Calcaneometatarsalis.**

This is an extremely small muscle overlying the quadratus plantae (38), joining the calcaneus with the proximal end of the fifth metatarsal.

ORIGIN. This muscle arises from the small area on the posterolateral aspect of the calcaneus immediately adjacent to the point of exit of the plantaris (31) tendon. This small muscle then tapers as it passes obliquely over the quadratus plantae (38) toward the base of metatarsal five. A thin tendon forms at the distal one-third, continues distally, and overlies the peroneus longus tendon (28) where it dips deeply into the sole, then underlies the medial side of the peroneus brevis (30).

INSERTION. This tiny tendon then inserts into the base of the fifth metatarsal just proximal to the insertion of the peroneus brevis (30).

ACTION. Just what the action of this muscle is would be difficult to determine. From the standpoint of origin and insertion, the muscle could support the longitudinal arch of the foot.

THE INTRINSIC MUSCLES OF THE FOOT

This group of small muscles has origin and insertion within the foot proper. They serve to balance the action of the longer and more powerful prime movers

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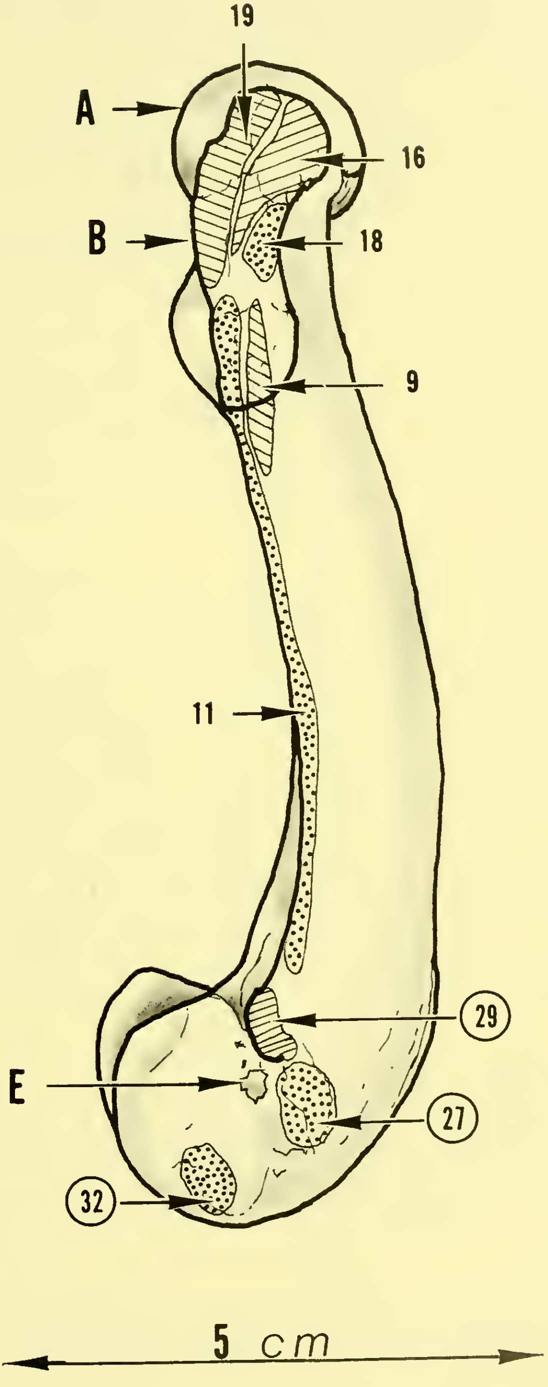
FIGURE 50. Lateral view of right femur. Key: A, head of femur; B, greater trochanter of femur; E, attachment of lateral collateral ligament of knee; 9, gluteus maximus; 11, caudofemoralis; 16, gluteus medius; 18, gluteus minimus; 19, piriformis; 27, extensor digitorum longus (origin); 29, peroneus digiti quinti (origin); 32, popliteus (origin).


19
A
16
B
18
9
11
29
E
27
32
5 cm

of the digits, and to give finer and more individualized skill motions to the digits. The broad webbing and elongated digits of the hind limb, as compared to the forelimb, permits more individualized digital motions.

The intrinsic muscles fall into three groups for descriptive purposes: the lumbrical muscles (48) which arise from the flexor digitorum longus (36) in the foot, the small muscles grouped about the first and fifth metatarsals, and the deeply situated interossei musculature (46).

The extensor digitorum brevis (47), although its origin and insertion are within the foot, is not considered an intrinsic muscle, but it is described in this general group for convenience.

INTRINSIC MUSCLES OF THE FIFTH DIGIT (40, 41, 42)

The fifth digit in the sea otter is the largest, and therefore the small muscles about this digit have a greater total volume than those about the first digit. The opponens muscle (42) is very small and, in view of its insertion, could hardly be expected to give opposition to this digit.

40. **Abductor digiti quinti.**

This is one of the three small muscles grouped about the fifth metatarsal.

ORIGIN. This largest of the small foot muscles is the most lateral in location. The muscle arises proximally from the heavy ligamentous capsule and small sesamoid bone overlying the plantar aspect of the base of the fifth metatarsal on the medial side and from the base of the metatarsal laterally adjacent to the insertion of the peroneus brevis (30). The origin continues distally from the lateral side of the fifth metatarsal for its full length. The muscle passes somewhat obliquely across the plantar surface of the fifth metatarsal, covering most of the ventral surface of the bone. At the metatarsal head, a short broad tendon develops which blends into the joint capsule, making attachments to the lateral sesamoid and the base of the proximal phalanx on its lateral side.

ACTION. This muscle serves to abduct and flex the proximal joint of the fifth digit.

41. **Adductor digiti quinti.**

This muscle is located opposite the abductor (40) and opposes its action.

ORIGIN. This muscle is considerably smaller than the abductor (40). It takes its origin from the capsular structures just medial to the abductor (40)

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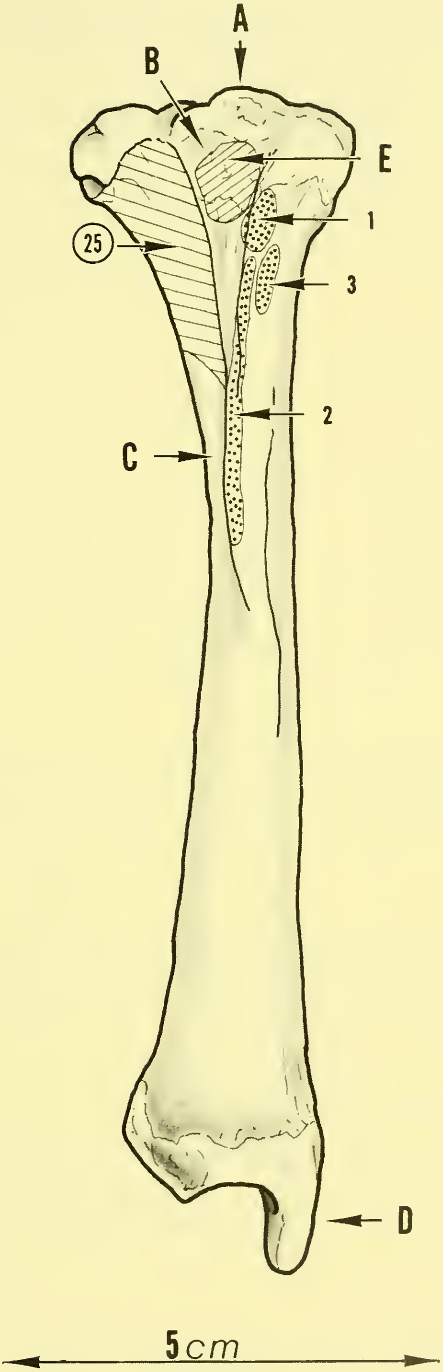
FIGURE 51. Anterior view of right tibia. Key: A, tibial plateau; B, tibial tuberosity; C, tibial crest; D, medial malleolus; E, patella tendon (combined tendons of 7, 10, and 14); 1, sartorius; 2, gracilis; 3, semitendinosus; 25, tibialis anterior (origin).


A
B
E
1
25
3
2
C
D
5 cm

and also from the medial side of the fifth metatarsal shaft in its proximal one-half. The muscle then courses distally to the medial side of the proximal joint where a short flattened tendon develops.

INSERTION. This tendon blends into the joint capsule, attaching to the medial sesamoid to make its insertion into the base of the proximal phalanx on the medial plantar aspect. Distally, the thin tendon of the opponens digiti quinti (42) courses over the tendinous expansion.

ACTION. This muscle serves to adduct and flex the proximal joint of the fifth digit.

42. **Opponens digiti quinti.**

This is a small intrinsic muscle and from its position is given the name opponens.

ORIGIN. The muscle arises from the midcentral area of the fibrous capsule of the tarsus and superficially overlies the proximal origin of all interossei (46) except the most medial one. The muscle tapers promptly into a very thin tendon at the level of the junction of the middle and proximal thirds of the fourth metatarsal. The tendon then continues obliquely toward the medial side of the proximal joint of the fifth digit. Keeping to the medial side, the tendon passes over the tendon of the adductor hallucis (44) and appears to join into the extensor aponeurosis one-third of the way down the proximal phalanx.

ACTION. This small muscle could assist in flexion of the proximal joint, adduction of the proximal joint, and possibly to the extensor aponeurosis, giving some assistance in the extension of the middle and distal joints. In spite of its name, its insertion would exclude any opposition motion of the fifth digit.

INTRINSIC MUSCLES OF THE FIRST DIGIT (43, 44)

The first digit with its two phalanges is the shortest toe in the foot, and the two associated intrinsic muscles are likewise small. There is no opponens muscle for this digit.

43. **Abductor hallucis.**

This muscle is the most medial of the small foot muscles.

ORIGIN. This muscle arises from the fibrous plantar capsule of the tarsus at the base of the first metatarsal. The muscle is fusiform in shape and passes

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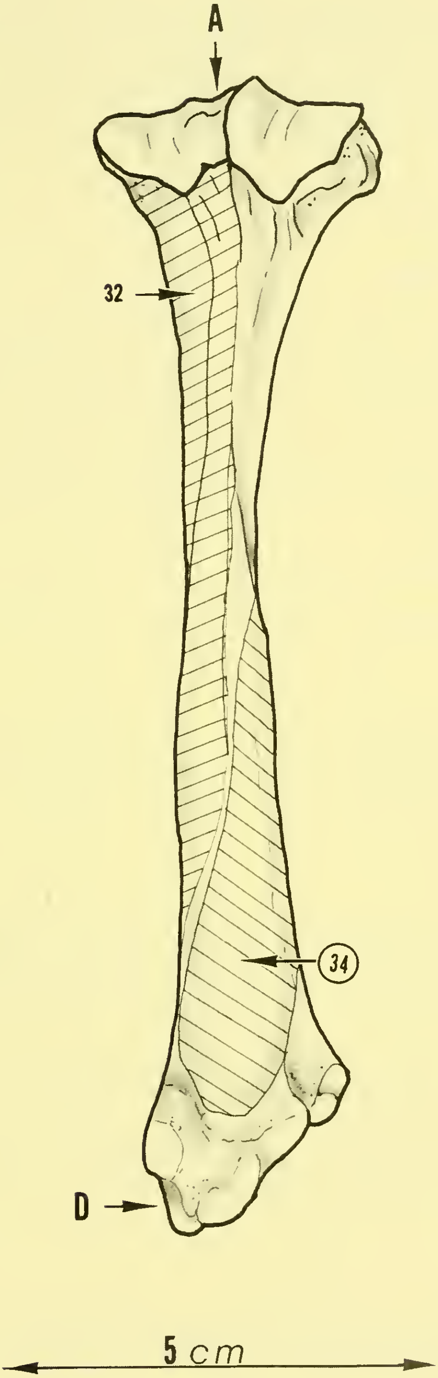
FIGURE 52. Posterior view of right tibia. Key: A, tibial plateau; D, tibia (medial malleolus); 32, popliteus; 34, tibialis posterior (origin).


A
32
34
D
5 cm

distally overlying the medial one-half of the first metatarsal. A short flat tendon develops just proximal to the proximal joint level and passes medially over the medial sesamoid to which it has fibrous attachment, then continues in an aponeurosis-like structure to the base and side of the proximal phalanx for its insertion.

Action. Flexion of the proximal joint and abduction of the proximal joint of digit one.

44. **Adductor hallucis.**

Origin. This small fusiform muscle and companion of the abductor (43) arises from the fibrous plantar capsule on the lateral side of the base of metatarsal one. Proceeding distally and parallel to the abductor, it overlies the lateral one-half of metatarsal one on its ventral surface. Distally, a short flat tendon develops which passes to the lateral side, inserting in a similar manner to the abductor. Fibrous attachments are present to the lateral sesamoid and joint capsular structures, and eventually insertion is into the proximal side of the proximal phalanx.

Action. Flexion and adduction of the proximal joint of digit one.

45. Dr. Howard omitted mention of any muscle numbered '45.' Editor.

The Interossei Musculature

The interossei muscles are six in number. They lie deep in the sole of the foot, being cradled in the transverse metatarsal arch. There are two interossei for each of digits two, three, and four, and they insert respectively on the medial and lateral sides of the digits.

46. **Interossei.**

Excluding the small muscles about the first and the fifth digits, there are six small interossei muscles: two each for digits two, three, and four. For descriptive purposes, they can be identified from the medial to the lateral side as 46a–f.

Origin. The interossei muscles arise in sequence from the heavy fascia covering the plantar surface of the tarsus, from the lateral side of the base of metatarsal one to the medial side of the base of metatarsal five. Muscle fibers also arise from the periosteum of the proximal ends of the metatarsal. The origin of 46a and b overlies the proximal end of metatarsal two. The origin

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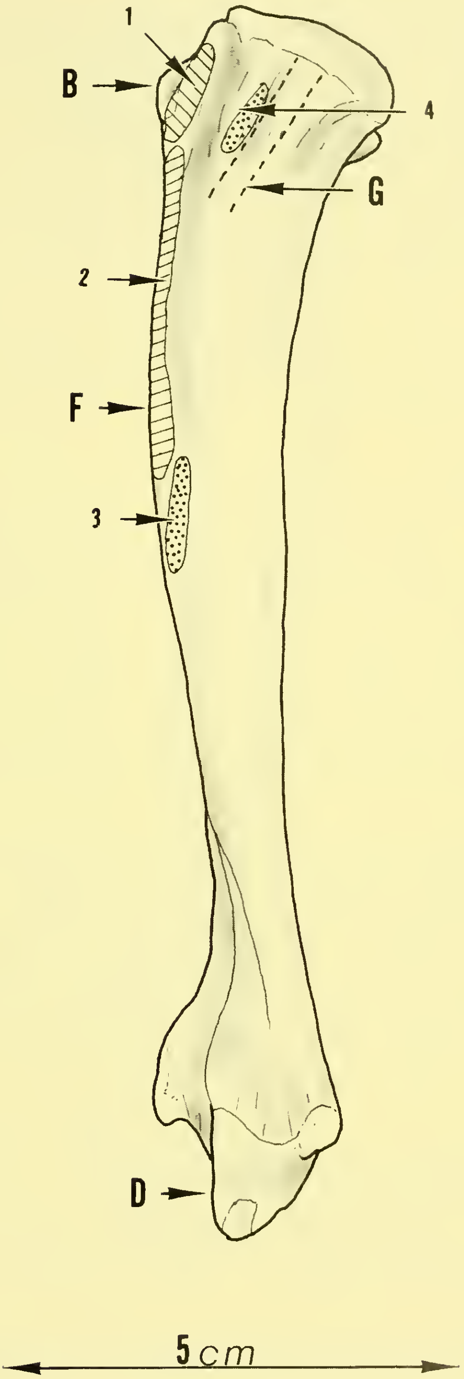
Figure 53. Medial view of right tibia. Key: B, tibial tubercle; D, medial malleolus of tibia; F, anterior crest of tibia; G, medial collateral ligament; 1, sartorius; 2, gracilis; 3, semitendinosus; 4, semimembranosus.


1
B
4
G
2
F
3
D
5 cm

of 46c and d overlies the proximal end of metatarsal three. The origin of metatarsal 46e and f overlies the proximal end of metatarsal four, with some additional overlapping of f onto the proximal end of metatarsal five.

INSERTION. The muscles pass distally to assume their respective positions on either side of metatarsals two, three, and four. Near the metatarsophalangeal joint, flat tendons form which spread out with attachments to the joint capsule and adjacent sesamoid in a more ventral area, and the more dorsal area of tendon extends distally and dorsally into the extensor hood to join the extensor aponeurosis of the digit.

ACTION. The action of the interossei muscles is to flex the metatarsophalangeal joint and to give a degree of lateral motion at this joint. Also, through the lateral bands, these muscles would act to extend the middle and distal interphalangeal joints.

47. Extensor digitorum brevis.

This muscle is an accessory digital extensor which lies deep to the extensor digitorum longus (27) and joins the ankle area with the digits.

ORIGIN. This muscle arises from the calcaneus and adjacent capsular structures on the dorsolateral aspect of the ankle. The origin lies directly under the extensor digitorum longus (27) tendons where they pass through the sheath in front of the ankle. Three distinct muscle bellies are present, and these extend distally to about the metatarsal junction of digits five, four, and three. The muscle terminates in three long flat tendons which pass to the ulnar sides of digits four, three, and two where they enter the hood structure and extensor aponeurosis.

INSERTION. These tendons enter the extensor aponeurosis to the ulnar side of the extensor digitorum longus (27) and the tendinous fibers continue distally to form a generally lateral border of the aponeurosis. At the interphalangeal joint level, the fibers are generally central with those of the longus, and the insertion is into the base of the middle phalanx. Tendinous fibers may continue to form, in part at least, the extensor tendon going to the distal joint. In the specimen dissected, there arose from the medial and lateral muscles tiny

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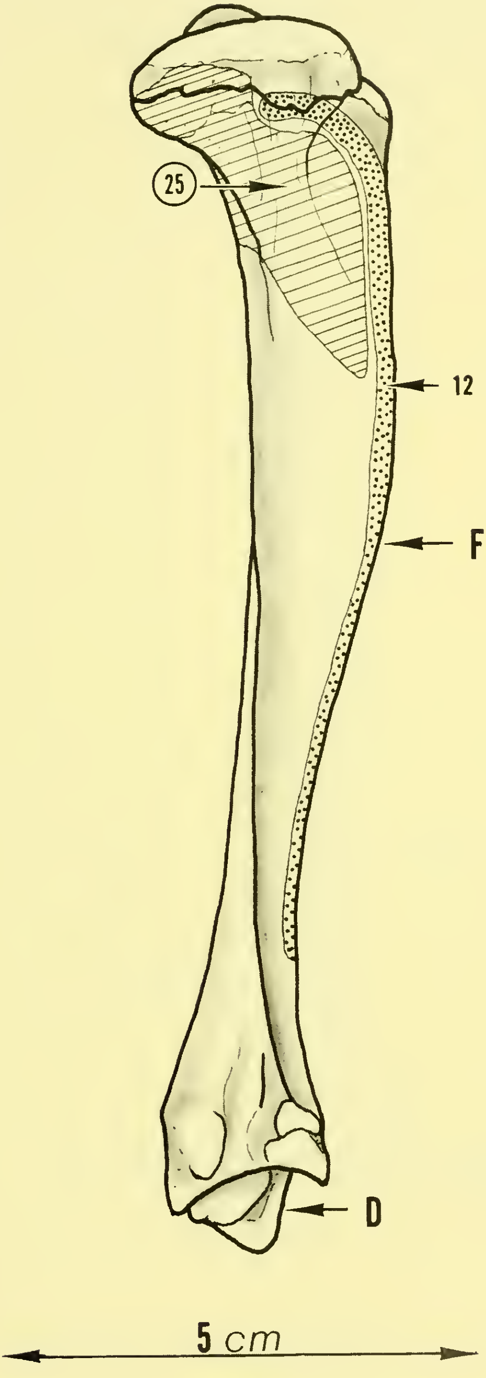
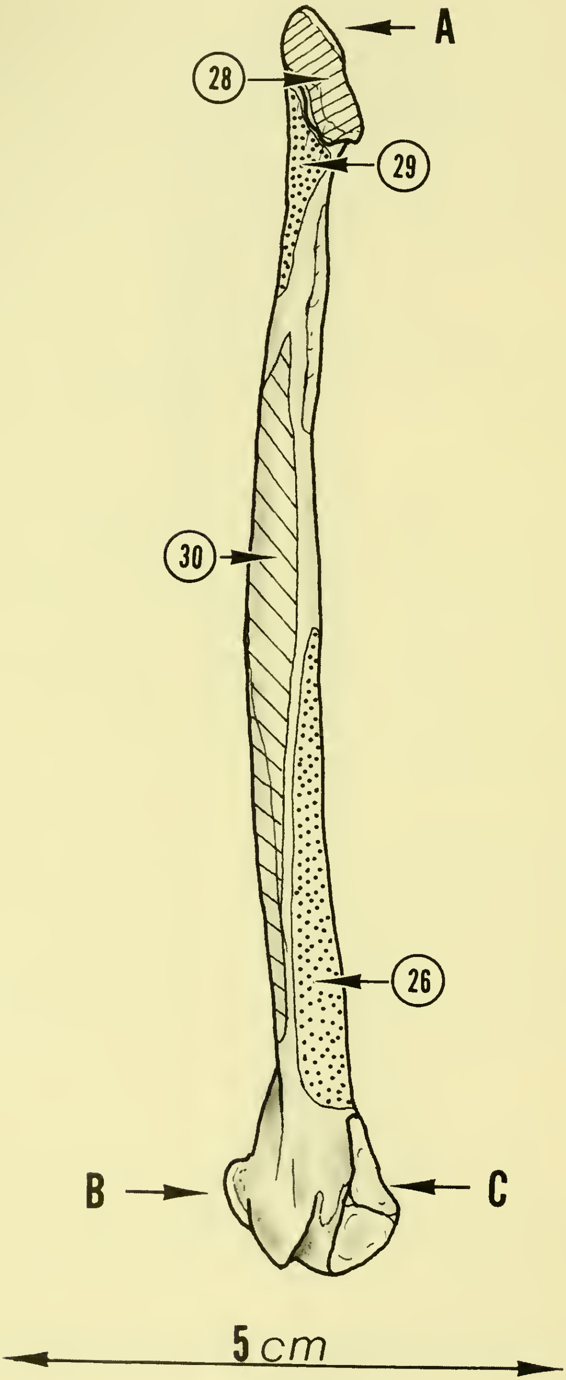
FIGURE 54. Lateral view of right tibia. Key: D, medial malleolus of tibia; F, tibial crest; 12, biceps femoris; 25, tibialis anterior (origin).

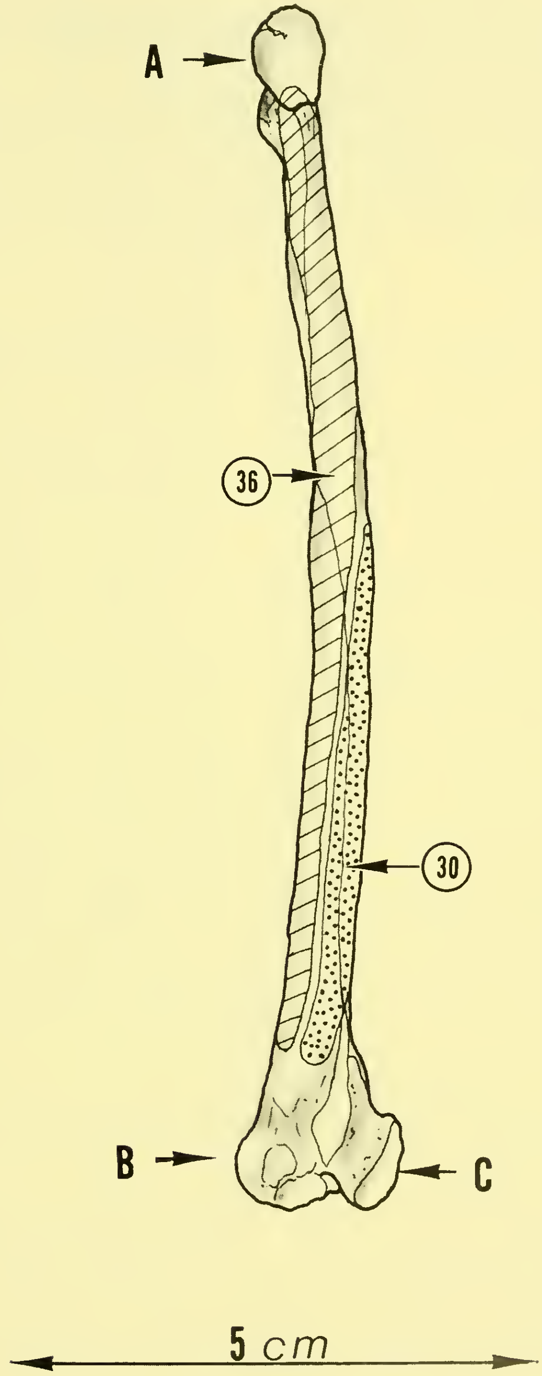
FIGURE 55. Anterior view of right fibula. Key: A, head of fibula; B, lateral malleolus; C, articulation with tibia; 26, extensor hallucis longus (proprius—origin); 28, peroneus longus (origin); 29, peroneus digiti quinti (anterior head—origin); 30, peroneus brevis (origin).

FIGURE 56. Posterior view of right fibula. Key: A, head of fibula; B, lateral malleolus; C, articulation with tibia; 30, peroneus brevis (origin); 36, flexor digitorum longus (origin).


25
12
F
D
5 cm



A
28
29
30
26
B
C
5 cm


A
36
30
B
C
5 cm

tendinous slips which joined respectively with the extensor digitorum longus (27) of the fifth and the extensor hallucis proprius (26) of the first. It is highly probable that individual variations occur.

ACTION. The tiny tendinous slips that go to the first and fifth digits are so small that the function would be minimal, if any. For the main tendons going to digits two, three, and four the action would be the same as the extensor digitorum longus (27), as both are acting through the extensor aponeurosis of the digits.

48. **Lumbricales.**

These small slender muscles arise from the long flexor tendons of digits two, three, four, and five, and are generally included in the intrinsic muscle group.

ORIGIN. Out of a total of six muscles, four follow a basic pattern of arising from the radial side of each flexor tendon (flexor digitorum longus—36) for each of the digits two, three, four, and five. They are thin fusiform muscles, each forming a small thin tendon just proximal to the metatarsophalangeal joint level on the radial side of each digit. The other two more superficial muscles arise more from the ventral surfaces of the flexor digitorum longus (36) tendon of four and five. They are closely associated proximally, but separate distally into two distinct muscles. Each forms a thin tendon, the more medial one passing toward the fourth digit and the more lateral toward the fifth digit.

INSERTION. Of the four lumbricales arising from the basic pattern, each has a thin long tendon which goes respectively to the radial sides of digits two, three, four, and five. For digits two, three, and four, a slender tendon inserts on the radial side of the proximal phalanx a short distance beyond the proximal joint and ventral to the extensor aponeurosis. For digit five, the tendon joins with the extensor digitorum longus (27) to form the radiolateral margin of the extensor aponeurosis.

The more superficial lumbrical muscles arising from the long flexor tendons of four and five, are much smaller than the others. Their thin tendons pass

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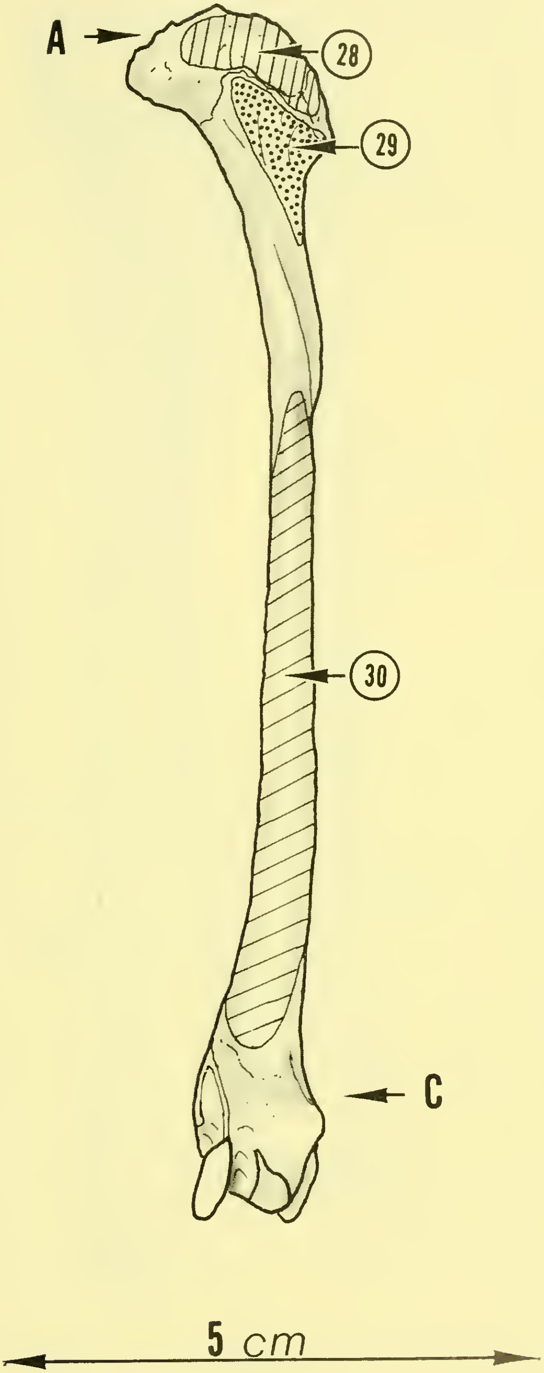
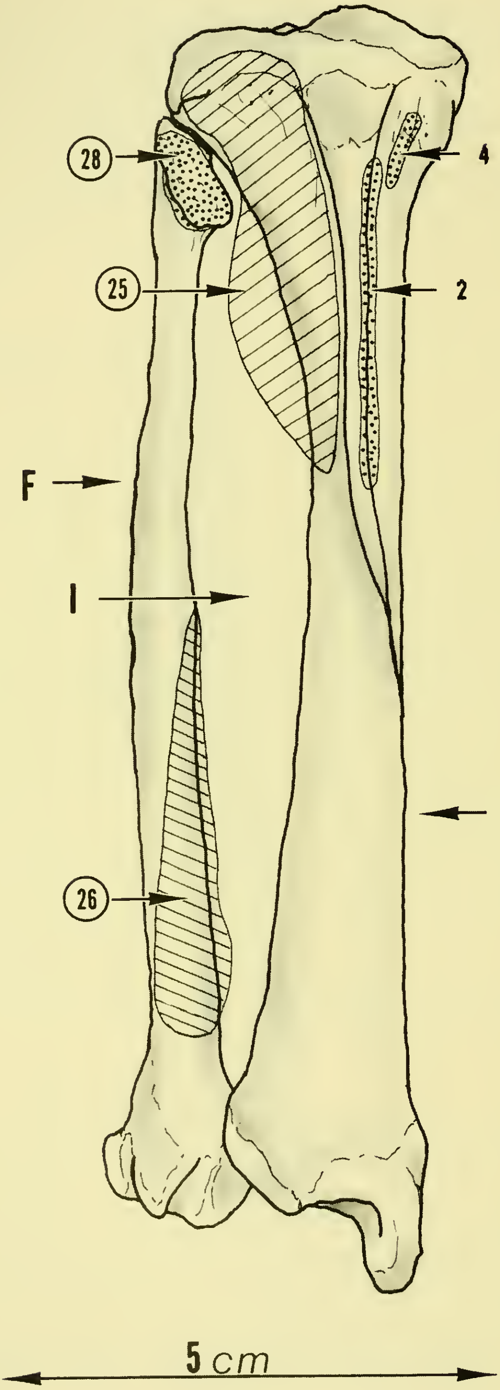
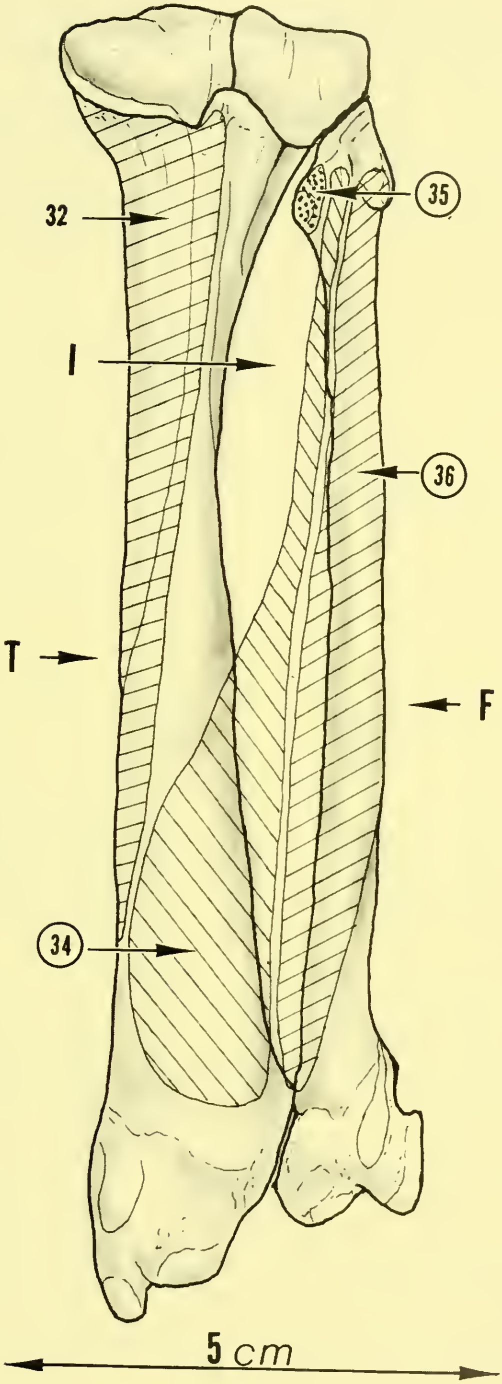
FIGURE 57. Lateral view of right fibula. Key: A, head of fibula; C, lateral malleolus of fibula; 28, peroneus longus (origin); 29, peroneus digiti quinti (anterior head—origin); 30, peroneus brevis (origin).

FIGURE 58. Anterior view of right tibia and fibula (articulated). Key: T, tibia; F, fibula; I, interosseus membrane; 2, gracilis; 4, semimembranosus; 25, tibialis anterior (origin); 26, extensor hallucis longus (proprius—origin); 28, peroneus longus (origin).

FIGURE 59. Posterior view of the right tibia and fibula (articulated). Key: T, tibia; F, fibula; I, interosseus membrane; 32, popliteus; 34, tibialis posterior; 35, flexor hallucis longus; 36, flexor digitorum longus.


A
28
29
30
C
5 cm


28
4
25
2
F
I
T
26
5 cm


32
③⑤
I
③⑥
T
F
③④
5 cm

ventrally and join respectively the ulnar sides of the sublimus flexor tendons just prior to their disappearance into the flexor tendon sheath at the metatarsal joint level.

Action. The action of the four lumbricales which follow the basic pattern would be to assist in flexion of the metatarsophalangeal joint. They would also give some radial lateral flexion of the joint. The one passing to digit five would also assist in extension of the distal two joints through the extensor aponeurosis. The more superficial lumbrical muscles, which serve to join the profundus and sublimus flexors, undoubtedly have some function but it would be difficult to state just what this function is.

Extensor Aponeurosis

The extensor mechanism for the digits is complicated and not completely understood. The tendinous flattened structure overlying the dorsum of digits 2 through 5 inclusive provides the mechanical arrangement for the insertion and action of the extrinsic and intrinsic musculature. By extrinsic is meant the extensor digitorum longus (27), the extensor digitorum brevis (47), the extensor hallucis longus (26), and the peroneus digiti quinti (29). By intrinsic musculature is meant the interossei (46) and for digit 5 the lumbrical (48) muscle.

The general plan of this mechanism is as follows: The long tendons of the extrinsic muscles for digits 2, 3, 4, and 5 join at the metatarsophalangeal joint level in a fibrous hood-like structure which marks the beginning of the aponeurosis and which attaches ventrally to the capsular structures on either side. The long tendons do not insert into the proximal phalanx, but act to extend the metatarsophalangeal joint by virtue of this hood-type structure. The aponeurosis now proceeds distally as a continuation of the tendons with the cross fibers, with the addition of the interrossei tendons medially and laterally for digits 2, 3, and 4, to form lateral bands; for the fifth digit the lumbrical performs this function on the radial side.

At proximal interphalangeal joint level, direct insertion at the base of the middle phalanx occurs for most of the extensor tendon fibers, but some continue on to insert terminally at the base of the distal phalanx. Both insertions are on the dorsal aspects. The fibers continuing beyond the interphalangeal joint level form a thin and rather poorly developed tendon.

In fresh specimens, traction on the extrinsic tendons will extend all three joints of digits 2, 3, 4, and 5, provided the metatarsophalangeal joint is not permitted to hyperextend. If the metatarsophalangeal joint is allowed to hyperextend, the distal two joints drop into slight flexion as the excursion of the long tendons is limited by the hood attachment. This claw-type deformity is corrected, for the most part, when traction is made along the lateral bands of the aponeurosis.

Although passive hyperextension is present for both proximal and distal interphalangeal joints, active hyperextension is not obtained by traction on the aponeurosis. In fact, the tendon action distal to proximal interphalangeal joint level seems limited and weak.

See figure 41 for a diagrammatic representation of the aponeurosis and the various tendon components for the specimen study. Undoubtedly, variations would be noted if many specimens were to be dissected.

ACKNOWLEDGMENTS

The State of California Department of Fish and Game was most cooperative in providing the specimen for anatomical study. The California Academy of Sciences provided the invaluable aid of a disarticulated sea otter skeleton.

The Anatomical Studies of the California River Otter, by Edna M. Fisher, proved to be an excellent guide during the dissection, and her unpublished notes on sea otter anatomy, which were made available through the courtesy of Mr. Fred Tarasoff, were also of value. Unpublished notes and sketches by Fred Tarasoff were also available and of some assistance.

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THE MORAY EELS (PISCES: MURAENIDAE) OF THE GALAPAGOS ISLANDS, WITH NEW RECORDS AND SYNONYMIES OF EXTRALIMITAL SPECIES

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ABSTRACT: Sixteen species of muraenid eels are recognized from the Galapagos Islands. These are (new records in boldface): *Anarchias galapagensis* (Seale), *Echidna nocturna* (Cope), **E. zebra** (Shaw), *Gymnothorax dovii* (Günther), **G. buroensis** (Bleeker), **G. castaneus** Jordan and Gilbert, *G. panamensis* (Steindachner), *G. pictus* (Ahl), *Enchelycore octaviana* (Myers & Wade), **E. lichenosa** (Jordan & Snyder), *Muraena lentiginosa* Jenyns, **M. clepsydra** Gilbert, **M. argus** (Steindachner), *Uropterygius polystictus* Myers & Wade, **U. necturus** (Jordan & Gilbert), and an undescribed species of *Uropterygius*. The following new synonymies are proposed: *Rabula* Jordan & Davis, 1891 = *Gymnothorax* Bloch, 1795. *Rabula davisi* Fowler, 1912 = *Gymnothorax mordax* (Ayres, 1859). *Sideria chlevastes* Jordan & Gilbert, 1883 = *Gymnothorax rueppelliae* (McClelland, 1845). *Echidna scabra* Garman, 1899; *E. chionostigma* Fowler, 1912; *Muraena acutis* Seale, 1917; and *Rabula rotchii* Clark, 1936 = *Echidna nocturna* (Cope, 1872). *Gymnothorax arae* Borodin, 1928 = *G. dovii* (Günther, 1870). *Gymnothorax thomsoni* Borodin, 1928 = *G. pictus* (Ahl, 1870). *Murenophis marmoreus* Valenciennes, 1855; *Muraena aquae-dulcis* Cope, 1872; *M. insularum* Jordan and Davis, 1891; and *Lycodontis xanthospilus* Fowler, 1944 = *Muraena lentiginosa* Jenyns, 1842. *Muraena albigutta* Hildebrand, 1946 = *M. argus* (Steindachner, 1870).

Introduction

The Galapagos Islands (Archipiélago de Colón) possess a large and diverse marine eel fauna, many species of which are muraenids. The moray fauna of the islands has not been treated as a whole since Jordan and Evermann (1896). We herein provide a listing of the 16 valid species, the first records of seven additional species, and comments on the validity of several Galapagos and extralimital nominal species of morays. A key is provided for the identification of known Galapagos species.

The following list includes those species whose existence at the Galapagos we have verified: *Anarchias galapagensis* (Seale), *Echidna nocturna* (Cope), *Gymnothorax dovii* (Günther), *G. buroensis* (Bleeker), *G. castaneus* Jordan & Gilbert, *G. panamensis* (Steindachner), *G. pictus* (Ahl), *Enchelycore octaviana* (Myers & Wade), *E. lichenosa* (Jordan & Snyder), *Muraena lentiginosa* Jenyns, *M. clepsydra* Gilbert, *M. argus* (Steindachner), *Uropterygius polystictus* Myers & Wade, *U. necturus* (Jordan & Gilbert), and an undescribed species of *Uropterygius*.

Fowler's (1938) record of *Lycodontis afer* from South Seymour (Baltra) Island is probably based on Herre's (1936, p. 44) listing of *Gymnothorax funebris* (James E. Böhlke, personal communication, 13 August 1974). We have reidentified Herre's specimen (SU 24386) as *G. panamensis*. Other doubtful records and invalid species have recently been treated. Rosenblatt *et al.* (1972) corrected Herre's (1936) erroneous records of Indo-Pacific species said to be from the Galapagos. Herre's listing of *Gymnothorax chilospilus* and *G. undulatus* was based on small specimens of *Muraena lentiginosa*. Randall and McCosker (in press) placed *Lycodontis umbra* Fowler (1944) in the synonymy of *Gymnothorax panamensis* (Steindachner).

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Key to the Galapagos Muraenids

1a Dorsal and anal fins developed as skin-covered ridges originating just before caudal 2
1b Dorsal and anal fins skin-covered but distinct, beginning ahead of gill opening and just behind anus, respectively 5

2a Tip of tail hard and pointed; posterior nostril closely associated with an enlarged interorbital pore, so that posterior nostril appears double; Gulf of California to Panama and Galapagos .... *Anarchias galapagensis* (Seale)

2b Tip of tail blunt, with a skin-covered caudal; posterior nostril not closely associated with an interorbital pore 3

3a Teeth blunt, molariform; body color dark brown to black, encircled by numerous, narrow white rings; Indo-west Pacific, oceanic islands of eastern Pacific and Gulf of California to Panama .... *Echidna zebra* (Shaw)

3b Teeth pointed; body color mottled but without definite rings 4

4a Head and trunk longer than tail; ground color light with dark mottling; posterior nostril tubular, located anterior to center of eye; Gulf of California (SIO 65-330) and Galapagos .... *Uropterygius polystictus* Myers & Wade

4b Head and trunk shorter than tail; ground color dark with rusty mottlings; posterior nostril with a raised rim, located behind center of eye; Gulf of California to Panama and Galapagos .... *Uropterygius necturus* (Jordan & Gilbert)

5a Teeth blunt, becoming molariform in adults; body color even brown to black with scattered white spots; anterior nostrils orange in life; Gulf of California to Peru and Galapagos .... *Echidna nocturna* (Cope)

5b Teeth pointed at all ages; coloration various, not as above 6

6a Posterior nostril tubular 7

6b Posterior nostril not tubular, at most with a raised rim 9

7a Dorsal and anal margins white; black spot at corner of mouth not preceded by white; body with three rows of large irregular yellow blotches and many scattered small white spots; teeth on shaft of vomer not depressible; Alijos Rocks, Baja California, to Peru and Galapagos .... *Muraena argus* (Steindachner)

7b Dorsal and anal margin not white, with at most a few white blotches; black spot at corner of mouth preceded by a white area on lower jaw; body either mostly plain or spotted, but without large yellow blotches; all vomerine teeth depressible 8

8a A large black spot, equal to 2.5 or more eye diameters, around gill opening; young with 5 or 6 series of small hour-glass shaped spots, adults speckled with numerous very small irregular spots on body and fins; Cape San Lucas, Mexico, to Peru and Galapagos .... *Muraena clepsydra* Gilbert

8b Black area surrounding gill opening not conspicuous or ringed with white, its diameter equal to 1.5 eye diameters or less; color not as above, either tan with rows of round to oblong yellow or white spots, or dark and reticulated with a few small white spots; Gulf of California to Peru and Galapagos .... *Muraena lentiginosa* Jenyns

9a Lower jaw curved, so that a gap is present and teeth are visible when mouth is closed 10

9b Lower jaw nearly straight so that there is no gap and the teeth are hidden when mouth is closed 11

10a Body coloration uniform brown to grey; pores along upper lip elongate slits with crenulate margins; Gulf of California (SIO 65-336) to Colombia and Galapagos .... *Enchelycore octaviana* (Myers & Wade)

10b Body coloration dark brown, head and throat overlain with numerous light spots, a series of large light blotches along sides; all head pores round; Galapagos and Japan .... *Enchelycore lichenosa* (Jordan & Snyder)

11a Body coloration white, profusely covered with dark brown speckling; vomerine teeth biserial, maxillary teeth uniserial; Indo-west Pacific and oceanic islands of eastern Pacific .... *Gymnothorax pictus* (Ahl)

11b Body background color various, if white not profusely speckled; vomerine teeth not in two equal rows, maxillary teeth uniserial or biserial 12

12a Dorsal origin about midway between occiput and gill opening; head pores ringed in white, a black ring around eye; outer series of teeth thickened, bent abruptly backward at tips, their posterior margins serrate; Gulf of California to Panama; Galapagos and Juan Fernandez and Easter Islands .... *Gymnothorax panamensis* (Steindachner)

12b Dorsal origin notably closer to occiput than gill opening; head pores not ringed in white, no dark ring around eye; teeth in jaws all conical, straight or evenly curved, their margins smooth 13

13a Teeth on maxillary in two rows, the outer row smaller than the inner; five longitudinal rows of teeth in the front of upper jaw; body ground color dark brown to black, overlain with a wavy, irregular mottling; Indo-west Pacific and oceanic islands of eastern Pacific .... *Gymnothorax buroensis* (Bleeker)

13b Maxillary teeth uniserial; three longitudinal rows of teeth in the front of upper jaw; body ground color brown to black or green, not overlain with a dark, irregular mottling 14

14a Body ground color dark brown to black, with numerous white spots; Panama to Colombia and Galapagos .... *Gymnothorax dovii* (Günther)

14b Body ground color brown to brownish green, usually plain although sometimes with a few white or yellow flecks, mostly on posterior half and dorsal fin; Gulf of California to Panama and Galapagos .... *Gymnothorax castaneus* Jordan & Gilbert

New Records

Muraena clepsydra Gilbert.

This species is known from Cape San Lucas, Baja California, Mexico, to Panama. Galapagos specimens have come from Barrington (Santa Fe) Island (SIO 55-259; 970 mm; UCLA 55-314; 3, 82-305 mm.).

Gymnothorax buroensis (Bleeker).

A single specimen (SIO 74-103; 465 mm.) was collected at Darwin Bay, Tower (Genovesa) Island by M. Anctil. *Gymnothorax buroensis* is known from the Indo-west Pacific and Hawaii, and in the eastern Pacific from Clipperton and Cocos islands and nearshore localities in Costa Rica and Panama (Rosenblatt *et al.*, 1972).

Echidna zebra (Shaw).

The Galapagos record is based on an observation of this species by Gerard M. Wellington, Charles Birkeland, and Peter Glynn at Tower (Genovesa) Island during January, 1975 (Wellington, personal communication, 31 Jan. 1975). Although the specimen was not collected, its unmistakable appearance would preclude its misidentification.

Figure 1. *Muraena argus*, photographed at Gordon Rocks, Galapagos Islands, in a cave at approximately 45 m. depth, by Carl Roessler.

Muraena argus (Steindachner).

This species is known from Alijos Rocks, Baja California, Mexico to Peru (see discussion under *Muraena albigutta*, page 426). A Galapagos specimen was collected at James Bay, James (San Salvador) Island (UCLA 67-33, 900 mm.), and we have a photograph from Gordon Rocks (fig. 1).

Uropterygius necturus (Jordan & Gilbert).

This species is known from the Gulf of California to Panama, the Revillagigedo and Clipperton islands, and has been taken at several Galapagos localities including Indefatigable (Santa Cruz) Island (UCLA 64-19, 230 mm.), Tower (Genovesa) Island (UCLA 67-35; 9, 174-232 mm.), and Charles (Santa Maria) Island (UCLA 67-43; 3, 220-280 mm.).

Enchelycore lichenosa (Jordan & Snyder).

Aemasia lichenosa was described by Jordan and Snyder (1901) as the type species of a new genus on the basis of Japanese market specimens from Wakanoura (the holotype, SU 6480, now at CAS, 52 cm.) and Misaki (a paratype, USNM 49976, 55 cm.). Except for Randall and McCosker's (in press) synonymy of *Aemasia* with *Enchelycore*, this species, to our knowledge, has been mentioned only in Japanese faunal works. We were somewhat surprised then, to discover four adult specimens of a hook-jawed moray that we have identified, by comparison with the type material, as this species. Galapagos specimens are from Punta Espinosa, Narborough (Fernandina) Island (UCLA 64-3, 70 cm.; UCLA 64-8, 76 cm.; ANSP 117435, 60 cm.; ANSP 109855, 63 cm.). We are unable to separate the Galapagos specimens from the Japanese type material on the basis of morphological characters, coloration, or dentition. The holotype has 148 vertebrae (56 preanal); Galapagos specimens ANSP 109855 and ANSP 117435 have 136 (57 preanal) and 142 (53 preanal) vertebrae, respectively.

The addition of *Enchelycore lichenosa* to the Galapagos' fauna represents the ninth Indo-Pacific muraenid species known from the eastern Pacific (see Rosenblatt *et al.*, 1972). It is curious that *E. lichenosa* has not been taken elsewhere in the Pacific.

IDENTITY OF INVALID GENERA AND SPECIES

Rabula Jordan & Davis.

Jordan and Davis (1891, pp. 589–590) erected the subgenus *Rabula* to include those species of *Gymnothorax* with a dorsal fin origin beginning over or behind the gill opening. They designated as type-species *Muraena aquae-dulcis* Cope 1872, on the basis of a specimen (USNM 6673) from San Diego, California or "probably . . . from farther south," and Cope's description of the holotype. Fowler (1912) subsequently found their specimen to differ from Cope's species and, in a footnote which we quote, described it as a new species, *Rabula davisi*:

> I may note that Jordan and Davis identify an eel from San Diego, Cal., with Cope's species, and as they do not explicitly designate Cope's fish the former must be taken as the type of their genus *Rabula*. Therefore, the *Gymnothorax aquae-dulcis* (nec *Muraena aquae-dulcis* Cope) Jordan and Davis requires a new specific name.

We examined the holotype of *R. davisi* and found it to be an aberrant specimen of *Gymnothorax mordax* (Ayres, 1859). The dorsal fin appears to arise in the mid-trunk region; however a radiograph (fig. 2) of the specimen clearly shows that the dorsal fin arises above the 4th vertebra, disappears above the 11th, then reappears above the 61st. The specimen has 145 total vertebrae with 64 before the anal fin, not differing significantly from combined data for 54 specimens of *Gymnothorax mordax* (K. McCleneghan, personal communication, and C. Clothier, unpublished data) with a range of 143–152 total vertebrae ($\bar{x} = 147.8$) and 61–67 preanal ($\bar{x} = 65$). The specimen also agrees with *G. mordax* in its coloration, dentition, and morphometry. *Rabula* thus becomes a synonym of *Gymnothorax* Bloch 1795.

Other morays currently referred to *Rabula* include *R. fuscomaculata*

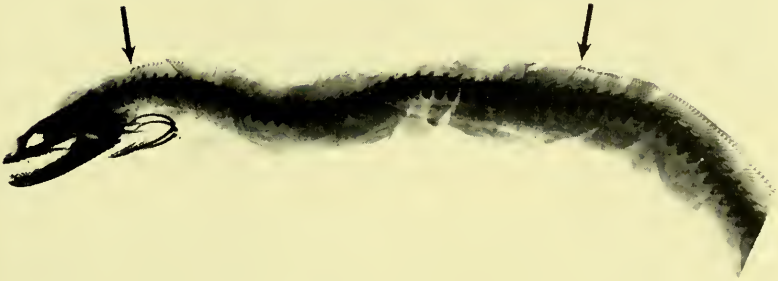

Figure 2. Radiograph of the head and trunk regions of the holotype of *Rabula davisi*. Arrows indicate dorsal fin origin above the 4th vertebra and reappearance above the 61st vertebra.

Schultz, *R. marshallensis* Schultz, and *R. acuta* (Parr). We have examined and radiographed specimens of '*fuscomaculata*' (CAS 31206) and '*marshallensis*' (CAS 31205) and, with the exception of the posterior dorsal fin origin, are unable to find characters which would allow their generic separation from *Gymnothorax*. We are hesitant to recognize them as generically distinct solely on the basis of their fin location.

Sideria chlevastes Jordan & Gilbert.

Examination of the holotype (USNM 20385) of *Sideria chlevastes* has shown the taxon to be a junior synonym of *Gymnothorax rueppelliae* (McClelland), a wide-ranging Indo-Pacific and Hawaiian species. The two common Indo-Pacific species of *Gymnothorax* with conspicuous broad bands have been called *G. ruppeli* (an unjustified emendation of *rueppelliae*) and *G. petelli*, respectively, by most modern authors. Randall (1973, p. 174) has shown however, that both names apply to the same species, and that the former has priority. Thus '*petelli*' of authors becomes '*rueppelliae*', and '*rupelli*' of most authors is without a name. Moreover, '*reticularis* Bleeker' is not available, as suggested by Randall, since that represents a misidentification of *Gymnothorax reticularis* Bloch, a distinctly different species.

Jordan and Gilbert's (1883) terse description of *Sideria chlevastes* merely states "obtained at the Galapagos Islands by Captain Herendeen." A search at the National Museum of Natural History by the senior author for further information concerning the type specimen revealed only that it was entered into the catalog on 13 August 1877, with a listing only of the collector and

"Galapagos Islands." No other specimens accompanied it. In that no subsequent Galapagos specimens have appeared since Herendeen's, we suspect that the locality was in error. It was not uncommon at that time for whalers such as Herendeen to stop at Hawaii and other islands, often returning with specimens to be deposited at the USNM. In that manner, it is not unlikely that a locality error might have originated. The 220 mm. holotype has 135 vertebrae, 51 before the anus.

Rabula rotchii Clark.

Clark's (1936) description is based on an abnormal specimen of *Echidna nocturna* (Cope, 1872) with a posterior dorsal insertion. The holotype (CAS 4964) in other proportions, coloration, and dentition fits *E. nocturna* well.

Echidna chionostigma Fowler.

While preparing this study we examined the type specimens (ANSP 14519 and 14520) of *E. chionostigma* Fowler, 1912, "probably from the Gulf of California," and found them also to be referable to *Echidna nocturna* (Cope, 1872).

Echidna scabra Garman.

Garman's (1899) type specimen (MCZ 28451) of *Echidna scabra*, from Cocos Island, is a juvenile of *Echidna nocturna* (Cope, 1872).

Muraena acutis Seale.

Seale's (1917) type specimen (MCZ 3960) of *Muraena acutis*, from the Gulf of Panama, is clearly referable to *Echidna nocturna* (Cope, 1872).

Gymnothorax thomsoni Borodin.

Borodin's (1928) feckless description but passable illustration of *G. thomsoni* clearly relates to an injured specimen of *Gymnothorax pictus* (Ahl, 1789), not *G. dovii* as suggested by Fowler (1938, p. 251).

Gymnothorax arae Borodin.

Borodin's (1928) inadequate description of *G. arae* from Darwin Bay, Tower (Genovesa) Island does mention scattered white dots, indicating that *G. arae* is a junior synonym of *G. dovii* (Günther, 1870).

Lycodontis xanthospilus Fowler.

Our examination of the holotype (ANSP 70026) of *L. xanthospilus* Fowler (1944) from James (San Salvador) Island revealed it to be a small specimen of *Muraena lentiginosa* Jenyns, 1842.

Muraena insularum Jordan & Davis.

A study of an adequate series of *Muraena* from the Galapagos Islands leads us to the conclusion that *M. insularum* Jordan & Davis, 1891, described from a Chatham (San Cristobal) Island specimen, also is identical with *M. lentiginosa* Jenyns, 1842. Two extreme color forms may be segregated in the Galapagos material. One has a color pattern of light brown with darker reticulations which almost form bars. In this dark sort there are a few light spots, but these are restricted to the throat. The dark color pattern has been described and figured by Morrow (1957, p. 16) and described by Jordan and Davis in the original description of *M. insularum*. Extremes of this kind are purplish brown, with a few scattered white spots on the throat. In the other sort, the ground color is light brown and there are several series of white spots down the sides and on the fins. These spots tend to line up in rows. The spots are surrounded by dark brown areas which tend to coalesce to form an interlocking network. There is, however, a complete range of variation between these sorts. Further, Jenyns' description of *M. lentiginosa* seems to have been based on a specimen of the dark sort.

The difference mentioned by Jordan and Davis concerning the number of rows of teeth in the upper jaw is invalid, since in all the known eastern Pacific species of *Muraena* the inner row of enlarged teeth is lost with increasing size.

It is of interest that such variability in coloration is not found in mainland populations. All of a large number of mainland specimens are much like the light island types in coloration, except that the dark brown areas surrounding the light spots are less extensive and never coalesce. However, all of our specimens are from Panama north, and Morrow (1957) has reported a specimen of the dark type from Peru. This seems to indicate that the Peruvian and Galapagos populations are genetically different from the northern populations. It is, however, difficult to evaluate differences in variability, and we do not feel that specific or even subspecific differentiation is indicated.

Muraena aquae-dulcis Cope.

Our examination of the Costa Rican type specimen (ANSP 14925) of *M. aquae-dulcis* Cope, 1872 indicates that it is a small and damaged specimen of *M. lentiginosa* Jenyns, 1842.

Murenophis marmoreus Valenciennes.

Although no specimens of this species have been reported since its description (Valenciennes, 1846), the name continues to appear as a species of *Gymnothorax* (Jordan & Davis, 1891) or *Rabula* (Jordan & Evermann, 1896; Fowler, 1938). Jordan and Evermann considered it to be "a doubtful species, perhaps based on *Muraena lentiginosa*." The illustration of the holotype leaves little doubt that this surmise is correct. The coloration (see discussion under *Muraena* *insularum*) is diagnostic. The indication in the figure of a dorsal origin behind the gill opening is likely an error and Valencienne's description of the posterior nostril as a slit beneath the eye applies to no known muraenid.

Muraena albigutta Hildebrand.

Hildebrand (1946), in describing *Muraena albigutta* from Peru, was apparently unaware of Steindachner's (1870) description of *Muraena argus* from Altata, Sinaloa, Mexico. Our material from the Gulf of California (SIO 60-1; UCLA 56-68) agrees well with Steindachner's description. We have compared the holotype of *M. albigutta* (USNM 127840) with a specimen from Guaymas, Sonora, Mexico. They agree, particularly in the distinctive coloration and in that the teeth on the shaft of the vomer are not depressible. *Muraena argus* is now known from Alijos Rocks, Baja California, Mexico (SIO 74-104); the Gulf of California; Isla La Plata, Ecuador (UCLA 53-419); Lobos de Afuera, Peru; and the Galapagos.

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THE TAXONOMIC STATUS OF THE SOUTHERN SEA OTTER

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Abstract: A recent review of the taxonomy of the sea otter (*Enhydra lutris*) by Roest (1973) concluded that all populations of this species extending from the Commander Islands to southern California should be considered to constitute a single subspecies (*E. l. lutris*). At present a 1700 mile gap (between Alaska and California) exists within this vast range. We re-examined Roest's data (and the available literature) for evidence which might suggest alternative taxonomic conclusions. In our opinion, the known facts strongly support the conclusion that the southern sea otter should continue to be recognized as a separate subspecies (*E. l. nereis*). Marked morphological and behavioral differences seem to exist, and at the present time complete genetic isolation as well. If a northwest-southeast cline in morphology existed formerly, the evidence suggests that there was a pronounced step or change in its slope in southwestern Alaska.

Introduction

Merriam (1904) described the Californian population of the sea otter (*Enhydra lutris*) as *Latax lutris nereis* on the basis of morphological differences between a single skull from San Miguel Island, Santa Barbara County, and skulls of typical *E. l. lutris* from the Aleutian Islands, Alaska. The validity of *E. l. nereis* has been variously accepted or questioned by subsequent workers (e. g., Grinnell, 1933; Grinnell, Dixon, and Linsdale, 1937; Scheffer and Wilke, 1950; Hall and Kelson, 1959; Kenyon, 1969). Until recently, lack of adequate material has been a severe handicap to critical evaluation of the taxonomic status of the Californian population. However, Roest (1971) compared large samples of adult skulls of known sex from Alaska (mainly from the Aleutians) and California. On the basis of skull differences and differences between the two populations in weight and total length, he recognized *E. l. nereis* as valid and as the proper subspecific designation for the southern sea otter. Subsequently additional skulls, from southwestern Alaska, became available to him. These specimens were intermediate in characters between those from the Aleutians and California and he proposed (Roest, 1973) that these characters varied clinally. On that basis he synonymized *E. l. nereis* and included all of the sea otters from the Commander Islands to California in *E. l. lutris*.

On the basis of Roest (1973), Miller (1974, p. 2), in an official publication of the California Department of Fish and Game, stated: "Now that *E. l. nereis* is no longer valid, *the question of sea otters in California being rare or endangered is void inasmuch as there are over 120,000 sea otters now extant in Alaskan waters, and over 1,600 in California*" (italics ours). In other words, according to Miller, the demographic status of the sea otter in California had been decided by the taxonomy proposed by Roest (1973).

Because of the possible importance of the taxonomy of the California sea otter to this animal's rare and endangered status, and to future management decisions, and because of the inherently challenging taxonomic questions involved, we re-examined Roest's data for evidence which might suggest alternative taxonomic conclusions to those chosen by him (1973). We found that there are, in fact, several alternative interpretations of the available data on geographic variation in the sea otter. Moreover, Roest's interpretation does not seem to fit the known facts as well as do other explanations. In the following discussion of geographic variation in *Enhydra lutris*, the subspecies *E. l. gracilis* of the Kurile Islands and the southern tip of Kamchatka is not reviewed critically.

Discussion

Roest (1971) assembled 214 adult sea otter skulls from Alaska, mainly from the Aleutian Islands, and 50 adult skulls from California. He took 24 skull measurements and, on the basis of stepwise discriminant analysis, selected four characters as being of taxonomic significance. Using a combination of these characters applied to skulls of known sex only, he designated each of 156 Alaskan and 40 Californian skulls as "Alaskan" or "Californian," with the following results:

Origin	N	Correctly identified	Incorrectly identified	Not referable
Alaska	156	141 (90.5%)	2 (1.3%)	13 (8.3%)
California	40	38 (95.0%)	0	2 (5.0%)

On the basis of the high degree of separability of Alaskan from Californian skulls, supplemented by differences in total length and in weight between the two populations, Roest recognized *E. l. nereis* as a valid subspecies and applied this name to the southern sea otter.

In 1972, skulls from southwestern Alaska (the Alaska Peninsula, southern Alaska, and Prince William Sound) became available and proved to be intermediate between those from the Aleutians and California (Roest, 1973). On the basis of this sequential shift in skull morphology from west to southeast, Roest proposed that variation in skull characters was clinal and that all of the sea otters from the Commander Islands to California pertain to a single race, *E. l. lutris*. From this viewpoint *E. l. nereis* was relegated to the synonymy of *E. l. lutris* although Roest (1973, pp. 8, 14) noted that the Californian population can be distinguished from the Aleutian population, but not from the population of southwestern Alaska.

There are, however, alternative interpretations of the variation in skull characters from the Aleutians to California. One of these has been suggested to us by Dr. Carl L. Hubbs (pers. comm.). Noting that Roest did not examine skulls from the area between southwestern Alaska and California, he points out that we do not therefore know the nature of variation over this distance of 1700 nautical miles (all distances given are great circle distances unless otherwise specified). Hubbs suggests that variation in skull characters may not have been gradually changing in the way suggested by Roest (1973), but they "may have been fairly constant throughout most of this vast distance; if so, we would have two well marked subspecies with a band of intergradation in southwestern Alaska."

Actually, Roest's own data suggest this. Of ten specimens from near Umnak Island and along the north shore of the Alaska Peninsula, "3 specimens show primarily Alaskan features, 6 are intermediate, and 1 could be considered Californian . . . . ," whereas of 16 specimens from Prince William Sound, he considered two Alaskan, two intermediate, and 12 Californian (Roest, 1973, pp. 8–9). These distributions differ significantly ($\chi^2 = 10.69$; $P < .01$). This pronounced shift toward the characters of the southern population, so far north in the sea otter's range, suggests that a population with Californian skull characters may well have extended far north into British Columbian waters. This would be quite compatible with Hubbs' suggestion of two well-marked subspecies intergrading in southwestern Alaska rather than clinal variation occurring within a single, widely distributed population.

If variation in skull characters was indeed clinal, there must have been a pronounced step or shift in slope steepness between the Alaska Peninsula and Prince William Sound. The great majority of specimens from Amchitka and Adak are of the Alaskan skull type. Between Adak and Port Heiden, the northeasternmost locality on the Alaskan Peninsula from which Roest had specimens, skull type has shifted from Alaskan to predominantly intermediate over a distance of 695 nautical miles. Between Port Heiden and Prince William Sound skull type has shifted from intermediate to predominantly Californian over a distance of 435 nautical miles. If the samples previously discussed indicate accurately the morphologic variation in the populations from which they were drawn, the slope of the cline over the 1700 nautical miles from Prince William Sound south to Monterey Bay must have been extremely gentle compared to that from Prince William Sound to Adak.

As regards weight differences between the northern and southern populations, the data presented by Roest (1973, p. 2) suggest that Californian males weigh considerably less than both Aleutian and southwestern Alaskan males; the same is true of females but the difference is less. However, some critical samples are small; further, most of his Alaskan specimens were weighed when fresh and most Californian specimens were weighed some time after death. Additional data on body weights are available from the literature (see summary in Harris, 1968; Kenyon, 1969; Wild and Ames, 1974). However, these do not permit critical geographic comparisons because it is not possible to compare comparable age groups. Nevertheless, they suggest in general that northern otters average heavier and reach a larger maximum weight (100 pounds for males, Kenyon, 1969, p. 21), thus supporting the trend suggested by Roest.

Data on total length (Roest, 1973, p. 7) indicate that males from California are considerably smaller than males from both southwestern Alaska and the Aleutians whereas females from both California and southwestern Alaska are smaller than those from the Aleutians. Unfortunately, total lengths of Alaskan specimens are curvilinear and those of Californian specimens are standard lengths (a fact not mentioned by Roest [1971] although means, ranges, and sample sizes indicate that the same samples were used in both papers). Thus, the generally larger size of Alaskan specimens may be accentuated by the difference in measurement techniques.

Student's *t* tests applied to Roest's 1973 data indicate significant differences in mean total length ($P < .001$) between males from California and males from both Adak and southwestern Alaska. However, males from the last two localities do not differ significantly. The mean length of females from Adak differs significantly from that of females from southwestern Alaska ($P < .01$) and California ($P < .001$), but females from California and southwestern Alaska do not differ significantly.

As regards color, "Alaskan otters are . . . dark, but those from California are most commonly medium brown in color" (Roest, 1973). It is not possible to estimate the degree of separability of the Alaskan and Californian populations on the basis of pelage color from this information, but apparently most southern sea otters can be distinguished by their color. Data summarized by Harris (1968, pp. 263–264) also support this conclusion.

To summarize the morphological data, the sea otter populations of the Aleutians and California can be differentiated at a level of better than 90% on the basis of skull characters. Aleutian otters are also larger and darker than those from California. Between these populations there is a population in southwestern

Alaska with intermediate skull characters; the males are larger than those from California but the females are similar in size. It is impossible, on the basis of available material, to determine with confidence whether the population in southwestern Alaska represents a point on a long west-southeast cline or whether it is a population intergradient between well-marked northern and southern subspecies. If, however, this population is on a cline, there must be a pronounced step or change in slope steepness between the Alaska Peninsula and Prince William Sound.

In addition to morphological differences, there are also behavioral differences between northern and southern sea otters. The use of hard objects placed on the chest as anvils for breaking open hard-shelled food items is rare in the otters of the Commander Islands and Amchitka, but is common in the otters of California. Since the diet of Alaskan otters includes a much higher proportion of fish than does the diet of southern otters, there may be simply less need for tool-using in the northern part of the species' range.

Hauling out on land is much more frequent in the northern population. In apparent association with this increased use of land is more efficient terrestrial locomotion in Alaskan otters. Kenyon (1969) states that northern otters walking unhurriedly move with a rolling gait, raising one foot at a time. When animals are startled "they arch the back and bound or hop, moving both forefeet then both hind feet forward in rapid succession. Speed of movement is somewhat less than the running speed of a normally agile man." In contrast, Californian otters do not arch the back and do not move their appendages alternately. Rather, "they either drag their hind quarters or repeatedly pivot their bodies up and forward with the help of their feet" (J. Vandevere, paper presented at AAAS meeting, San Francisco, California, 27 February 1974). These differences suggest possible genetic differences in both behavior and anatomy between northern and southern sea otters. In this regard it is of considerable interest that the Asian sea otter (*E. l. gracilis*) is also relatively clumsy on land (Lydekker, 1895; Barabash-Nikiforov, 1947).

The ability of Alaskan sea otters to move relatively long distances out of water has been documented by Schneider and Faro (1975). In 1971 a number of otters were trapped by rapidly forming pack ice along the north shore of the Alaska Peninsula, and a number died because they could find no open leads in which to forage. Two dead sea otters were found 8 km. inland from Port Heiden Bay and one dead otter was seen "15 km inland, half way to Pavlof Bay on the Pacific Ocean." These animals may have been trying to reach the Pacific Ocean in an attempt to find open water where foraging was possible.

Vandevere (1970) described a number of differences in reproductive behavior between northern and southern sea otters. Most striking of these were differences in the posture of the female during copulation. The sequence of events leading to copulation also differed, the nose or side of the face of the female being grasped by the northern male rather late in precopulatory struggling whereas this occurs early in this stage of copulation in southern otters.

The present distribution of the southern sea otter in relation to its nearest conspecifics is also of critical importance in assessing the distinctiveness of this population. As of early December 1974, the northernmost established Californian sea otters were located off Sunset State Beach, Santa Cruz County, about 15 airline miles south-southeast of the city of Santa Cruz. A few individuals have been seen north of this point but none has stayed long enough to suggest establishment. The nearest naturally occurring northern sea otters are in Prince William Sound, 1700 nautical miles to the north, although Pedersen and Stout (1963) reported the sighting of what was probably a single otter off Neahkahnie, northern Oregon, between August 1961 and February 1962. A small introduced population is located near Port Orford, Oregon, 365 nautical miles to the north, where a number of otters from Amchitka were released in 1970 and 1971; about 23 are still present.

At this time, the southern sea otter is well removed from its nearest conspecifics and there is no exchange of genetic material between this population and any other. Since 1914, the sea otter has extended its range north in California from Point Sur, Monterey County (Wild and Ames, 1974, p. 23, fig. 5) to Sunset State Beach, a great circle distance of only 35 nautical miles in 60 years. The isolation of the Californian population is thus likely to continue for many years if the present natural situation persists.

Although complete disruption of gene flow between Californian and other sea otters may be relatively recent, resulting from the decimation of the species by fur traders in the last two centuries, the severe reduction of the southern population may well have had profound effects on its genetic constitution. This is strongly suggested by the findings of Bonnell and Selander (1974) on the northern elephant seal (*Mirounga angustirostris*). Electrophoretic analysis of blood samples from five isolated breeding colonies in California and Mexico indicated no polymorphisms among 21 proteins encoded by 24 loci. The authors concluded that this homozygosity may have resulted from fixation of alleles brought about by the decimation of the species by sealers in the 19th century. Although comparable evidence is not available for the sea otter, it seems highly likely that the severe reduction in numbers suffered by the southern population, followed by strong geographic isolation, has had some effect on that population's genetic constitution.

Conclusions

In the application of formal scientific nomenclature to naturally occurring populations, the taxonomist frequently faces the problems inherent in trying to fit a myriad of biological situations into the rigid framework of a fixed nomenclatural system. The best that one can do is to use that nomenclature which best expresses the natural situation with which he is dealing.

In the case of the sea otter, at least two interpretations may be made of the morphological variation observed in the populations between the Commander Islands and Monterey Bay. If we regard this variation as clinal, then the nature of the cline must influence our choice of nomenclature. Three characteristics of this presumed cline are of particular importance: 1) the terminal populations are separable at a level of at least 90% on the basis of skull morphology; 2) there is either a step in the cline, or a pronounced change in slope steepness, between the Alaska Peninsula and Prince William Sound; 3) the population at the southern terminus has been much reduced and has been completely isolated for at least 100 years, with a strong possibility that its genetic constitution has undergone significant change.

Given these characteristics, whether one includes the entire cline in a single subspecies or treats the terminal populations as distinct subspecies becomes a matter of professional judgement. If we are dealing with a case of primary intergradation in which a gradual cline along western North America sharply changes slope in southern Alaska, it may still be appropriate scientifically to recognize the northern and southern sea otters as distinct subspecies. There are many instances in vertebrate taxonomy in which the terminal populations of a cline are regarded as distinct subspecies if they are distinctly separable in a variety of traits, and/or if they are separated by a pronounced step in the cline. If, in fact, variation is actually clinal in this way, it is just as proper taxonomically to regard the northern and southern sea otters as distinct subspecies as it is to combine them in *E. l. lutris*.

However, it is by no means clear that we are dealing with a case of primary intergradation. It is equally possible that there are two distinct subspecies which in recent history intergraded (secondarily) in southwestern Alaska and, indeed, this is strongly suggested by the nature of the variation described by Roest in the samples available to him. Moreover, some taxonomists have advocated that subspecies designations be applied only to portions of species which are not only genetically distinct, but which are at least partially independent (separately evolving) evolutionary units (e.g., Lidicker, 1962). The southern sea otter clearly meets even these stringent criteria by virtue of its genetic isolation, its morphological and behavioral differentiation, and its recent derivation from what must have been an extremely small remnant population. Further, there are important differences between the habitats occupied by the northern and southern sea otters. Formation of pack ice as described by Schneider and Faro (1975) never occurs within the range of the southern population. Water temperatures are much lower in the north. Daily sea-water surface temperatures at Scotch Cap in the Aleutians over a five-year period ranged from –1.39° C to 12.22° C, and at Monterey, California, over a similar period, they ranged from 10.1° C to 16.7° C

(Ricketts and Calvin, 1948, p. 263, fig. 117). Many other habitat differences undoubtedly occur as well. All of these factors imply that the two otter populations are subjected to quite different selective regimes.

Thus, whether one views the evidence as indicating that the southern sea otter population is part of a stepped cline, a remnant of two historically well marked subspecies intergrading in southwestern Alaska, or a recently differentiated and unique evolutionary unit, its formal designation as a subspecies is justified on scientific grounds. Given that such designation is scientifically sound, one may still ask what are the advantages and disadvantages to advocating this nomenclatural arrangement.

There seems to be no particular advantage to including these populations in one subspecies, but there are a number of disadvantages to doing so. This course of action would conceal the high degree of separability between the southern and northern populations; it would conceal the pronounced step or shift in slope in the indicated cline in southern Alaska; it would fail to consider certain behavioral differences, and possible related anatomical differences, between the northern and southern populations; and it would give no idea of the present geographic isolation of the southern population. To us, formal recognition of the southern population as a distinct subspecies, to which the already available name *E. l. nereis* may be applied, much more accurately reflects the existing natural situation than would any other nomenclatural arrangement. Furthermore, it is an arrangement which is consistent with recognition of the Asian subspecies *E. l. gracilis* (*cf.* Barabash-Nikiforov, 1947; Roest, 1973), a form which appears to be of comparable distinctiveness to *E. l. nereis* (differing in size, cranial features, pelage color, and behavior), but much less isolated by distance. We therefore propose that three subspecies continue to be recognized for this unique and important mammal.

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HERALDIA NOCTURNA, A NEW GENUS AND SPECIES OF PIPEFISH (FAMILY SYNGNATHIDAE) FROM EASTERN AUSTRALIA, WITH COMMENTS ON *MAROUBRA PERSERRATA* WHITLEY

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Abstract: *Heraldia nocturna* is described as a new genus and species in the fish family Syngnathidae. The type locality is Sydney Harbour in eastern Australia. The species occurs on rocky reefs and is nocturnally active. The male has a brood area on the belly that lacks pouch folds or plates; the new genus is related to the *Doryrhamphus* complex of spiny, belly-pouch pipefishes. Variation in another related Sydney area pipefish, *Maroubra perserrata*, previously known from a single specimen is described.

Introduction

In the course of a survey of the fishes of Sydney Harbour, a number of small pipefishes were collected that resembled *Doryrhamphus*, but differed in the trunk and tail ridges, brood pouch, and head ornamentation. The capture of specimens with quinaldine and hand net allowed aquarium observations on the habits of the new pipefishes.

Australia is richly endowed with pipefishes and seahorses; Munro (1958) lists 71 Australian species in the family Syngnathidae, including such distinctive forms as the endemic sea dragons *Phyllopteryx* and *Phycodurus*. Scuba collecting in both tropical and temperate waters is adding to the known fauna.

Methods

Methods for making counts and measurements follow Herald (1940). The first trunk ring is twice as long as the other rings and although actually

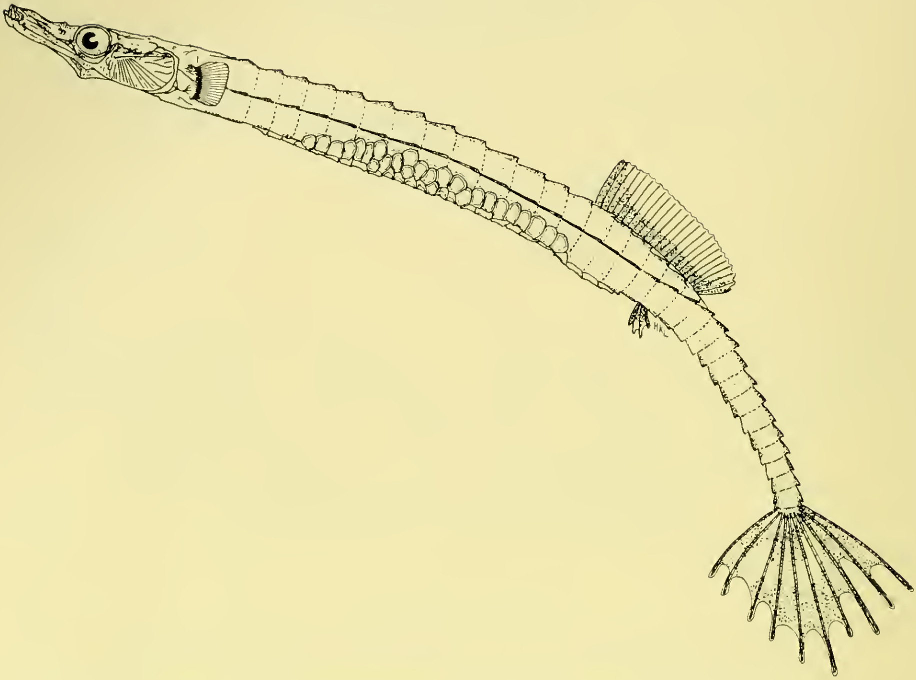

Figure 1. Holotype of *Heraldia nocturna*, AMS I.17328-001, 74.8 mm. SL.

double, is counted as a single ring (Herald and Randall, 1972). Four specimens were maintained in aquaria for varying periods up to two months. Observations on swimming behavior were made during light and dark periods. Abbreviations of measurements are as follows: SL—standard length; TL—total length; HL—head length.

Institutional abbreviations are as follows: AMS—Australian Museum, Sydney; BMNH—British Museum Natural History, London; BPBM—Bernice P. Bishop Museum, Honolulu; CAS—California Academy of Sciences, San Francisco; QM—Queensland Museum, Brisbane; WAM—Western Australian Museum, Perth.

Acknowledgments

Rudi Kuiter, diver aquarist from Sydney, collected the majority of specimens of the new genus and species. His sure hand with the dipnet and knowledgeable observations are much appreciated. Clarrie Lawler, Barry Goldman, and Paul Zorn each collected a specimen. Helen Larson drew the figures and Bronwyn Wright typed the manuscript. C. E. Dawson and R. A. Fritzsche improved the paper with their critical comments.

Heraldia Paxton, new genus

Diagnosis. Very stout, *Doryrhamphus*-like pipefish with abdominal brood area lacking lateral membranous folds or protecting plates. Lateral trunk ridge continuous with lateral tail ridge, which in turn becomes superior tail ridge; inferior trunk and tail ridges continuous and superior trunk ridge ending free on 1st, 2nd, or 3rd tail ring. Snout without spines in either sex; head intricately sculptured; body ridges pronounced—those of first 2–4 trunk rings with rounded edges but thereafter with points at posterior edge of each ring. Base of dorsal fin very dark; caudal fin large and deeply emarginate with individual rays extending beyond web. Trunk rings 16–17; tail rings 13–15; dorsal rays 23–26 located on 5½–7 rings, of which 3½–4¾ are trunk rings and 2–3 are tail rings. Pectoral rays 19–22; anal 4; caudal 10–11. Maximum length 74.8 mm SL, 84.2 mm TL.

Heraldia is related to the other pipefish genera with an abdominal brood area and small spines on the posterior ends of the body ring ridges. *Heraldia* differs from *Doryrhamphus* and *Dentirostrum* in lacking brood pouch flaps, from *Dunckerocampus* in its shorter snout and fewer tail rings, and from *Oostethus* and *Maroubra* in having the dorsal fin mostly on the trunk.

The type species of *Heraldia, H. nocturna,* is new and the only known member of the genus. The first two specimens were sent to Dr. Earl Herald, who recognized them as a new genus and provided a brief description and diagnosis before his untimely death. His help and encouragement are gratefully acknowledged. *Heraldia* is named in honor of Earl Stannard Herald, whose contributions to syngnathid systematics and help to other ichthyologists were considerable.

Heraldia nocturna Paxton, new species.

(Figures 1–2).

Material examined. All 14 type specimens were collected with scuba from rocky reefs at depths from 2–15 meters in Sydney Harbour, New South Wales, Australia (33° 50′S., 151° 15′E.), or Seal Rocks, N.S.W. about 190 kilometers northeast of Sydney (32° 25′S., 152° 35′E.).

Holotype. AMS I.17328–001, male, 74.8 mm. SL (84.2 mm. TL), Village Point, Watson's Bay, Sydney Harbour, Australia, 3 m., quinaldine, R. Kuiter, 8 September 1973.

Paratypes. AMS I.17328–002, female?, 69.5 mm. SL, collected with the holotype; AMS I.16516–001, 64.0 mm. SL, Green Point, Sydney Harbour, 15 m., rotenone, B. Goldman, 23 Sept. 1972; AMS I.17033–008, 67.6 mm. SL, off Store Beach, Sydney Harbour, 1–7 m., rotenone, G. Allen, D. Hoese, J. Paxton, D. Pollard, 6 April 1972; AMS I.17112–003, 60.6 mm. SL, Seal Rocks, 10 m., quinaldine, R. Kuiter, 29 April 1973; AMS I.17641–001, 65.5

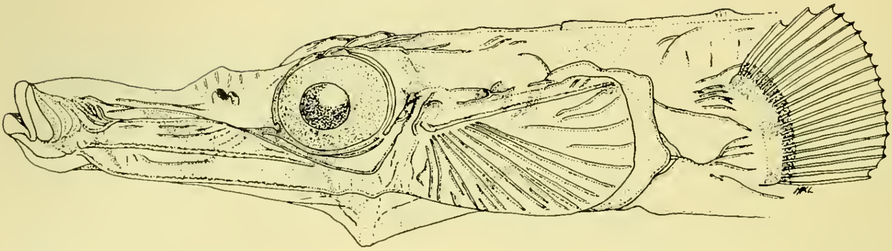

Figure. 2. Head of holotype of *Heraldia nocturna.*

mm. SL, Seal Rocks, 10 m., quinaldine, R. Kuiter, 5 May 1973; AMS I. 17642–001, 40.6 mm. SL, Green Point, Sydney Harbour, 2 m., quinaldine, R. Kuiter, 31 Dec. 1973; AMS I.18075–001, 33.4 mm. SL, Watson's Bay, Sydney Harbour, 5 m., quinaldine, P. Zorn, 3 Nov. 1974; BMNH 1975. 2.19.1, 60.9 mm. SL, Parsley Bay, Sydney Harbour, quinaldine, R. Kuiter, 26 Dec. 1973; BPBM 18034, 66.5 mm. SL, Seal Rocks, 12 m., quinaldine, R. Kuiter, 27 Oct. 1974; CAS 32366, 66.4 mm. SL, Camp Cove, Sydney Harbour, 5 m., hand net, C. Lawler, 13 April 1969; CAS 32367, male, 62.7 mm. SL, Green Point, Sydney Harbour, quinaldine, R. Kuiter, 10 Aug. 1974; QM I.12920, 47.8 mm. SL, Camp Cove, Sydney Harbour, 15 m., quinaldine, R. Kuiter, 6 Jan. 1974; WAM P.25167–001, 61.0 mm. SL, Watson's Bay, Sydney Harbour, quinaldine, R. Kuiter, 3 Aug. 1974.

Diagnosis. Counts and characteristics as given under *Heraldia* above; total rings 30–32; total rings plus dorsal fin rays 54–57; head in standard length 4.9–5.5; snout in head 2.3–2.7; dorsal fin base in head 1.4–1.6.

Description. The measurements of the holotype (74.8 mm. SL) in mm. are followed in parentheses by the range as percent SL for the 16 types. Head length 13.7 mm. (18.2–20.4%), snout length 5.8 mm. (5.9–8.7%), eye diameter 2.9 mm. (3.7–4.0%), dorsal fin base length 8.8 mm. (11.8–13.8%), pectoral fin length 2.8 mm. (3.4–4.4%), anal fin length 2.8 mm. (3.0–5.7%), caudal fin length 10.6 mm. (12.2–17.6%).

The head has a remarkable scrollwork of tiny ridges, some of which are not a part of the typical pipefish head ridge pattern; the ridges vary in number and development with individual specimens. The median snout ridge is without spines and is elevated slightly at the nostril area in front of the eyes; between the eyes it divides into two ridges, and is paralleled by at least four additional smaller ridges. The sides of the snout have a series of parallel ridges, two of which are more pronounced, those on the lateral median and on the lateral inferior surface. The supraorbital crest extends backward to the end of the eye, then divides into a series of radiating ridges. The principal opercular ridge extends diagonally completely across the upper portion of the opercle; radiating outward from it are 2–12 small ridges on the upper side and 13–18 on the lower side. The supraopercular ridge has two sections, each with smaller radiating ridges present or absent. The prenuchal, nuchal, and occipital ridges are present but only slightly elevated. The pectoral cover plate has two ridges in upper and lower positions; the upper has several smaller ridges running parallel above it and the lower ridge has conspicuous ridges branching off the axis.

The brood area of the only male carrying eggs extends from the second to the penultimate (16th) trunk ring. The eggs are embedded in a gelatinous matrix; no lateral skin folds or protective plates are present and the matrix either dissolves or is absorbed shortly after the larvae are hatched. No other external sexual dimorphism is evident.

The anal and caudal fins are quite large, the latter measuring 10.6 mm. in length on the holotype; this is equivalent to a width of more than 5 trunk rings. The caudal rays number 10 in the holotype and 11 in all paratypes. There is no indication of regenerated rays.

The predominant color of the freshly killed male holotype was yellow-brown. The head is yellow-green with reddish brown blotches present on the snout, under and behind the eyes, and on the opercle. The pectoral fins are clear with a dark brown base. All of the body ridges are dark brown, anteriorly appearing as narrow dashed lines and posteriorly as wider solid lines. The base of the dorsal fin is dark reddish brown, as are the first 2 rays; the dark pigment decreases in extent in a descending line on the sixth ray. The basal third of the middle 14 rays are light yellow-green, the outer two-thirds are clear; the posterior 2 rays are dark brown. The basal two-thirds of the anal is brown tinged with red; the distal one-third of the anal is yellow-green. The caudal is reddish brown with yellow-green basal blotches; the tips of the caudal rays are white. Three yellow blotches are present on the ventral surface of the tail rings between the anal and caudal, each blotch covering one to two rings. Three less pronounced light blotches are present on the ventral surface of the trunk rings. In preserved specimens the basic body color varies from light yellow-brown to darker brown and the ventral light areas are white.

Biology. Two males carrying eggs were collected in September and October. A few hours after the holotype was placed in an aquarium, many of the eggs hatched. After formalin preservation, the remaining developing larvae fell from the egg sockets. The gelatinous matrix forming the sockets was firm and covered slightly less than half of each of the developing eggs. Sockets were present on the ventral surface of trunk rings 2–16 and extended onto the inferior lateral surfaces of rings 4–13; 173 sockets were present. The second egg-bearing male was collected on 10 September 1974 and placed in an aquarium; by 23 September all eggs had hatched or been lost and the male was preserved on 30 September. By this time almost all remnants of the matrix had dissolved or been absorbed; only a few dark areas representing the edges of the sockets remained. No other sexually dimorphic character was evident and none of the remaining specimens were sexed. However, the holotype was collected under a rocky ledge with one other individual, possibly a female. Two of the Seal Rocks specimens were taken one week apart at the back of the same rocky hole and may represent a male and female. All other specimens were taken singly.

Newly hatched larvae measured 5–6 mm. TL and had fin folds but no fin rays present. The head was bent at an angle to the body, in this regard resembling a seahorse. The color was bright yellow-green with a few scattered melanophores. A bright silver and gold reflecting layer prominently surrounded the lens of the eye. All of the unhatched eggs appeared in much the same state of development, with the colors visible through the transparent egg case.

All of the Sydney Harbour specimens were taken in the outer harbor within 1.5 kilometers of the entrance, where the environment is similar enough to the open coast to support large brown kelp. Seal Rocks is on the open coast. The absence of this species from earlier collections is probably due to lack of scuba collecting from rocky regions in other areas. All specimens were collected in rocky areas—under rocky ledges, in crevices, holes, or small caves. Unlike many pipefishes, *H. nocturna* does not necessarily live in association with vegetation, as there was none at a number of collection sites (R. Kuiter, pers. comm.).

Four individuals were maintained in aquaria for periods of from one week to two months. During the day the pipefish remained in a small rock cave, swimming near the under surface of the overhanging rock in an upside down position. Only after some weeks in the aquarium would an individual leave the cave during periods of light and swim around the aquarium. During these brief forays, the fish righted itself and swam in a horizontal position close to the bottom, but did not come to rest. During most of this swimming, the tail was slightly bent in the region of tail rings 10–12. The large caudal was usually kept open and only rarely closed halfway like a fan, giving a propulsive burst forward. The fish swam equally well backward and forward and most of the propulsion appeared to be from the pectoral fins. At night the pipefish swam freely to all corners of the aquarium in a normal horizontal posture. When the lights were turned on the fish swam to the cave and resumed the diurnal upside down swimming. After five minutes of darkness, swimming about the bottom of the tank was resumed. Aquarium behavior indicates *Heraldia nocturna* is nocturnally active, residing in protected rocky areas during the day. *Doryrhamphus melanopleura* from the Gulf of California exhibits the same type of upside down swimming behavior (R. Fritzsche, pers. comm.).

NAME. The specific name of *Heraldia nocturna* is in reference to the nocturnal activity of the species. The diurnal swimming posture suggests the common name 'Upside down pipefish.'

RELATIONSHIPS. The genera *Heraldia*, *Doryrhamphus*, *Dunckerocampus*, *Dentirostrum*, *Oostethus*, and *Maroubra* appear to constitute a related group of pipefishes. All have abdominal brood areas, body ridges with spines, and the first body ring much longer than those remaining. The possible relationships of *Maroubra* are discussed in the next section. *Heraldia*, with a stout body and trunk rings more numerous than tail rings, appears most closely related to *Doryrhamphus*. The relationship between *Doryrhamphus* with brood pouch folds and *Heraldia* without folds is similar to that of another pair of related belly-pouch genera, *Dentirostrum* which has folds, and *Dunckerocampus* which lacks them.

Heraldia nocturna has several characteristics that are rarely or never found in other pipefishes. For example, the basal color pattern in the dorsal fin is unique among syngnathids. The anal fin is relatively larger than that of other species. Highly emarginate caudal fin rays are known in few pipefishes, *Dorichthys retzi* of the tropical Indo-Pacific and juveniles of *Oostethus* being examples. The magnificently sculptured head of *Heraldia* is without equal in the pipefish world.

Maroubra perserrata Whitley, 1948.

Whitley (1948) described *Maroubra perserrata* as a new genus and species of pipefish from a single specimen collected from Maroubra Beach near Sydney by McCulloch in 1912. Eight specimens of this species were taken in August and November, 1974 from outer Sydney Harbour at depths from 3 to 20 m. in rocky areas. As the species previously was known only from the holotype, it is redescribed below; counts and measurements of the holotype (AMS I.12659) are followed in parentheses by ranges of the 8 new specimens, 4 males and 4 females, 46.1–72.9 mm. SL.

Slender pipefish with abdominal brood area lacking lateral membranous folds or protective plates; small cutaneous fold extending from midventral ridge of trunk rings in males only. Lateral trunk ridge continuous with lateral tail ridge, which in turn becomes superior tail ridge; inferior trunk and tail ridges continuous and superior trunk ridge ending free on 4th or 5th tail ring. Snout ridge without spines; small spine at anterior border of orbit. Body ridges pronounced, with points at posterior edge of each ring. Small caudal fin slightly emarginate, darkly pigmented on ventral half; other fins clear. Trunk rings 17(16); tail rings 26(24–27); dorsal rays 24(21–25), located on 5¼(5–5½) total rings, of which ¼(0–¾) are trunk rings and 5(4¼–5½) are tail rings. Pectoral rays 18(15–18); anal 4(4); caudal 10(9–10).

Total rings 43(40–43); total rings plus dorsal fin rays 67(61–68); head in standard length 6.9(6.7–7.6); snout in head 2.0(1.9–2.1); dorsal fin base in head 1.6(1.4–1.7). The median snout ridge is elevated in front of the eyes; posteriorly it divides into two short, low ridges. Secondary head ridges are present, but not as well developed as those in *Heraldia.* The main opercular ridge extends completely across the opercle and curves dorsally posteriad. Smaller ridges radiate ventrally from the main ridge, but none are present dorsally.

In four males a small cutaneous fold is present on the midventral ridge of all trunk rings. Egg-carrying males were collected in August and November, but no eggs remained after preservation. No gelatinous matrix was present in either specimen and the way in which the low midventral skin fold protects the eggs is not clear; no lateral folds or protective plates are present. The well developed midventral ridge must separate the eggs into two groups.

In preserved specimens the reddish brown color markings of the males are slightly more pronounced than those of the females, particularly on the head. A dark stripe is present on the side of the snout from the tip to the eye and stripes and bands are present on the anterior trunk rings dorsally and laterally, while the remaining rings are evenly pigmented. One male that had been carrying eggs is much more darkly pigmented laterally with white spots in the dark pigment.

The genus *Maroubra* appears to be related to the doryrhamphine pipefishes, with an abdominal brood area, well defined body rings with posterior points, and an elongate first trunk ring. The peculiar brood area with a midventral fold is a distinguishing feature, while the small caudal fin and posteriorly placed dorsal are not found in most of the related genera. The slender shape and large number of tail rings distinguish *Maroubra* from *Doryrhamphus* and *Heraldia.*

While comparing *Heraldia* and *Maroubra* with other pipefishes in the AMS collections, the holotypes of *Choeroichthys suillus* Whitley (1951) from Port Denison, Queensland, and *Choeroichthys suillus malus* Whitley (1954) from Masthead Island, Queensland were examined. The latter has all the characteristics of *Doryrhamphus,* and the presence of two dark stripes behind each eye indicates that *C. s. malus* is a synonym of *D. negrosensis* Herre. The holotype of *C. suillus* is a male with protective plates extending ventrally from the trunk rings; this feature, plus the lack of a lateral tail ridge, is diagnostic for the genus *Choeroichthys.*

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INDEX TO VOLUME XL

FOURTH SERIES

(Compiled by Lillian J. Dempster)

New names and principal references in **boldface** type. References to figures in *italics*.

ERRATA

Page 30.	Line 21 from top: for **Cercidium X sonorae** Rose and Johnston read **Cercidium X sonorae** Rose and Johnston (pro sp.).
Page 69.	Line 20 from bottom: for *wakijai* read *wakiyai.*
Page 98.	Line 6 from top: for *L. h. teniculus* read *L. h. tenuiculus.*
Page 265.	Line 3 of Abstract: for *Phenacoscorpius nebris* read *Phenacoscorpius megalops.*
Page 294.	Line 1 of figure caption: for *Phenacoscorpius nebris* read *Phenacoscorpius megalops.*