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Frank A. Taylor
Director, United States National Museum

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CLASSIFICATION OF THE WESTERN HEMISPHERE BALCLUTHA

(HOMOPTERA: CICADELLIDAE)[1]

By H. DERRICK BLOCKER [2]

The genus *Balclutha* is cosmopolitan in distribution. This paper treats 36 taxa found in the Western Hemisphere including 2 which are given new status, 4 in new combinations, and 15 new to science. Although specimens of *Balclutha* are commonly collected in numbers in grassy areas, some taxa are based on single specimens or very short series. The genus is placed in the subfamily Deltocephalinae. It is considered a member of the tribe Balcluthini by Oman (1949) but is placed in Macrostelini by Linnavuori (1959); the former tribal designation is followed here. There have been few taxonomic works restricted to this tribe and these have included only a portion of the Western Hemisphere. This geographical restriction and the wide distribution of certain taxa have resulted in some confusion as to the identity of a number of species and subspecies. Ecological and biological data published on Balcluthini are infrequent. The host plants are usually considered to be grasses and sedges.

In this study, the internal male genitalia were dissected using techniques described by Oman (1949) and Young (1952). Illustrations

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[1] Contribution from the Entomology Department, North Carolina Agricultural Experiment Station, Raleigh, N.C. Published with the approval of the Director of Research as Paper No. 2171 of the Journal Series.

[2] Department of Entomology, Kansas State University, Manhattan, Kans.

were drawn, using a camera lucida. The aedeagus, style, and connective were drawn at 150X; the male plate, valve, and pygofer, as well as the posterior margin of the female abdominal sternum VII, at 100X. A 0.1 mm scale for both magnifications is found in figure 1; all illustrations were drawn to this scale. The writer has used the terminology of Kramer (1950) for external structures, and of Young (1952) for internal. Descriptions and illustrations were made from long series of specimens unless stated otherwise. Geographical or seasonal variations were not found. Individual variations are illustrated. New scientific names, other than patronyms, should be considered arbitrary combinations of letters. A selective bibliography is included. Metcalf (in press) has compiled a complete list of references through 1955.

The Balcluthini can be separated from the closely related tribe Macrostelini by the appearance of the basal hind tarsomere which is distinctly sulcate basally in the Balcluthini. Both tribes can be separated from the remainder of the Deltocephalinae by the presence of only two anteapical cells in the forewing; there are almost always three anteapicals in the forewing of the remainder of the Deltocephalinae. The dorsal width of the head, including the eyes, compared to the width of the pronotum has been used to separate the Balcluthini into two genera by some workers. The author found no other characters correlated with head width and agrees with those workers who feel that this character is not stable enough for generic distinction.

The median length of the vertex compared to its length next to the eyes and the distance of each ocellus from its adjacent eye are useful, although they vary somewhat within species. Other characters include the width of the anteclypeus and its relationship to the genae. Color of the head and of the species in general is quite variable, and its diagnostic value is generally secondary. The oblique brown lines present on each side of the midline of the face in many species, referred to as muscle maculae in an unrelated species of Cicadellidae by Kramer (1950), are of some value and are noted, when present, in the species descriptions. Few characters of the thorax and abdomen are used except those of the genital capsule and genitalia. Hind femoral chaetotaxy used so effectively by Ribaut (1952) as a generic character varies from 2–2–1 to 2–1–1 within *Balclutha*. The pronotal length in relation to the median length of the vertex is sometimes useful.

The most important structure used in differentiating species is the aedeagus. The shape of the male pygofer and plates as well as the connective and styles is used to supplement the characters found on the aedeagus. The shape of the apex of the connective is particularly useful in separating groups of species.

Females are usually quite similar to the males but are usually slightly larger. The only female character used in this study is the shape of the posterior margin of the abdominal sternum VII. This structure separates several taxa within the Balcluthini, but there is much variation; hence, its use is supplementary.

The author is indebted to Professor David A. Young of North Carolina State University at Raleigh, who suggested this study and made several suggestions. Dr. Paul H. Freytag and Dr. James P. Kramer provided study facilities at Ohio State University and the U.S. National Museum, respectively, during visits to these institutions and made useful suggestions. Dr. S. L. Tuxen of Copenhagen, Denmark, has been most cooperative in answering questions concerning Fabrician type material.

Individuals and institutions who lent specimens were: Dr. Dwight M. DeLong of Ohio State University, specimens from his personal collection; Dr. Jîrí Dlabola, the National Museum of Natural History, Prague, Czechoslovakia; Dr. Paul H. Freytag and Dr. C. A. Triplehorn, Ohio State University; Dr. T. Ishihara of Japan, personal collection; Dr. James P. Kramer, U.S. National Museum; Dr. Jean L. Laffoon, Iowa State University; R. Linnavuori of Finland, personal collection; Dr. George W. Byers, Snow Entomological Museum, University of Kansas; Dr. W. R. Richards, Canadian National Collection; Dr. Edward S. Ross, California Academy of Science; Dr. Jerome G. Rozen, American Museum of Natural History; Dr. A. Soós, Hungarian Natural History Museum, Budapest, Hungary; Miss Amy Suehiro, Bernice P. Bishop Museum; Dr. H. Weidner, Zoological Museum, Hamburg, West Germany; Dr. C. J. Davis, Hawaiian Department of Agriculture; Dr. G. G. E. Scudder, University of British Columbia; Dr. Jerry A. Powell, University of California at Berkeley.

Tribe Balcluthini Baker

Tribal nomenclature.—Baker (1915) proposed the name Balcluthini as a replacement name for Gnathodini, the generic name *Balclutha* Kirkaldy having earlier replaced *Gnathodus* Fieber, which was preoccupied.

Description.—Slender leafhoppers; variable in size; head from slightly wider than to distinctly narrower than pronotum; vertex from as long next to eye as medially, to distinctly longer medially; interocular width approximately three times median length; ocelli usually small, variable in their distance from adjacent eye; anteclypeus parallel margined or slightly wider apically; postclypeal sutures extending well past antennal pits to ocellocular area; transclypeal suture arched so that basal margin of anteclypeus is convex; gena slightly notched next to eye, joining anteclypeus as a very narrow band.

Thorax with pronotum slightly widest posteriorly, approximately three times as long as vertex; macropterous; forewings with four apical and two anteapical cells of which outermost is closed and innermost is open basally, appendix well developed; hindwings with inner fork of radius and outer fork of media confluent distally, only three apical cells; hind femoral chaetotaxy 2–1-1 or 2–2–1; basal hind tarsomere distinctly sulcate basally.

Male pygofer deeply incised on ventral border, setae pubescent, microsetae present in irregular patterns, with heavily sclerotized process present in several species; plates usually triangular, setae uniseriate along exterior margin; style with apical extension usually digitiform; connective Y-shaped; aedeagus usually simple but with processes arising on base or shaft in several species.

Color variable, from stramineous to brown to green; face with or without oblique brown lines on each side of midline; thoracic venter commonly darker than general body color; forewings hyaline to subhyaline with dark brown to reddish spots or stripes present in some species.

Genus *Balclutha* Kirkaldy

Gnathodus Fieber, 1866 (not Pander, 1856, [Polychaeta]), Verhandl. Zool.-Bot. Ges. Wien., vol. 16, p. 505. [Type by monotypy, *Cicada punctata* F. 1775.]

Balclutha Kirkaldy, 1900, Entomologist, vol. 33, p. 243. [New name for *Gnathodus* Fieber.]

Eugnathodus Baker, 1903, Invert. Pacifica, vol. 1, p. 1. [Type by original designation, *Gnathodus abdominalis* Van Duzee, 1892.]

Nesosteles Kirkaldy, 1906, Bull. Hawaiian Sugar Planters' Assoc. Expt. Sta. Div. Ent., vol. 1, p. 343. [Type by original designation, *Nesosteles hebe* Kirkaldy, 1906.]

Anomiana Distant, 1918, Fauna British India, vol. 7, p. 109. [Type by original designation, *Anomiana longula* Distant, 1918.]

Agellus DeLong and Davidson, 1933, Ohio Journ. Sci., vol. 33, p. 210. [Type by original designation, *Eugnathodus neglecta* DeLong and Davidson 1933.]

Key to Males of the Western Hemisphere[3]

1. Head as wide as or wider than pronotum, if narrower, then pygofer with a heavily sclerotized process which is bifid apically 2
Head narrower than pronotum 18
2(1). Connective bifid apically, or at least with apical margin concave . . . 3
Connective truncate apically 11
3(2). Pygofer with distinct heavily sclerotized process present on posteroventral margin 4
Pygofer without a process 6
4(3). Pygofer process distinctly bifid apically, arising on inner surface; aedeagus with dorsal apodeme simple, shaft unevenly curved (fig. 19). **rufofasciata** (Merino)

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[3] *B. rosacea* (Osborn) is omitted because it is known only from the female.

Pygofer process not bifid apically, arising on posteroventral margin; aedeagus not as above 5

5(4). Pygofer process directed ventrally, not dentate; aedeagus with dorsal apodeme expanded into two lateral lobes (fig. 20). **guajanae** (DeLong)

Pygofer process directed posteromesally, dentate or not; aedeagus with three pairs of processes arising on dorsal apodeme (fig. 21). **hebe** (Kirkaldy)

6(3). Aedeagus in posteroventral view with shaft broad and deeply bifid apically; forewing with third apical cell dark (fig. 27). **lineata** (Osborn)

Aedeagus in posteroventral view with shaft not broad nor bifid apically; forewings with apical cells not dark 7

7(6). Aedeagus with shaft narrowed apically and strongly recurved (fig. 32). **knulli** (Davidson and DeLong)

Aedeagus with shaft not recurved apically 8

8(7). Aedeagus with dorsal apodeme approximately one-third as long as shaft 9

Aedeagus with dorsal apodeme much less than one-third as long as shaft 10

9(8). Aedeagus with shaft evenly curved; style with preapical lobe broadly produced (fig. 29) . . . . **flavescens** (Baker)

Aedeagus with shaft unevenly curved; style with preapical lobe as in figure 30 . . . . **robusta** (Caldwell)

10(8). Aedeagus with shaft long, slender, curving anteriorly (fig. 22). **floridana** (DeLong and Davidson)

Aedeagus with shaft short, expanded basally, curving dorsally (fig. 33). **sandersi** (Davidson and DeLong)

11(2). Aedeagal shaft apex with overlapping lobes (fig. 28). **chiasma,** new species

Aedeagal shaft without such lobes. 12

12(11). Aedeagus with pair of processes arising basally and dentate on posterior margin (fig. 26) . . . . **denticula,** new species

Aedeagus without processes 13

13(12). Aedeagus with preatrium conspicuous 14

Aedeagus with preatrium very short or absent 15

14(13). Aedeagal shaft with apical one-half curved dorsally, preatrium conspicuously curved ventrally then anteriorly (fig. 24). **aridula** Linnavuori

Aedeagal shaft with apical two-thirds curved dorsally, preatrium not or inconspicuously curved ventrally (fig. 23). **neglecta** (DeLong and Davidson)

15(13). Aedeagus strongly curved anteriorly; connective with apex rectangular; style with preapical lobe subacutangular (fig. 31) . **curvata** Caldwell

Aedeagus curved dorsally or anterodorsally; connective with apex expanded and truncate; style with preapical lobe rounded . . . 16

16(15). Aedeagus with shaft as wide apically as dorsal apodeme, unevenly curved ventrally then dorsally (fig. 25) . . . . **cochrani,** new species

Aedeagus with shaft much narrower apically than dorsal apodeme, or if not then shaft evenly curved dorsally or anterodorsally 17

17(16). Aedeagus with shaft regularly curved dorsally or slightly anterodorsally, forming less than a semicircle (fig. 34) . . . . **incisa** (Matsumura)
Aedeagus with shaft curved conspicuously anterodorsally, semicircular; (fig. 35) . . . . **diluta,** new species
18(1). Connective truncate apically 19
Connective bifid apically, or at least with apical margin concave . 27
19(18). Aedeagus with a pair of conspicuous long slender processes arising from dorsal apodeme; plates short and blunt (fig. 16) **youngi,** new species
Aedeagus not as above, processes, if present, arising from shaft; plates elongate 20
20(19). Aedeagus with preatrium conspicuous; shaft not bifid apically (fig. 15) . . . . **obunca,** new species
Aedeagus with preatrium absent or inconspicuous; shaft bifid apically 21
21(20). Aedeagus with pair of processes arising from ventral margin of shaft and extending nearly to apex (fig. 9) . . . . **krameri,** new species
Aedeagus not as above, processes, if present, greatly reduced and occurring as expansions on lateral margins of shaft 22
22(21). Aedeagus with shaft approximately four times as long as height of dorsal apodeme; plates extending as far posteriorly as pygofer apex; distance from eye to ocellus less than diameter of latter (fig. 18).
caldwelli, new species
Aedeagus with shaft approximately twice as long as height of dorsal apodeme; plates not extending as far posteriorly as pygofer apex; distance from eye to ocellus equal to or greater than diameter of latter 23
23(22). Aedeagus deeply bifid apically, gonoduct in posteroventral view widest apically. 24
Aedeagus not deeply bifid apically, or if so then gonoduct parallel margined. . . . . **abdominalis** (Van Duzee) . . 25
24(23). Aedeagus not expanded apically, shaft in posteroventral view sagittate apically (fig. 14) . . . . **distincta** Linnavuori
Aedeagus conspicuously expanded apically, shaft not shaped as above (fig. 13) . . . . **diversa,** new species
25(23). Aedeagus in posteroventral view with a pair of distinct small triangular processes on lateral margins at midlength of shaft, length 3.9 mm or greater . . . . **abdominalis** (Van Duzee) . . 26
Aedeagus without such processes, or if present then rounded and inconspicuous; length 3.5 mm or less (fig. 10).
abdominalis abdominalis (Van Duzee)
26(25). Aedeagus with shaft expanded apically, deeply bifid in posteroventral view; from Panama (fig. 12) . . . . **a. amplissima,** new subspecies
Aedeagus with shaft not expanded apically, only slightly bifid in posteroventral view; from Brazil and Argentina (fig. 11).
a. fuscipennis Linnavuori, new status
27(18). Aedeagus with pair of processes arising from lateroventral margin of shaft near base (fig. 17) . . . . **fuscina,** new species
Aedeagus without such processes. 28
28(27). Aedeagus with shaft short, curved dorsally; connective shallowly emarginate apically; from South America or Puerto Rico 29
Aedeagus with shaft long, curved anteriorly or distinctly anterodorsally; connective bifid apically; from North America or Mexico 30

29(28). Aedeagus irregularly curved dorsally, shaft conspicuously narrowed only at apex; connective with stem irregular anteapically, not strongly expanded apically; from Puerto Rico (fig. 7) . . **apicula,** new species

Aedeagus evenly curved dorsally, shaft gradually narrowed; connective with stem regular and expanded apically; from South America (fig. 8). **incompta,** new species

30(28). Aedeagus with shaft elongate, in profile always exceeding dorsal prolongation of an imaginary vertical line drawn across atrium; vertex usually slightly to conspicuously longer medially than next to eye. 31

Aedeagus with shaft not as elongate, not exceeding such a line, or only slightly so; vertex usually as long next to eye as medially (exceptions not uncommon) 33

31(30). Aedeagus with base nearly parallel margined; shaft narrowed abruptly, slender apically (fig. 6) . . . . **arctica** Beirne

Aedeagus with base distinctly wider anteriorly, shaft gradually narrowed, slender apically (fig. 4) . . . . **impicta** (Van Duzee) . . 32

32(31). Aedeagus with base greatly narrowed before shaft curves dorsally. **i. impicta** (Van Duzee)

Aedeagus with base gradually narrowed before shaft curves dorsally (fig. 5) . . . . **i. arizona** Delong and Davidson, new status

33(30). Aedeagus with base very wide, shaft narrowed abruptly, appears to arise from posterodorsal margin of base; connective usually shallowly bifid at apex (fig. 3) . . . . **mexicana,** new species

Aedeagus with base gradually narrowed, connective usually deeply bifid at apex . . . . **punctata** (F.) . . 34

34(33). Aedeagus with shaft curved anterodorsally, base about four times as wide as apex of shaft (fig. 1) . . . . **p. punctata** (F.)

Aedeagus with shaft curved conspicuously anteriorly, base more than six times as wide as apex of shaft (fig. 2) . . **p. patula,** new subspecies

Balclutha punctata punctata (Fabricius)

Figure 1

Cicada punctata Fabricius, 1775, Systema entomologiae, vol. 7, p. 687.

Cicada punctata Thunberg, 1784, Nova Acta Reg. Soc. Sci. Upsaliensis, vol. 4, p. 21. [Primary homonym.]

Typhlocyba rosea Provancher, 1872, Nat. Canadien, vol. 4, p. 378.

Typhlocyba jocosa Provancher, 1890, Petite faune entomologique du Canada, vol. 3, p. 300.

Gnathodus confusus Gillette and Baker, 1895, Bull. Colorado Agric. Expt. Sta., vol. 31, p. 104.

Gnathodus manitou Gillette and Baker, 1895, Bull. Colorado Agric. Expt. Sta., vol. 31, p. 105.

Gnathodus medius Baker, 1896, Canadian Ent., vol. 28, p. 38. [New synonymy.]

Gnathodus occidentalis Baker, 1896, Canadian Ent., vol. 28, p. 41.

Gnathodus livingstoni Baker, 1896, Canadian Ent., vol. 28, p. 42.

Balclutha california Davidson and DeLong, 1935, Proc. Ent. Soc. Washington, vol. 37, p. 102.

Length of male 3.6 to 4.4 mm, of female 3.7 to 4.4 mm; head width of male .775 to .900 mm, of female .850 to .950 mm; pronotal width of male .850 to 1.025 mm, of female .900 to 1.050 mm.

Head distinctly narrower than pronotum; vertex usually no longer medially than next to eye, but distinctly longer medially in some specimens, interocular width more than 3 times median length; ocellus located at a distance of from 1½ to 2 times its diameter from eye; anteclypeus widest apically, exceeding gena; postclypeal sutures parallel above antennal pits; pronotum more than three times as long as vertex; hind femoral chaetotaxy 2–1–1; female with posterior margin of abdominal sternum VII truncate, occasionally slightly sinuate.

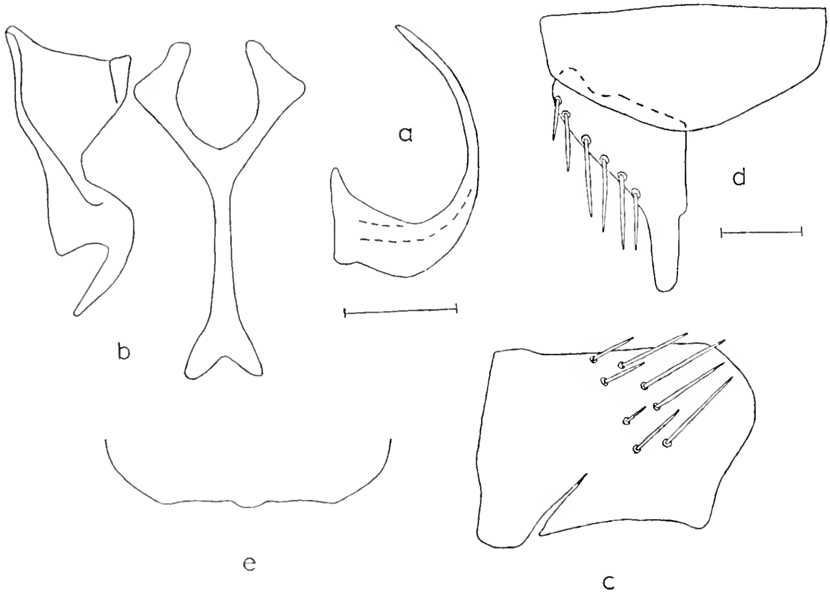

FIGURE 1.—*B. p. punctata: a*, aedeagus, lateral view, 0.1 mm scale; *b*, style and connective, dorsal view; *c*, male pygofer, lateral view; *d*, valve and plate, ventral view, 0.1 mm scale; *e*, female abdominal sternum VII, ventral view.

Male pygofer with less than 15 setae, posteroventral margin with a small rounded projection; plates broadly triangular, extending posteriorly as far as pygofer apex; connective expanded apically and bifid, longer than style, stem longer than arms, angle between arms rounded; style with preapical lobe rounded, apical extension rounded apically; aedeagus broad at base, parallel margined for approximately basal one-third then narrowed, shaft slender.

Color from pale green to dull brown; face commonly with oblique brown lines on each side of midline; vertex and pronotum commonly with orange markings, pronotum commonly with dark longitudinal bands; forewings hyaline to subhyaline commonly with an irregular number of brown spots; abdominal dorsum dark.

Fabricius' type material, according to Dr. S. L. Tuxen (in litt., Universitets Zoologiske, Krystalgade, Copenhagen, Denmark) has been lost. A neotype male from Alt. Reddewitz at Rugen leg., VIII-1930 (Korschefsky), is hereby designated and deposited in the Zoological Museum of Copenhagen. *Cicada punctata* Thunberg is here regarded not only as a primary homonym, but also as a junior synonym, but his type material has not been located. A paratype male of *B. california* from the DeLong collection has been examined. Holotype female of *G. medius* Baker and two cotypes (female) of *G. livingstoni* Baker from the U.S. National Museum have been examined. Cotypes (one male and one female) of *G. occidentalis* Baker from the U.S. National Museum have also been examined; the male specimen is hereby designated lectotype. Type material of *T. rosea* Provancher, *T. jocosa* Provancher, *G. confusus* Gillette and Baker, and *G. manitou* Gillette and Baker has not been examined. These species have been listed as synonyms of *B. punctata* by Beirne (1950), and he is followed here. Additional specimens examined were from Alaska, Arizona, California, Colorado, Florida (one specimen), Idaho, Maine, Michigan, Montana, New Hampshire, New Mexico, New York, Oregon, Utah, Vermont, Washington, Wisconsin, Wyoming, Ontario, British Columbia, and Quebec.

B. punctata (F.) is holarctic in distribution and is commonly found throughout its range. It is closely related to *B. impicta* (Van Duzee), but can be distinguished by the shape of the aedeagal shaft which is much shorter than *impicta* (see key).

***Balclutha punctata patula*, new subspecies**

FIGURE 2

Length of male 4.0 to 4.7 mm, of female 4.0 to 4.3 mm; head width of male .850 to .950 mm, of female .925 to .950 mm; pronotal width of male .950 to 1.025 mm, of female .975 to 1.050 mm.

As *B. p. punctata* but aedeagus with basal one-third broad, shaft slender.

Holotype male and paratype males from Moscow Mountain, Idaho, June 4, 1936 (C. B. Philip), deposited in the collection at The University of Kansas. Additional specimens examined from Arizona (July), Idaho (June), Minnesota (Aug.), Maine (Aug.), New Hampshire (July), New Mexico, New York (Aug.), Washington (July), West Virginia (June), British Columbia (Aug.), and Manitoba (Aug.).

B. punctata patula, new subspecies, can be distinguished from *B. punctata* (Fabricius) only by the broader base of the aedeagus. This structure is also similar to *B. arctica* Beirne but can be distinguished by the shorter length of the shaft of the aedeagus in *p. patula.*

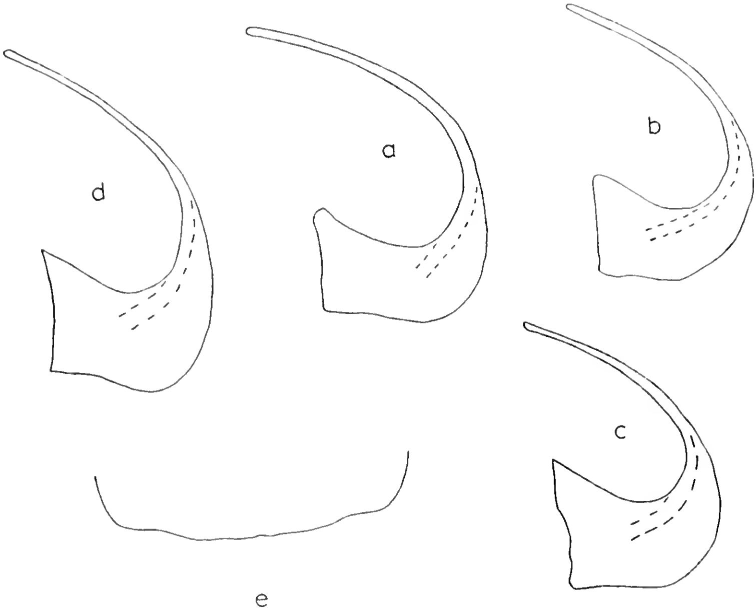

FIGURE 2.—*B. punctata patula: a–d,* aedeagus, lateral view; *e,* female abdominal sternum VII, ventral view.

Balclutha mexicana, new species

FIGURE 3

Length of male 3.5 to 3.7 mm, of female 3.8 to 3.9 mm; head width of male .825 to .875 mm, of female .850 to .875 mm; pronotal width of male .875 to .925 mm, of female .925 to .975 mm.

Head narrower than pronotum; vertex as long next to eye as medially or occasionally slightly longer in some specimens, interocular width more than three times median length; ocellus located at a distance approximately twice its diameter from eye; anteclypeus widest apically, slightly exceeding gena; postclypeal sutures parallel above antennal pits; pronotum more than three times as long as vertex; hind femoral chaetotaxy 2–2–1; female with posterior margin of abdominal sternum VII sinuate posteriorly.

Male pygofer with less than 15 setae; plates broadly triangular, extending posteriorly as far as pygofer apex; connective expanded apically, only slightly bifid, longer than style, stem longer than arms, angle between arms rounded; style with preapical lobe rounded, apical extension acute apically; aedeagus very broad basally, shaft slender, curved dorsally then anteriorly.

Color greenish brown; face without oblique brown lines; thoracic venter dark; forewings hyaline, tinted greenish brown; abdominal dorsum dark.

Holotype and paratype males from Saltillo Coah. [Mexico], Sept. 23, 1941 (DeLong, Good, Caldwell, and Plummer), deposited in the DeLong collection. A female specimen, same label data, and three specimens from Distrito Federal, Mexico, have also been examined.

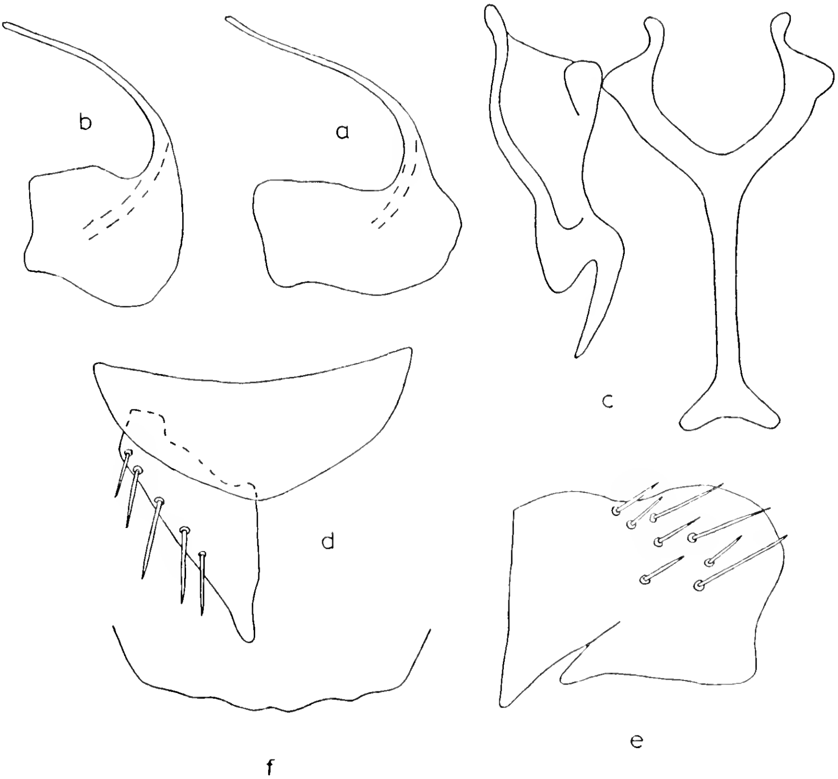

Figure 3.—*B. mexicana: a, b,* aedeagus, lateral view; *c,* style and connective, dorsal view; *d,* valve and plate, ventral view; *e,* male pygofer, lateral view; *f,* female abdominal sternum VII, ventral view.

B. mexicana, new species, is closely related to *B. punctata* (Fabricius) but can be readily distinguished by the shape of the aedeagus which is much broader basally in *mexicana*.

Balclutha impicta impicta (Van Duzee)

FIGURE 4

Gnathodus impictus Van Duzee, 1892, Canadian Ent., vol. 24, p. 113.
Gnathodus impictus var. *flavus* Baker, 1896, Canadian Ent., vol. 28, p. 38.
Gnathodus viridis Osborn, 1905, Bull. New York State Mus., vol. 97, p. 541.
Balclutha impicta var. *maculata* Davidson and DeLong, 1935, Proc. Ent. Soc. Washington, vol. 37, p. 101.
Balclutha osborni Van Duzee, 1916, Check list of Hemiptera, p. 75.

Length of male 3.5 to 4.2 mm, of female 3.6 to 4.0 mm; head width of male .750 to .875 mm, of female .750 to .850 mm; pronotal width of male .825 to 1.000 mm, of female .825 to .950 mm.

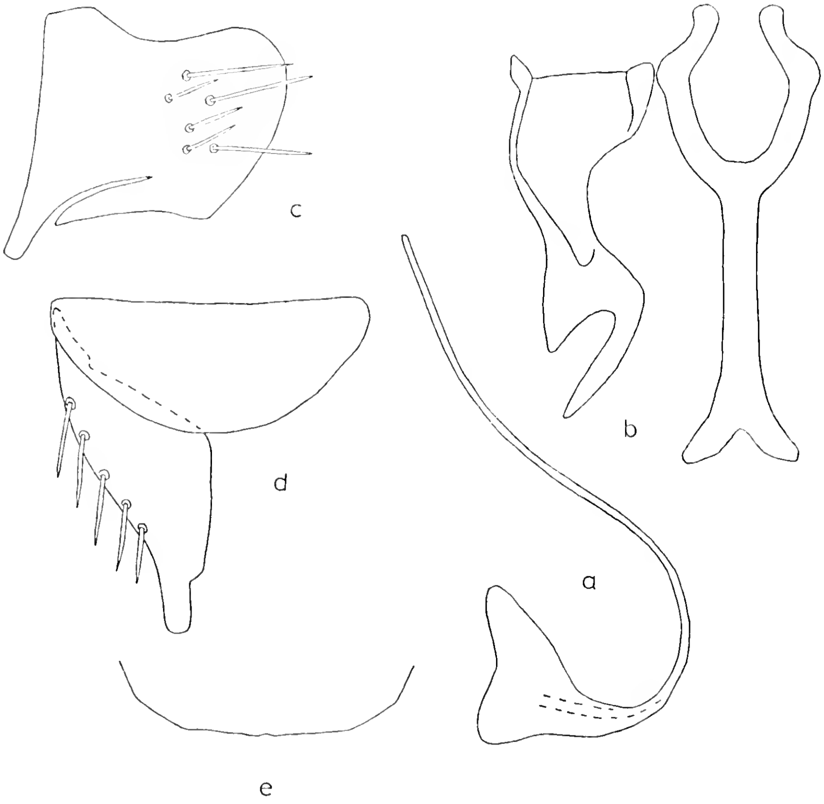

FIGURE 4.—*B. i. impicta: a*, aedeagus, lateral view; *b*, style and connective, dorsal view; *c*, male pygofer, lateral view; *d*, valve and plate, ventral view; *e*, female abdominal sternum VII, ventral view.

Head distinctly narrower than pronotum; vertex usually slightly longer medially than next to eye, interocular width more than 3 times median length, ocellus located at a distance of from 1½ times its diameter or farther from eye; anteclypeus widest apically, exceeding gena; postclypeal sutures parallel above antennal pits; pronotum 3 times as long as vertex, hind femoral chaetotaxy 2–2–1; female with posterior margin of abdominal sternum VII truncate, occasionally slightly sinuate apically.

Male pygofer with less than 15 setae; plates broadly triangular; connective widest apically and deeply bifid, longer than style, stem longer than arms, angle between arms rounded; style with preapical lobe acute, apical extension long, acute apically; aedeagus broad basally, shaft very narrow, long, curved dorsally then anteriorly.

Color from stramineous to green or brown; face commonly with faint oblique brown lines on each side of midline; vertex, pronotum, and scutellum commonly with brown and orange markings; thoracic venter commonly dark; forewings hyaline to subhyaline, commonly tinted as body color, less commonly with irregular number of dark brown spots; abdominal dorsum dark.

The male lectotype (selected by P. W. Oman) from New Jersey, located at Iowa State University, has been examined. Cotype females of *G. impictus* var. *flavus* Baker from the U.S. National Museum and paratype males of *B. impicta* var. *maculata* Davidson and DeLong from the DeLong collection have been examined. The female holotype of *B. osborni* Van Duzee from the collection of Ohio State University has also been examined. Additional specimens examined were from Arkansas, Connecticut, Delaware, District of Columbia, Georgia, Indiana, Iowa, Kansas, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Nebraska, New Hampshire, New Jersey, New York, North Carolina, Ohio, Pennsylvania, South Carolina, Tennessee, Vermont, Virginia, Wisconsin, Ontario, and the Virgin Islands (one specimen).

B. i. impicta (Van Duzee) is closely related to *B. punctata* (F.) and *B. arctica* Beirne. It is quite variable in color and is generally common throughout its range. It can be distinguished from other species by the shape of the aedeagus (see key).

Balclutha impicta arizona **Davidson and DeLong, new status**

FIGURE 5

Balclutha arizona Davidson and DeLong, 1935, Proc. Ent. Soc. Washington, vol. 37, p. 100.

Length of male 4.1 to 4.6 mm, of female 4.1 to 5.1 mm; head width of male .900 to .975 mm, of female .925 to 1.025 mm; pronotal width of male .950 to 1.050 mm, of female .950 to 1.125 mm.

Characters as in *B. i. impicta* with some variations; anteclypeus parallel margined or slightly wider apically; pronotum three times as long as vertex or slightly less; female with posterior margin of abdominal sternum VII truncate or occasionally slightly produced apically; aedeagus broad basally, shaft with only basal three-fourths narrowed.

Paratype male from Arizona located in the Delong collection has been examined. Additional specimens were from Arizona (June to Sept.), Colorado, New Mexico (June and July), and Mexico (Sept.).

B. impicta arizona Davidson and DeLong is herein considered a western subspecies of *B. impicta* (Van Duzee) since the only definite morphological difference is found in the base of the aedeagus which is not narrowed as abruptly as in *impicta*. The subspecies is also generally larger in size.

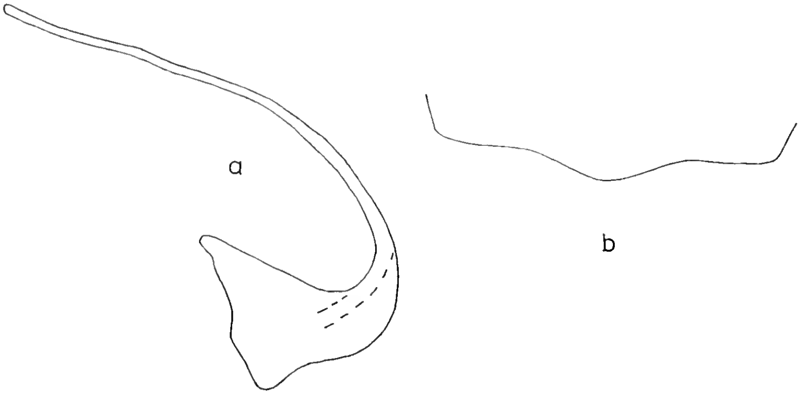

FIGURE 5.—*B. impicta arizona: a*, aedeagus, lateral view; *b*, female abdominal sternum VII, ventral view.

***Balclutha arctica* Beirne**

FIGURE 6

Balclutha arctica Beirne, 1950, Canadian Ent., vol. 82, p. 124.

Length of male 4.0 to 4.6 mm, of female 4.5 to 5.0 mm; head width of male .900 to 1.000 mm, of female .950 to 1.000 mm; pronotal width of male .975 to 1.100 mm, of female .975 to 1.150 mm.

Head narrower than pronotum; vertex longer medially than next to eye, interocular width more than three times median length; ocellus located at a distance of from twice its diameter or farther from eye; anteclypeus parallel margined or slightly wider apically, usually slightly exceeding gena; postclypeal sutures parallel above antennal pits; pronotum more than three times as long as vertex; hind femoral chaetotaxy 2-2-1; female with posterior margin of abdominal sternum VII truncate posteriorly.

Male pygofer as *impicta* but sometimes with rounded projection on posteroventral margin; plates as *impicta*; connective expanded apically, slightly bifid, longer than style, stem longer than arms, angle between arms rounded; style with preapical lobe rounded, apical extension long, rounded apically; aedeagus broad basally, with basal one-third approximately parallel margined, shaft narrowed, slender, curved dorsally then anteriorly.

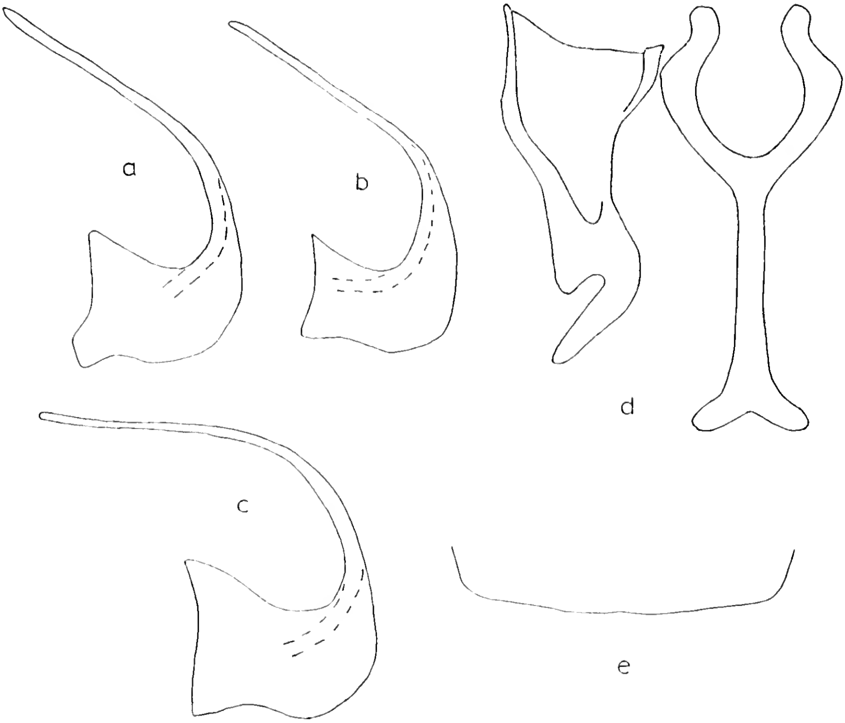

FIGURE 6.—*B. arctica: a–c*, aedeagus, lateral view; *d*, style and connective, dorsal view; *e*, female abdominal sternum VII, ventral view.

Color from stramineous to light green to brown; face commonly with faint oblique brown lines on each side of midline; thoracic venter commonly dark; forewings hyaline to subhyaline; abdominal dorsum dark.

The male holotype from Dawson, Yukon (June), is in the Canadian National collection. Material compared with type by B. P. Beirne has been examined. Additional material examined was from British Columbia and Northwest Territory (July), Idaho (July), Montana (June and July), New Mexico (June and July), Wyoming (July), and Frio, D. F. [Mexico] (Oct. and Nov.).

B. arctica Beirne is very closely related to *B. impicta* (Van Duzee) but can be distinguished from this species by the shape of the aedeagus which is broad with the basal one-third almost parallel margined in *arctica*.

Balclutha apicula, new species

Figure 7

Length of male 3.5 mm; head width .875 mm; pronotal width 1.000 mm; female unknown.

Head narrower than pronotum; vertex longer medially than next to eye, interocular width three times median length; ocellus located at a distance approximately twice its diameter from eye; anteclypeus wider apically, exceeding gena; postclypeal sutures parallel above antennal pits; pronotum three times as long as vertex; hind femoral chaetotaxy 2–2–1.

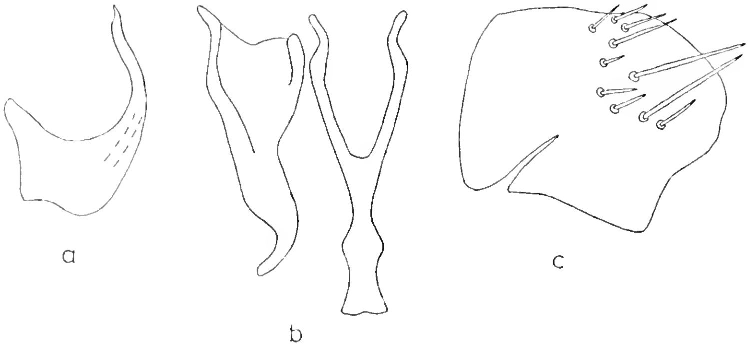

Figure 7.—*B. apicula*: *a*, aedeagus, lateral view; *b*, style and connective, dorsal view; *c*, male pygofer, lateral view.

Male pygofer with less than 15 setae, ventral margin broadly produced; connective slightly longer than style, stem irregular anteapically, not strongly expanded apically and slightly bifid, approximately equal in length to arms which are slender; style with preapical lobe inconspicuous, apical extension curved laterally, rounded apically; aedeagus broad basally, shaft gradually tapered, irregularly curved dorsally, acute apically.

Color stramineous; forewings subhyaline.

Holotype male from Mayaguez, Puerto Rico, Aug. 24–29, 1914, deposited in the American Museum of Natural History.

B. apicula, new species, appears to be related to *B. punctata* (F.) but can be distinguished by the shape of the aedeagus, style and connective (see key).

Balclutha incompta, new species

FIGURE 8

Length of male 3.2 mm; head width .700 mm; pronotal width .800 mm; female unknown.

Head narrower than pronotum; vertex as long next to eye as medially, interocular width more than three times median length; ocellus located at a distance more than its diameter from eye; anteclypeus widest apically, slightly exceeding gena; postclypeal sutures parallel above antennal pits; pronotum more than three times as long as vertex; hind femoral chaetotaxy 2–2–1.

Male pygofer with less than 10 setae, posteroventral margin slightly produced; plates slender, triangular, extending posteriorly as far as pygofer apex; connective expanded apically, slightly bifid, equal in length to style; stem and arms equal in length with angle between arms rounded; style with preapical lobe rounded, apical extension slightly curved and rounded apically; aedeagus simple, shaft gradually tapered and curved dorsally, apex acute.

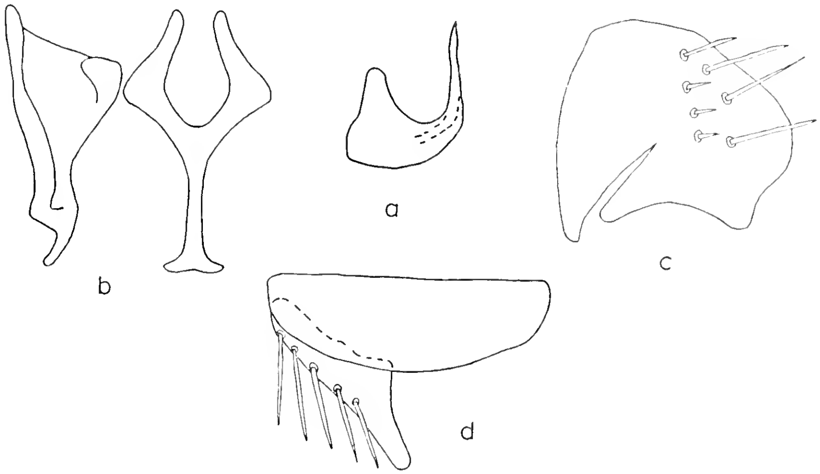

FIGURE 8.—*B. incompta: a*, aedeagus, lateral view; *b*, style and connective, dorsal view; *c*, male pygofer, lateral view; *d*, valve and plate, ventral view.

Color green; face without oblique brown lines; thoracic venter not dark; forewings subhyaline with green tint.

Holotype male from Rio Huagra-Yacu, Oriente, Ecuador, April 1941, 900 meters (Clarke-Macintyre), on indefinite loan to the U.S. National Museum from N.C. State University.

B. incompta, new species, appears to be closely related to *B. apicula*, new species, but can be distinguished by the shape of the aedeagus (see key).

***Balclutha krameri*, new species**

FIGURE 9

Length of male unknown; head width of male .925 mm; pronotal width of male .975 mm; female unknown.

Head narrower than pronotum; vertex as long next to eye as medially, interocular width more than three times median length; ocellus located at a distance approximately its diameter from eye; anteclypeus widest apically, slightly exceeding gena; postclypeal sutures parallel above antennal pits; pronotum more than three times as long as vertex.

Male pygofer with less than 15 setae, incised on posterior margin; plates triangular, slender, not extending as far posteriorly as pygofer apex; connective expanded apically and truncate, equal to style in length, stem longer than arms; style with preapical lobe rounded, apical extension slightly curved, rounded apically; aedeagus with dorsal apodeme prominent, shaft slender, curved dorsally with a pair of processes arising from ventral margin and extending nearly to apex.

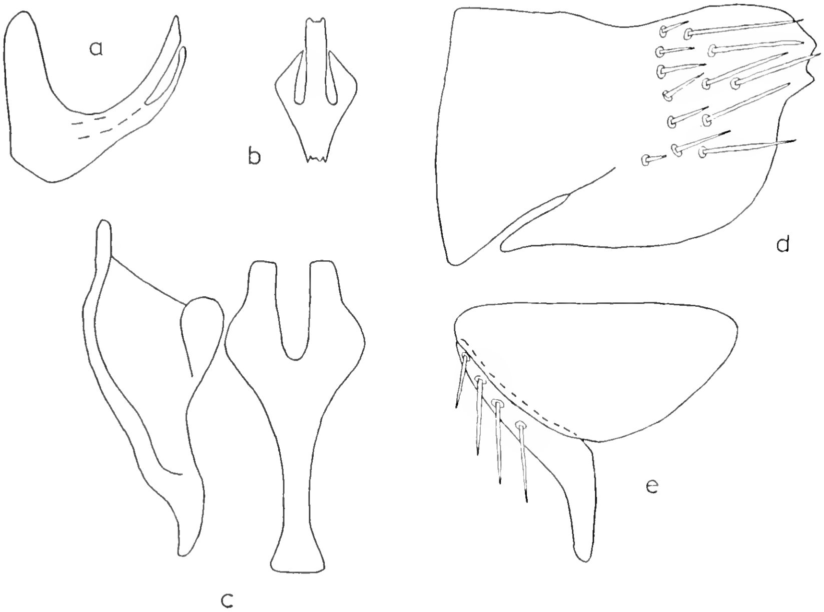

FIGURE 9.—*B. krameri:* *a*, aedeagus, lateral view; *b*, aedeagal shaft, posteroventral view; *c*, style and connective, dorsal view; *d*, male pygofer, lateral view; *e*, valve and plate, ventral view.

Color green.

Holotype male, Costa Rica (Pablo Schild), in U.S. National Museum. This species was described from a single specimen of which only the head, prothorax, and abdomen remain.

B. krameri, new species, is related to *B. abdominalis* (Van Duzee) but can be easily distinguished by the shape of the aedeagus which is distinctive (see key). This species is named in honor of Dr. James P. Kramer of the U.S. National Museum, who furnished the author much of the material used in this study and made many valuable suggestions during the time that this research was being conducted.

Balclutha abdominalis abdominalis (Van Duzee)

Figure 10

Gnathodus abdominalis Van Duzee, 1892, Canadian Ent., vol. 24, p. 113.
Balclutha hyalina Osborn, 1926, Ann. Ent. Soc. America, vol. 19, p. 352. [New synonymy.]

Length of male 3.0 to 3.5 mm, of female 3.5 to 3.6 mm; head width of male .675 to .775 mm, of female .775 to .850 mm; pronotal width of male .700 to .850 mm, of female .825 to .875 mm.

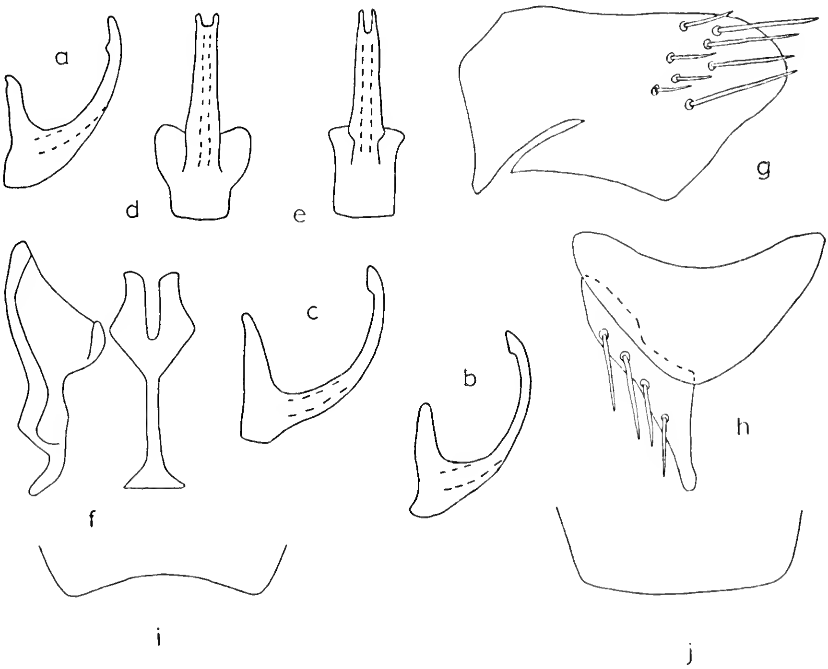

Figure 10.—*B. a. abdominalis: a–c*, aedeagus, lateral view; *d, e*, aedeagus, posteroventral view; *f*, style and connective, dorsal view; *g*, male pygofer, lateral view; *h*, valve and plate, ventral view; *i, j*, female abdominal sternum VII, ventral view.

Head narrower than pronotum but only slightly so in some specimens; vertex usually as long next to eye as medially but occasionally longer medially, interocular width more than three times median length; ocellus located at a distance of from one to two times its diameter from eye; anteclypeus parallel margined or slightly wider apically, not exceeding gena; postclypeal sutures parallel above antennal pits; pronotum approximately three times as long as vertex; hind femoral chaetotaxy 2–2–1; female with posterior margin of abdominal sternum VII truncate or slightly concave posteriorly.

Male pygofer with less than 15 setae, ventral margin produced, posteroventral border more heavily sclerotized, a heavily sclerotized band extending vertically through setal area; plates slender, triangular, not extending as far posteriorly as pygofer apex; connective expanded and truncate apically, two-thirds length of style, stem slightly longer than arms, arms thickened, with angle between arms acute; style with preapical lobe rounded, apical extension curved laterally and rounded; aedeagus with dorsal apodeme conspicuous, shaft evenly curved dorsally, slightly expanded apically, bifid apically in posteroventral view; processes on shaft inconspicuous if present.

Color stramineous to green; face with or without faint oblique brown lines on each side of midline; thoracic venter not dark; forewings hyaline to subhyaline, commonly tinted as body color.

The male lectotype (selected by P. W. Oman) from Jamesburg, N. J., is deposited in the collection at Iowa State University and has been examined. The male holotype of *B. hyalina* Osborn, from Cuba, is located at the U.S. National Museum and has also been examined. This is a widespread and variable species. Additional specimens have been examined from the states of Alabama, Arizona, Connecticut, District of Columbia, Florida, Georgia, Iowa, Kansas, Maryland, Michigan, Mississippi, Missouri, New Hampshire, New York, North Carolina, Ohio, Oklahoma, Pennsylvania, Tennessee, Texas, Virginia, West Virginia, Wisconsin, and Ontario. Other specimens examined were from Mexico, Puerto Rico, Cuba, Trinidad Island, British Honduras, Guatemala, Costa Rica, and Peru. This species has been collected from sedge in Cuba.

B. a. abdominalis (Van Duzee) appears to be closely related to several other species. It can be distinguished best by the shape of the aedeagus of which the shaft is evenly curved, expanded apically and on which, if lateral projections are present, they are inconspicuous.

Balclutha abdominalis fuscipennis Linnavuori, new status

Figure 11

Balclutha fuscipennis Linnavuori, 1954, Ann. Ent. Fennici, vol. 20, pp. 60, 61.

Length of male 3.9 or 4.5 mm; head width .850 mm; pronotal width .925 mm; female unknown.

Characters as in *B. a. abdominalis* except connective not greatly expanded apically, stem widened; aedeagus wide basally, shaft curved anterodorsally, not expanded apically, in posteroventral view with a distinct pair of lateral triangular processes, slightly bifid apically.

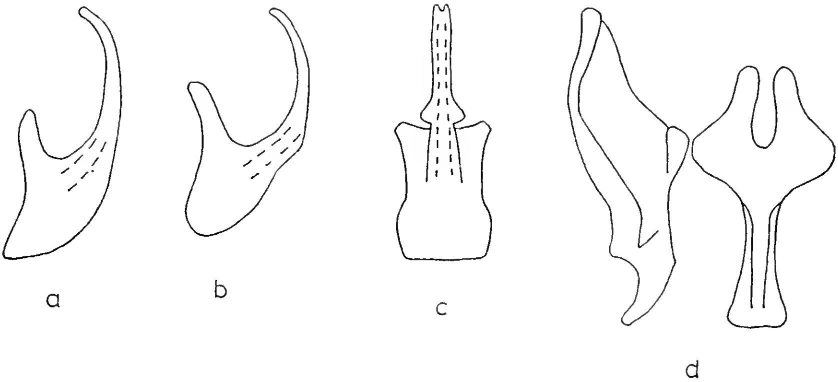

Figure 11.—*B. abdominalis fuscipennis: a, b*, aedeagus, lateral view; *c*, aedeagus, posteroventral view; *d*, style and connective, dorsal view.

Color brown to brownish green; face with faint oblique brown lines on each side of midline; thoracic venter not dark; forewings subhyaline with brown tint.

The male holotype from Tucaman, Lules, Argentina, Nov. 13, 1953 (Wygodzinsky), is in the collection of R. Linnavuori and has been examined. An additional specimen from Curitiba, Parana, Brazil, July 1961 (N. L. H. Krauss), in the U.S. National Museum has been examined.

B. a. fuscipennis Linnavuori is closely related to the nominate subspecies but can be distinguished by the pair of lateral triangular processes on the aedeagus. This subspecies is also distinctly larger in size.

Balclutha abdominalis amplissima, new subspecies

FIGURE 12

Length of male 4.6 to 4.7 mm, of female 4.7 mm; head width of male .950 to .975 mm, of female, .975 mm; pronotal width of male 1.075 to 1.100 mm, of female 1.100 mm.

Characters as *B. a. abdominalis;* connective as *B. a. fuscipennis;* aedeagus robust, slightly expanded apically; shaft in posteroventral view with pair of distinct lateral triangular processes, deeply bifid apically.

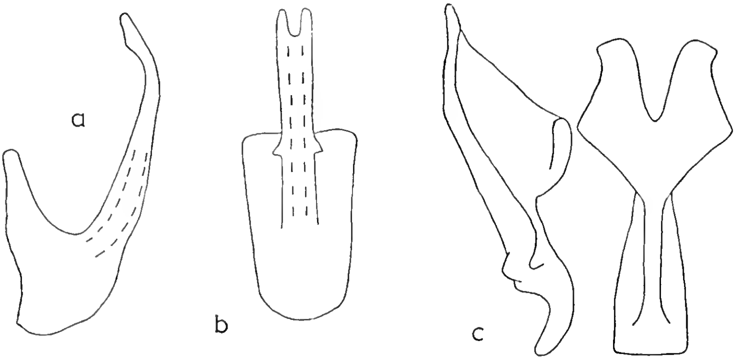

FIGURE 12.—*B. abdominalis amplissima: a,* aedeagus, lateral view; *b,* aedeagus, posteroventral view; *c,* style and connective, dorsal view.

Color brown; face with faint oblique brown lines on each side of midline; thoracic venter slightly darkened; forewings subhyaline with tan tint.

Holotype male, Cerro Punta, Panama, Dec. 10, 1952 (F. S. Blanton), in the U.S. National Museum. One male paratype at North Carolina State University. This subspecies was described from a series of three male specimens and one female specimen, all with the same label data.

B. abdominalis amplissima, new subspecies, can be distinguished from the nominate subspecies by its larger external size and by the larger size of the aedeagus. It can be distinguished from *B. a. fuscipennis* Linnavuori by the larger size of the aedeagus and by the expanded apex of the shaft which is also more deeply bifid.

Balclutha diversa, new species

FIGURE 13

Length of male 3.9 to 4.2 mm, of female 3.7 to 4.2 mm; head width of male .825 to .850 mm, of female .825 to .975 mm; pronotal width of male .925 to .975 mm, of female .925 to 1.025 mm.

Head distinctly narrower than pronotum; vertex as long next to eye as medially or occasionally slightly longer medially, interocular width more than three times median length; ocellus located at a distance of from one to two times its diameter from eye; anteclypeus slightly wider apically, not exceeding gena; postclypeal sutures parallel above antennal pits; pronotum more than three times as long as vertex; hind femoral chaetotaxy 2–2–1; female with posterior margin of abdominal sternum VII truncate or slightly concave posteriorly.

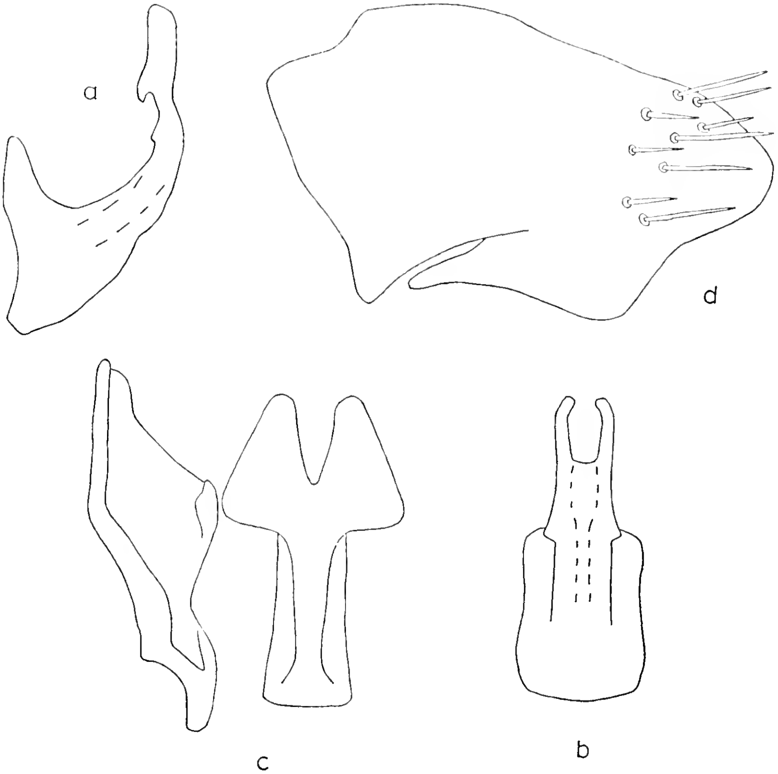

FIGURE 13.—*B. diversa: a,* aedeagus, lateral view; *b,* aedeagus, posteroventral view; *c,* style and connective, dorsal view; *d,* male pygofer, lateral view.

Male pygofer and plates as *B. abdominalis* (Van Duzee); connective truncate apically, not expanded, shorter than style, stem longer than arms which are broad, angle between arms acute; style with preapical lobe angled, apical extension only slightly curved, rounded apically;

aedeagus broad basally, shaft irregularly curved dorsally, conspicuously expanded apically, in posteroventral view with a pair of small triangular processes present on lateral margin, deeply bifid apically.

Color green; face without oblique brown lines; thoracic venter dark; forewings subhyaline.

Holotype male, Orizaba, V. C. [Mexico], Oct. 8, 1941 (DeLong, Good, Caldwell, and Plummer), and male paratypes, same data, in the DeLong collection. This species was described from a series of six male and five female specimens. An additional specimen from Fortin, V. C., Mexico, Oct. 9, 1941, was also examined.

B. diversa, new species, is very closely related to *B. abdominalis amplissima*, new subspecies, but can be distinguished by the shape of the aedeagus which is conspicuously more expanded apically and more deeply bifid.

Balclutha distincta Linnavuori

Figure 14

Balclutha distincta Linnavuori, 1959, Ann. Zool. Soc. 'Vanamo,' vol. 20, p. 345.

Length of male 3.8 mm; head width .800 mm; pronotal width .875 mm; female unknown.

Head narrower than pronotum; vertex slightly longer medially than next to eye, interocular width approximately three times median length; ocellus located at a distance of approximately 1½ times its diameter from eye; anteclypeus wider apically, exceeding gena; postclypeal sutures parallel above antennal pits; pronotum three times as long as vertex.

Male pygofer with less than 10 setae, narrowed posteriorly, dorsal and posteroventral margins heavily sclerotized; plates slender, triangular, not extending as far posteriorly as pygofer apex; connective expanded apically and truncate; stem slightly longer than arms which are thickened, with angle between arms acute; style with preapical lobe rounded, apical extension curved laterally, rounded apically; aedeagus broad basally, shaft with irregular margins, curved dorsally, in posteroventral view with small lateral triangular processes, apex deeply bifid, expanded.

Color tan to green.

The male holotype, Coronado, Costa Rica, Aug. 15, 1931 (F. Nevermann), in the Hungarian Natural History Museum, Budapest, has been examined. An additional male specimen from Costa Rica in the U.S. National Museum has also been examined.

B. distincta Linnavuori is closely related to *B. diversa*, new species, but can be distinguished by the shape of the aedeagus which, in posteroventral view, is more expanded apically than *diversa*. The apex of the aedeagus is sagittate in *distincta*.

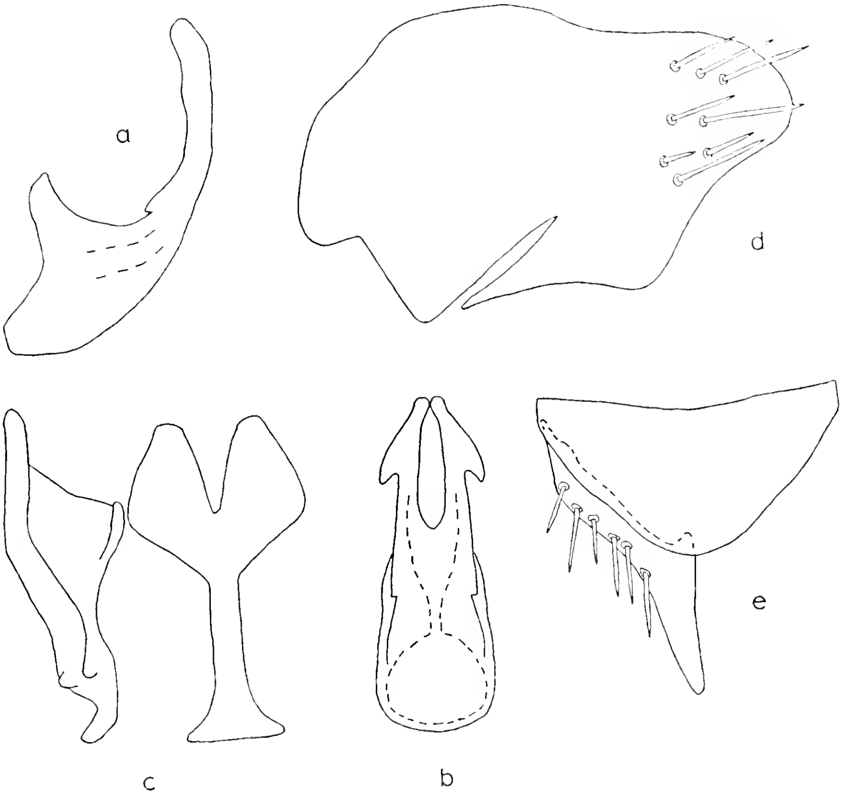

FIGURE 14.—*B. distincta*: *a*, aedeagus, lateral view; *b*, aedeagus, posteroventral view; *c*, style and connective, dorsal view; *d*, male pygofer, lateral view; *e*, valve and plate, ventral view.

***Balclutha obunca*, new species**

FIGURE 15

Length of male 4.0 to 4.1 mm, of female 4.1 to 4.5 mm; head width of male .875 to .925 mm, of female .925 to .950 mm; pronotal width of male .975 to 1.000 mm, of female 1.025 to 1.075 mm.

Head narrower than pronotum; vertex as long next to eye as medially or occasionally slightly longer medially, interocular width three times median length; ocellus located at a distance of from one to two times its diameter from eye; anteclypeus slightly wider apically, equal to or slightly exceeding gena; postclypeal sutures parallel above antennal pits; pronotum three times as long as vertex; hind femoral chaetotaxy 2–2–1; female with posterior margin of abdominal sternum VII truncate apically, posteroventral margins oblique.

Male pygofer with less than 15 setae, deeply incised in apical half of dorsal margin, ventral margin broadly produced; plates broadly triangular, not constricted apically, extending posteriorly as far as pygofer apex; connective not expanded apically, truncate, approximately equal in length to style, stem longer than arms, angle between arms rounded; style with preapical lobe rounded, apical extension strongly curved laterally, rounded apically; aedeagus robust basally, preatrium conspicuous, dorsal apodeme short and rounded, shaft slender, curved dorsally.

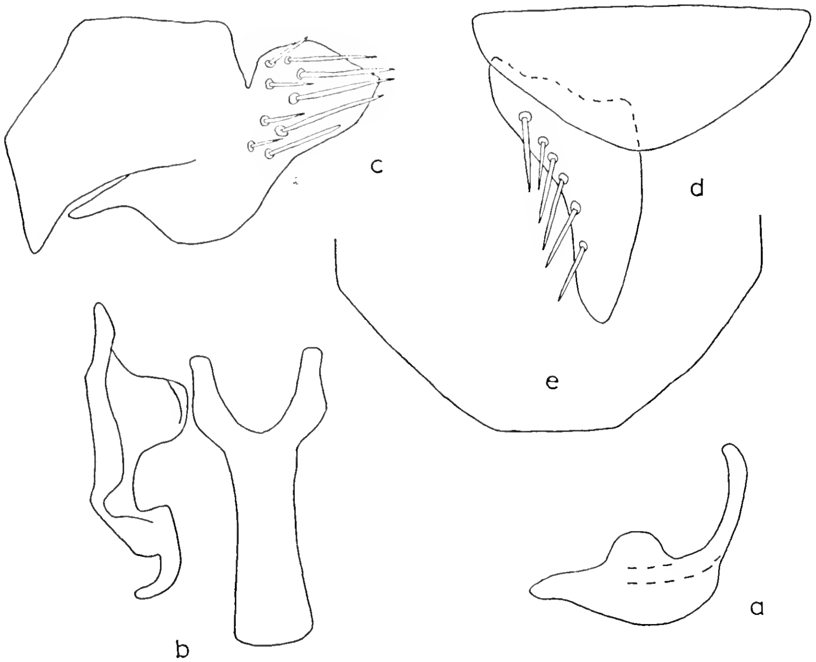

Figure 15.—*B. obunca: a*, aedeagus, lateral view; *b*, style and connective, dorsal view; *c*, male pygofer, lateral view; *d*, valve and plate, ventral view; *e*, female abdominal sternum VII, ventral view.

Color light to dark brown; face without oblique brown lines; pronotum commonly with longitudinal orange or brown lines, scutellum with orange areas; thoracic venter not dark; forewings hyaline with brown tint.

Holotype male, Nova Teutonia, Santa Catarina, Brazil, Apr. 27, 1950 (F. Plaumann), on indefinite loan to U.S. National Museum from North Carolina State University. Three male paratypes at North Carolina State University. This species was described from seven male and seven female specimens, all from Brazil (March, April, and July).

B. obunca, new species, appears to be related to *B. abdominalis* (Van Duzee) but can be distinguished by the shape of the aedeagus and the deeply incised ventral margin of the pygofer (see key).

Balclutha youngi, new species

FIGURE 16

Length of male 4.4 to 4.6 mm; head width .900 to .950 mm; pronotal width .925 to 1.000 mm; female unknown.

Head distinctly narrower than pronotum; vertex usually no longer medially than next to eye, interocular width more than three times median length; ocellus located at a distance of from one to two times its diameter from eye; anteclypeus slightly wider apically, not exceeding gena; postclypeal sutures parallel above antennal pits; pronotum more than three times as long as vertex; hind femoral chaetotaxy 2–2–1.

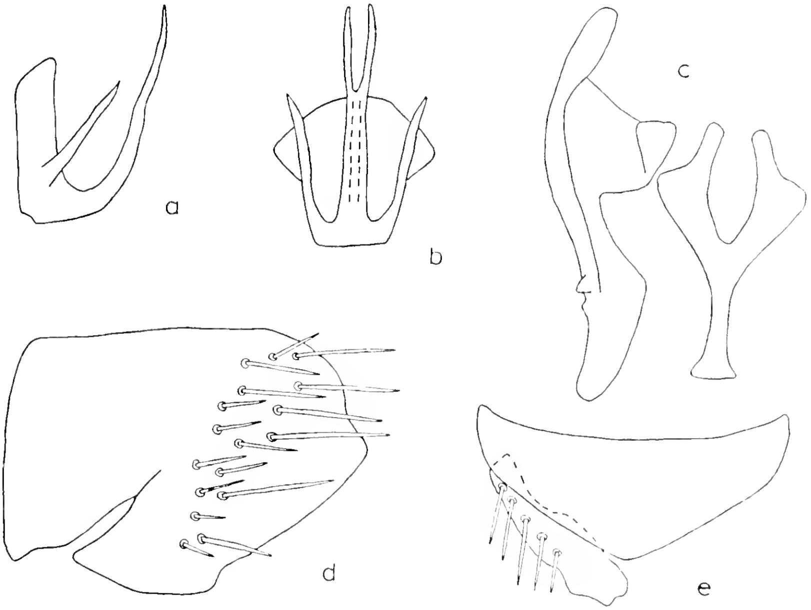

FIGURE 16.—*B. youngi: a*, aedeagus, lateral view; *b*, aedeagus, posteroventral view; *c*, style and connective, dorsal view; *d*, male pygofer, lateral view; *e*, valve and plate, ventral view.

Male pygofer with posterior margin not rounded, usually with more than 15 setae; plates short, blunt apically; connective expanded apically and truncate, two-thirds as long as style, stem and arms approximately equal in length; style with preapical lobe inconspicuous, apical extension stout, rounded apically and only slightly curved: aedeagus with dorsal apodeme conspicuous with a pair of long slender processes extending posteriorly, shaft slender, deeply incised apically, curved dorsally.

Color stramineous to green; face without oblique brown lines; vertex, pronotum, and scutellum with longitudinal yellow lines; thoracic venter not dark; forewings subhyaline with several small brown spots present in irregular patterns.

Holotype male, Nova Teutonia, Santa Catarina, Brazil, April 1953 (F. Plaumann), on indefinite loan to the U.S. National Museum from North Carolina State University. This species was described from four male specimens from Brazil (Apr., Oct., and Jan.).

B. youngi, new species, appears to be related to *B. hebe* (Kirkaldy). It can be readily distinguished from the latter by the shape of its aedeagus, the shape of the male plates, and the shape of the styles (see key). This species is named in honor of Dr. David A. Young of North Carolina State University.

***Balclutha fuscina*, new species**

Figure 17

Length of male 4.0 mm; head width .825 mm; pronotal width .850 mm; female unknown.

Head slightly narrower than pronotum; vertex as wide next to eye as medially, interocular width more than three times median length; ocellus located at a distance of slightly more than its diameter from eye; anteclypeus widest apically, exceeding gena; postclypeal sutures slightly curved mesally above antennal pits; pronotum approximately three times as long as vertex; hind femoral chaetotaxy 2–1–1.

Male pygofer with less than 15 setae, posteroventral margin with a short heavily sclerotized process extending posteriorly as far as pygofer apex; connective wide, expanded apically and bifid, approximately equal in length to style, stem slightly longer than arms; style with preapical lobe rounded, apical extension slightly curved and acute apically; aedeagus with shaft long and slender, a pair of short processes arising from base and extending posteriorly.

Color green to stramineous; face without oblique brown lines; thoracic venter not dark; forewings subhyaline with green tint.

Holotype male, Nova Teutonia, Santa Catarina, Brazil, May 1953 (F. Plaumann), on indefinite loan to the U.S. National Museum from

North Carolina State University. This species was described from this single specimen.

B. fuscina, new species, is closely related to *B. floridana* (DeLong and Davidson) but can be easily distinguished by the shape of the aedeagus (see key).

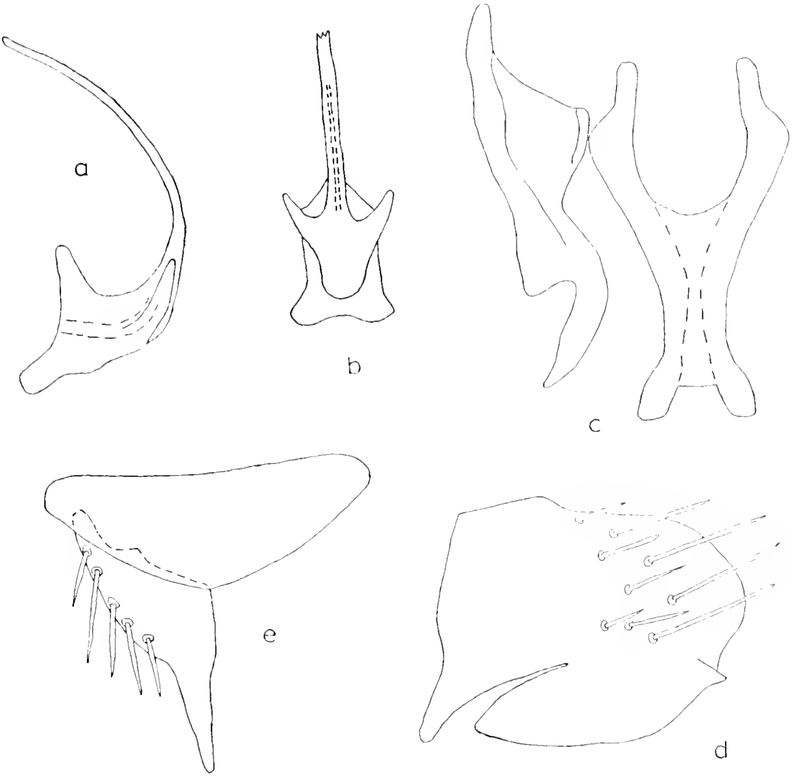

FIGURE 17.—*B. fuscina: a*, aedeagus, lateral view; *b*, aedeagus, posteroventral view; *c*, style and connective, dorsal view; *d*, male pygofer, lateral view; *e*, valve and plate, ventral view.

Balclutha caldwelli, new species

FIGURE 18

Length of male 3.1 to 3.4 mm, of female 3.1 to 3.8 mm; head width of male .725 to .850 mm, of female .800 to .875 mm; pronotal width of male .750 to .900 mm, of female .825 to .900 mm.

Head narrower than pronotum (occasionally very nearly as wide as pronotum); vertex usually longer medially than next to eye, interocular width three times median length or slightly less; ocellus located at a distance less than its diameter from eye; anteclypeus slightly wider apically, equal to or slightly exceeding gena; postcylpeal sutures curved mesally above antennal pits; pronotum three times as long as vertex or slightly less; hind femoral chaetotaxy 2–1–1; female with posterior margin of abdominal sternum VII sinuate posteriorly, a heavily sclerotized band extending across posterior margin.

Male pygofer with less than 15 setae, ventral margin produced; plates slender, triangular, extending posteriorly as far as pygofer apex, connective expanded apically and truncate, equal in length to style, stem and arms equal in length, angle between arms approximately 45 degrees; style with preapical lobe rounded, apical extension slightly curved and acute; aedeagus tapered gradually from base to apex, curved dorsally, shaft in posteroventral view with apex troughlike, dorsal margin exceeding ventral margin, slightly notched apically.

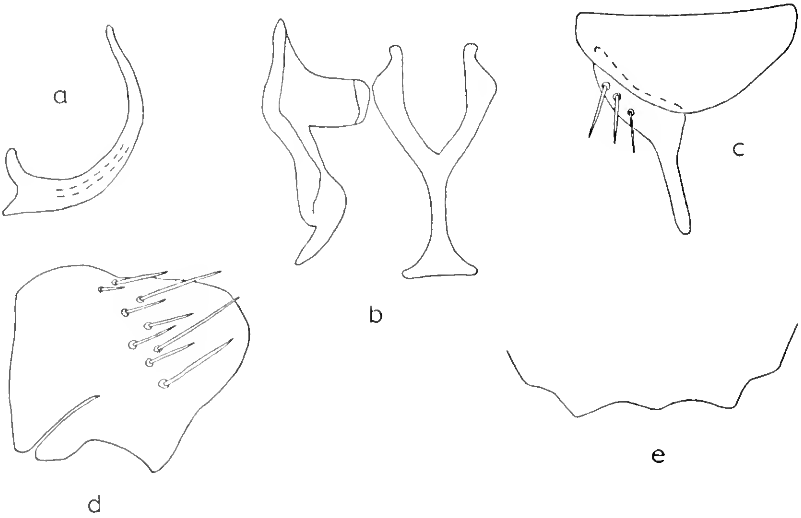

FIGURE 18.—*B. caldwelli: a*, aedeagus, lateral view; *b*, style and connective, dorsal view; *c*, valve and plate, ventral view; *d*, male pygofer, lateral view; *e*, female abdominal sternum VII, ventral view.

Color stramineous to brown; face without oblique brown lines; vertex and pronotum commonly irregularly marked with faint darker longitudinal lines or other orange-brown areas; scutellum usually with orange markings; thoracic venter usually dark; forewings hyaline to subhyaline, commonly concolorous with body color.

Holotype male from Experiment Station, Rio Piedras, Puerto Rico, July 11, 1917 (H. Morrison), in the U.S. National Museum. Paratype males, same data, in the U.S. National Museum and at North Carolina State University. This is a widespread subtropical and tropical species, and numerous specimens have been examined from Flordia, Mexico, Puerto Rico, Cuba, Trinidad Island, Dominican Republic, Haiti, Jamaica, British Honduras, Panama, El Salvador, Surinam, Colombia, Peru, and British Guiana.

B. caldwelli, new species, appears to be related to *B. neglecta* (DeLong and Davidson) but can be distinguished from this species by the shape of the aedeagus (see key) and by the head which is narrower than the pronotum. Caldwell (1952) and Linnavuori (1959) applied the specific name of *virescens* (Osborn) to this taxon. In typical *virescens* the head is wider than the pronotum, and the female abdominal sternum VII does not resemble that of *caldwelli.* This species is named in honor of Dr. John S. Caldwell, formerly of Ohio State University.

Balclutha rufofasciata (Merino)

FIGURE 19

Nesosteles rufofasciatus Merino, 1936, Philippine Journ. Sci., vol. 61, p. 381.

Length of male 3.3 to 3.9 mm, of female 3.7 to 4.2 mm; head width of male .800 to .875 mm, of female .875 to .925 mm; pronotal width of male .825 to .925 mm, of female .875 to 1.000 mm.

Head usually as wide as pronotum; vertex as long next to eye as medially, interocular width three times median length; ocellus located at a distance of from less than to equal to its diameter from eye; anteclypeus parallel margined, exceeding gena; postclypeal sutures curved mesally above antennal pits; pronotum three times as long as vertex; hind femoral chaetotaxy 2–1–1; female with posterior margin of abdominal sternum VII notched medially.

Male pygofer with less than 15 setae, with a bifurcate heavily sclerotized process on inner surface extending posteriorly; plates broadly triangular, with many setae, apical one-fourth constricted, curved ventrally; connective expanded apically and deeply bifid, approximately equal in length to style, stem slightly longer than arms; style with preapical lobe acute, apical extension long, strongly curved laterally, acute apically; aedeagus with preatrium conspicuous, dorsal apodeme extending anterodorsally, shaft gradually narrowed, slender in apical one-half, curved dorsally then anteriorly.

Color stramineous; face without oblique brown lines; thoracic venter not dark; forewings subhyaline with third apical cell dark brown, other cells commonly partially or wholly brown or red in color.

Type not located; the above redescription is from a series of specimens from St. Thomas, Virgin Islands (Nov.) located at the U.S. National Museum. It is also reported from Puerto Rico, Africa, the Philippines, and Oceania.

B. rufofasciata (Merino) appears to be related to *B. guajanae* (DeLong) but can be distinguished by the shape of the aedeagus, the shape of the pygofer process, and the forewing coloration (see key).

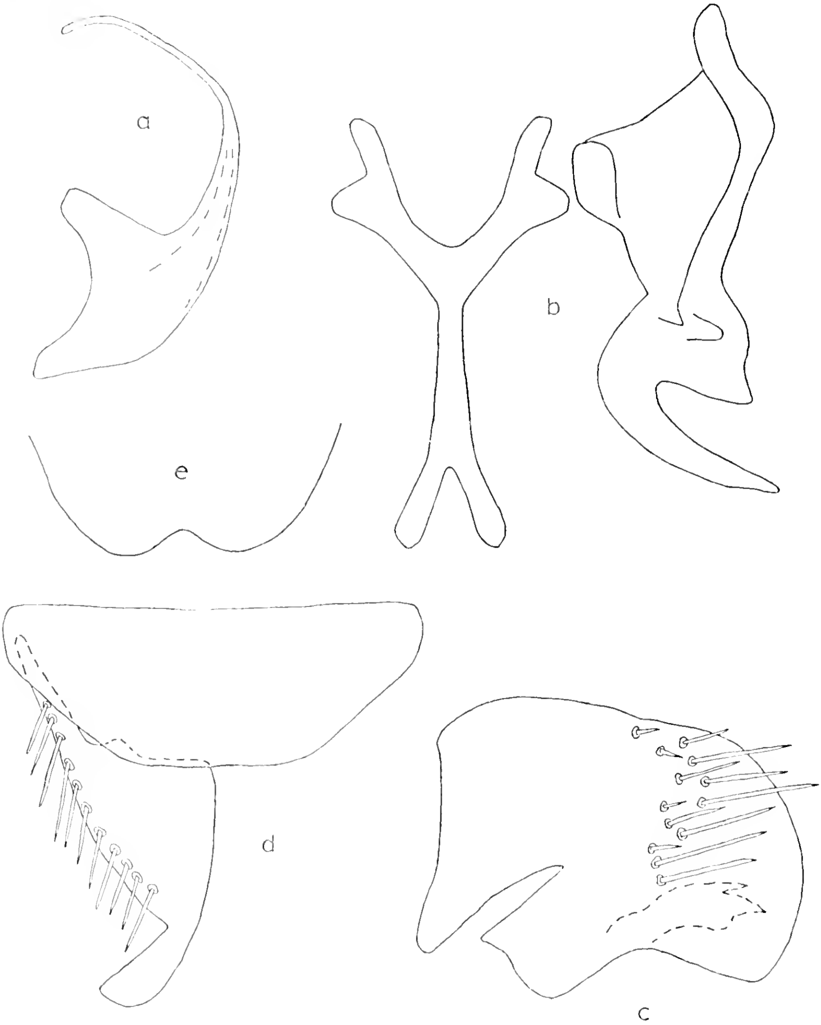

FIGURE 19.—*B. rufofasciata*: *a*, aedeagus, lateral view; *b*, style and connective, dorsal view; *c*, male pygofer, lateral view; *d*, valve and plate, ventral view; *e*, female abdominal sternum VII, ventral view.

Balclutha guajanae (DeLong), new combination

FIGURE 20

Eugnathodus guajanae DeLong 1923, *in* Wolcott, Journ. Dept. Agric. Porto Rico, vol. 7, p. 267.

Eugnathodus calcara DeLong and Davidson, 1933a, Ohio Journ. Sci., vol. 33, p. 57.

Length of male 3.2 to 3.7 mm, of female 3.3 to 4.0 mm; head width of male .800 to .875 mm, of female .875 to .925 mm; pronotal width of male .750 to .850 mm, of female .825 to .900 mm.

Head as wide as or wider than pronotum; vertex as long next to eye as medially, interocular width more than three times median length; ocellus located at a distance less than its diameter from eye; anteclypeus widest apically, exceeding gena; postclypeal sutures either parallel or slightly curved mesally above antennal pits; pronotum three times as long as vertex; hind femoral chaetotaxy 2–1–1; female with posterior margin of abdominal sternum VII rounded, notched mesally.

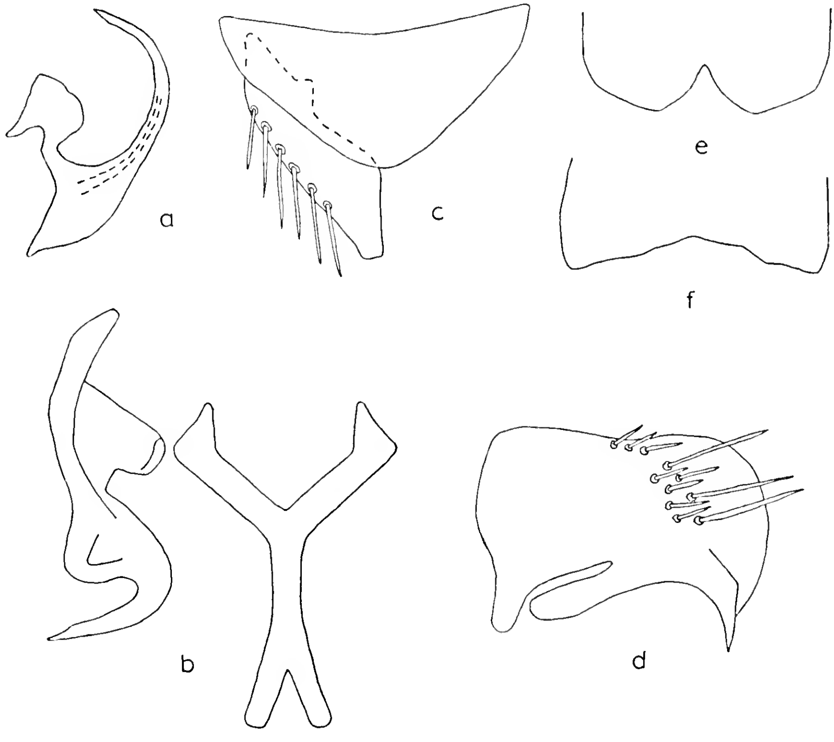

FIGURE 20.—*B. guajanae: a,* aedeagus, lateral view; *b,* style and connective, dorsal view; *c,* valve and plate, ventral view; *d,* male pygofer, lateral view; *e, f,* female abdominal sternum VII, ventral view.

Male pygofer with less than 15 setae, a tapered process at posteroventral margin extending ventrally, its margin entire; plates broadly triangular; connective expanded apically, deeply bifid, equal in length to style, stem longer than arms which diverge at approximately 90 degrees; style with preapical lobe rounded, apical extension strongly curved laterally, acute apically; aedeagus with dorsal apodeme conspicuous, expanded laterally and forming two lobes, shaft gradually narrowed, curved anteriorly.

Color tan; face without oblique brown lines; thoracic venter not dark; scutellum commonly with orange areas present; forewings hyaline to subhyaline.

The holotype of *E. guajanae,* a female from Rio Piedras, Puerto Rico, and the male holotype of *E. calcara,* both in the DeLong collection, have been examined. Linnavuori (1959, p. 339) placed *guajanae* in synonymy under *rosea* (Scott), but on the basis of material studied, Linnavuori's illustrations and Ribaut's (1952, p. 69) illustrations of *rosea* (Scott), *guajanae* is here removed from synonymy. This species is commonly found in Florida, Georgia, and Texas. One specimen from North Carolina has also been examined. Other localities from which material has been examined are Brazil, Mexico, Puerto Rico, Cuba, Jamaica, British Honduras, Panama, and British Guiana. It is commonly collected on sugarcane flowers.

B. guajanae (DeLong) appears to be closely related to *B. hebe* (Kirkaldy) but can be readily distinguished by the unique shape of the aedeagus and by the position of the pygofer process (see key). The apical end of the connective is also more bifid in *guajanae.*

Balclutha hebe **(Kirkaldy)**

FIGURE 21

Nesosteles hebe Kirkaldy, 1906, Bull. Hawaiian Sugar Planters' Assoc. Exp. Sta. Div. Ent., vol. 1, p. 343.

Eugnathodus bisinuatus DeLong, 1923, *in* Wolcott, Journ. Dept. Agric. Porto Rico, vol. 7, p. 266.

Eugnathodus pallidus Osborn, 1926, Ann. Ent. Soc. America, vol. 19, p. 352.

Eugnathodus bifurcata DeLong and Davidson, 1933a, Ohio Journ. Sci., vol. 33, p. 58.

Length of male 3.0 to 3.7 mm, of female 3.3 to 4.0 mm; head width of male .750 to .800 mm, of female .775 to .900 mm; pronotal width of male .725 to .800 mm, of female .750 to .900 mm.

Head as wide as or wider than pronotum; vertex as long next to eye as medially, interocular width more than three times median length; ocellus located at a distance equal to or slighly less than its diameter from eye; anteclypeus widest apically, exceeding gena; postclypeal sutures curved mesally above antennal pits; pronotum more than three times as long as vertex; hind femoral chaetotaxy 2–1–1; female with posterior margin of abdominal sternum VII with rounded median heavily sclerotized lobe which is indented on each side.

Male pygofer heavily setose (usually 15 or more setae), a tapered process at posteroventral margin extending mesally, process with margins entire or irregularly dentate; plates broadly triangular, apical one-third sharply curved dorsally; connective expanded apically, slightly bifid, slightly less than style in length, stem twice as long as arms; style with preapical lobe rounded, apical extension prominent, acute apically, aedeagus with dorsal apodeme greatly expanded, three pairs of processes extending posteriorly from its base, shaft slender, curved anteriorly.

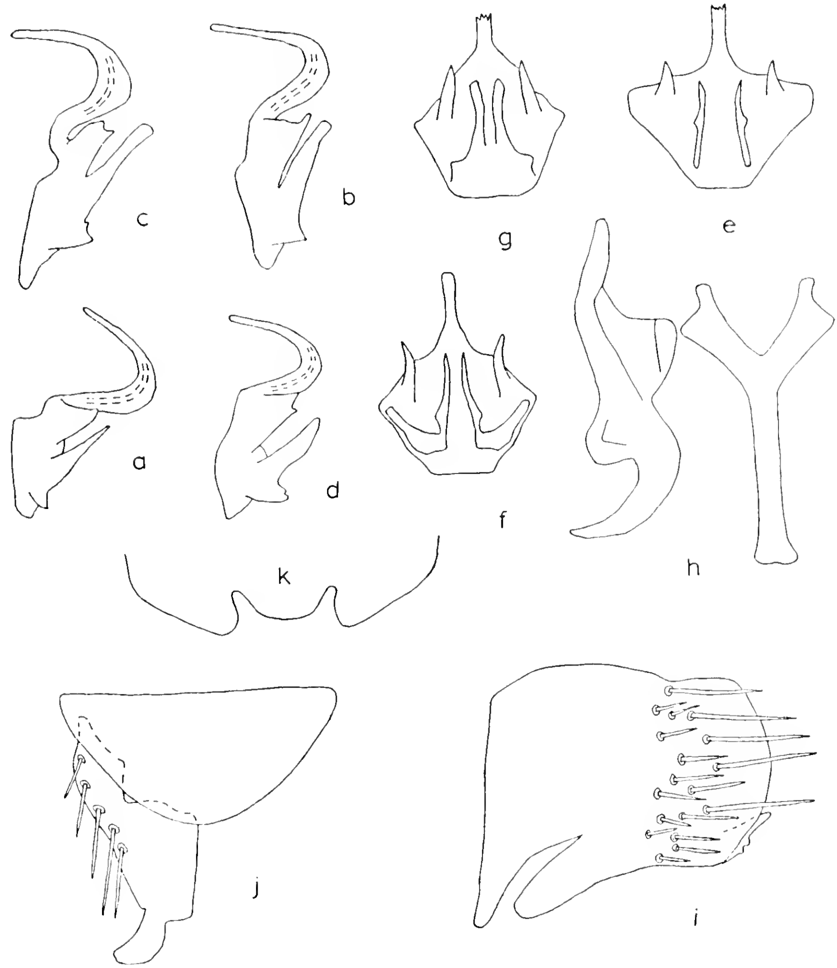

FIGURE 21.—*B. kebe: a–d*, aedeagus, lateral view; *e–g*, aedeagus, posteroventral view; *h*, style and connective, dorsal view; *i*, male pygofer, lateral view; *j*, valve and plate, ventral view; *k*, female abdominal sternum VII, ventral view.

Color including thoracic venter from green to light brown; forewings hyaline or subhyaline; abdominal dorsum dark.

Holotype not located; however, the holotypes of *E. bisinuatus* DeLong, *E. bifurcata* DeLong and Davidson, and *E. pallidus* Osborn have been examined. This is one of the most common species found in tropical and subtropical areas. Numerous specimens have been examined from Florida, Georgia, Mississippi (one specimen), North Carolina (one specimen), and Texas. Specimens from Mexico, Puerto Rico, Cuba, Haiti, Dominican Republic, British Honduras, Panama, Guatemala, Costa Rica, Surinam, Colombia, Brazil, Ecuador, Peru, Bolivia, and Paraguay have also been examined. Host data taken from labels include *Flaveria linearis* Laq., *Panicum purpurascens* Raddi, *P. barbinode* Trin., and Johnson grass. *F. linearis* is a member of the family Compositae. Since grasses and sedge are considered to be the food hosts of *Balclutha* species, there is some question about the authenticity of this plant as a food host.

B. hebe (Kirkaldy) appears to be related to *B. guajanae* (DeLong) but can be easily distinguished by the three pairs of processes arising from the base of the aedeagus in *hebe*.

Balclutha floridana (DeLong and Davidson)

FIGURE 22

Eugnathodus floridana DeLong and Davidson, 1933a, Ohio Journ. Sci., vol. 33, p. 56.

Nesosteles marquesana Osborn, 1934, Bull. Bernice P. Bishop Mus., vol. 114, p. 265.

Length of male 2.5 to 3.4 mm, of female 2.5 to 3.5 mm; head width of male .625 to .775 mm, of female .625 to .825 mm; pronotal width of male .625 to .750 mm, of female .600 to .800 mm.

Head as wide as or wider than pronotum; vertex as long next to eye as medially or occasionally slightly longer medially, interocular width more than three times median length; ocellus located at a distance of from less than to equal to its diameter from eye; anteclypeus widest apically, exceeding gena; postclypeal sutures usually parallel above antennal pits; pronotum three times as long as vertex; hind femoral chaetotaxy 2–1–1; female with posterior margin of abdominal sternum VII rounded posteriorly, slightly sinuate.

Male pygofer with less than 15 setae; plates triangular, apical half constricted, extending posteriorly as far as pygofer apex; connective wide, expanded apically and bifid, distinctive, approximately equal in length to style; style with preapical lobe rounded, apical extension slightly curved and acute apically, anterior margin oblique; aedeagus with shaft long and slender, curved sharply dorsally then anteriorly, commonly extending into abdominal segment VIII.

Color from light green to stramineous; face without oblique brown lines; thoracic venter not dark; forewings hyaline to subhyaline commonly tinted as body color.

The male holotype, La Belle, Fla., Apr. 21, 1921, is in the DeLong collection and has been examined. This species is commonly found in tropical and subtropical areas. Specimens have been examined from Florida, Georgia, South Carolina, Texas, Mexico, Puerto Rico, Cuba, Haiti, Dominican Republic, Jamaica, British Honduras, Panama, Guatemala, Brazil, Ecuador, and Peru.

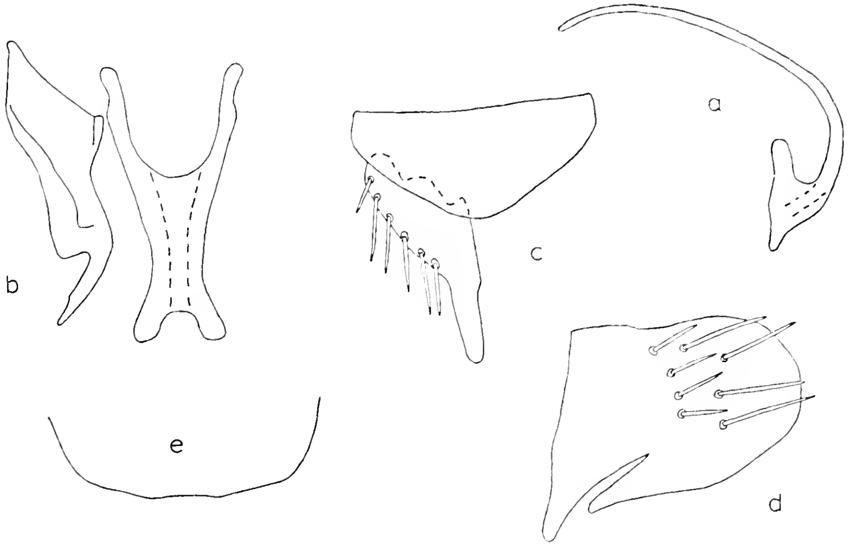

Figure 22.—*B. floridana: a*, aedeagus, lateral view; *b*, style and connective, dorsal view; *c*, valve and plate, ventral view; *d*, male pygofer, lateral view; *e*, female abdominal sternum VII, ventral view.

B. floridana (DeLong and Davidson) is related to *B. fuscina*, new species, but can be distinguished by the absence of processes on the shaft of the aedeagus and by the head width which is as wide as or wider than the pronotum in *floridana*.

Balclutha neglecta (DeLong and Davidson)

Figure 23

Eugnathodus neglecta DeLong and Davidson, 1933a, Ohio Journ. Sci., vol. 33, p. 55.

Length of male 2.8 to 3.8 mm, of female 3.2 to 4.0 mm; head width of male .675 to .875 mm, of female .775 to .900 mm; pronotal width of male .675 to .875 mm, of female .725 to .925 mm.

Head as wide as or wider than pronotum; vertex usually as long next to eye as medially (longer medially in some specimens), interocular width more than three times median length; ocellus variable, located at a distance of from less than to greater than its diameter from eye; anteclypeus parallel margined, apex attaining or exceeding gena slightly; postclypeal sutures curved mesally above antennal pits; pronotum three times as long as vertex; hind femoral chaetotaxy 2–1–1; female with posterior margin of abdominal sternum VII irregularly truncate or slightly convex posteriorly, with or without a small median projection, with a heavily sclerotized band across posterior margin.

Male pygofer not heavily setose; plates slender; triangular; connective expanded apically and truncate, approximately equal in length to style, stem slightly longer than arms which diverge at approximately 45 degrees; style with preapical lobe rounded, apical extension only slightly curved and rounded apically; aedeagus with preatrium conspicuous, curved ventrally only slightly if at all, shaft with apical two-thirds curved dorsally.

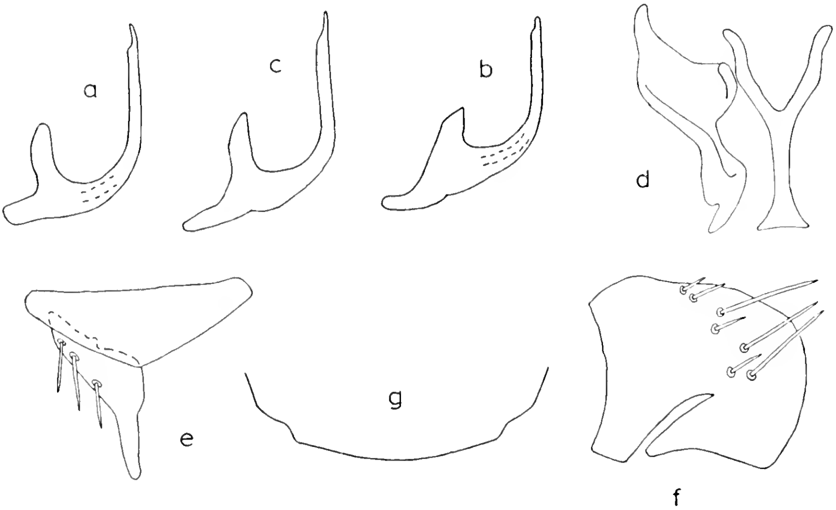

FIGURE 23.—*B. neglecta: a–c*, aedeagus, lateral view; *d*, style and connective, dorsal view; *e*, valve and plate, ventral view; *f*, male pygofer, lateral view; *g*, female abdominal sternum VII, ventral view.

Color light brown; face with or without oblique brown lines on each side of midline; pronotum commonly with brown longitudinal lines; thoracic venter dark; scutellum commonly with faint orange areas; forewings hyaline to subhyaline, usually with a tan tint; abdominal dorsum dark.

The male holotype from Mount Manitou, Mont., is in the DeLong collection and has been examined. This is a widespread species, and specimens have been examined from Arizona, California, Colorado, Florida, Idaho, Iowa, Kansas, Mississippi, Missouri, Montana, Nebraska, Nevada, New Mexico, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, South Dakota, Texas, Utah, Washington, Wisconsin, Wyoming, Ontario, and Manitoba. Other material examined was from Mexico, Puerto Rico, Panama, Ecuador, Peru, and Chile.

B. neglecta (DeLong and Davidson) is closely related to *B. aridula* Linnavuori from which it can be distinguished by the curvature of the aedeagus (see key).

Balclutha aridula Linnavuori

FIGURE 24

Balclutha aridula Linnavuori, 1959, Ann. Zool. Soc. 'Vanamo,' vol. 20, p. 344.

Length of male 2.8 to 3.5 mm, of female 3.1 to 3.8 mm; head width of male .700 to .850 mm, of female .750 to .900 mm; pronotal width of male .675 to .825 mm, of female .725 to .900 mm.

Head as wide as or wider than pronotum; vertex as long next to eye as medially or slightly longer medially, interocular width approximately three times median length; ocellus located at a distance of from 1 to 1½ times its diameter from eye; anteclypeus parallel sided, exceeding gena; postclypeal sutures usually curved mesally above antennal pits; pronotum with length varying from slightly less than to 3 times as long as vertex; hind femoral chaetotaxy 2–1–1, female with posterior margin of abdominal sternum VII shallowly concave, with a heavily sclerotized band extending along posterior margin.

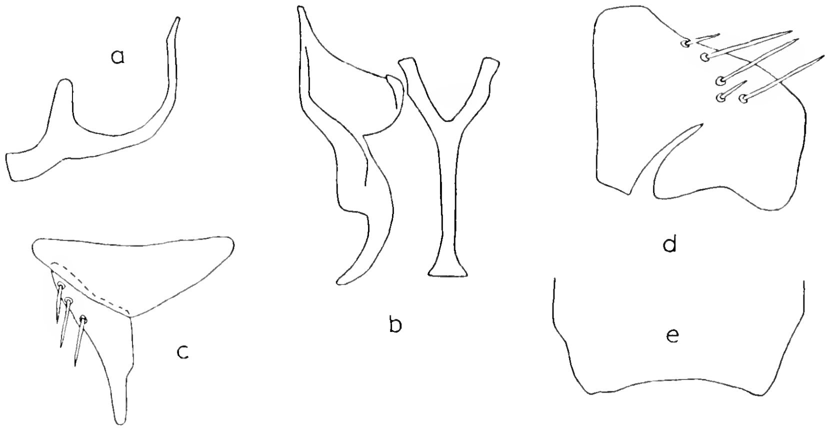

FIGURE 24.—*B. aridula*: *a*, aedeagus, lateral view; *b*, style and connective, dorsal view; *c*, valve and plate, ventral view; *d*, male pygofer, lateral view; *e*, female abdominal sternum VII, ventral view.

Male pygofer and plates as *B. neglecta;* connective expanded apically and truncate, slightly shorter than style, stem approximately twice as long as arms; style with preapical lobe and apical extension rounded; aedeagus with preatrium prominent, curved ventrally then anteriorly, shaft extending posteriorly for more than one-half its length, then curved dorsally, tapered at apex.

Color from brown to greenish yellow; face commonly with oblique brown lines on each side of midline; head and pronotum commonly with longitudinal brown stripes and/or orange areas on dorsal surface; thoracic venter dark; forewings hyaline to subhyaline.

The female holotype in the Hungarian Natural History Museum, Budapest, and a male paratype from the collection of R. Linnavuori have been examined. A large number of additional specimens have been examined from Chile, Peru, and some from Costa Rica.

B. aridula Linnavuori is closely related to *B. neglecta* (DeLong and Davidson) but can be distinguished by the shape of the preatrium of the aedeagus and by the curvature of the shaft (see key).

***Balclutha cochrani*, new species**

Figure 25

Length of male 3.1 to 3.2 mm, of female 3.4 to 3.6 mm; head width of male .850 mm, of female .875 to .950 mm; pronotal width of male .800 mm, of female .825 to .875 mm.

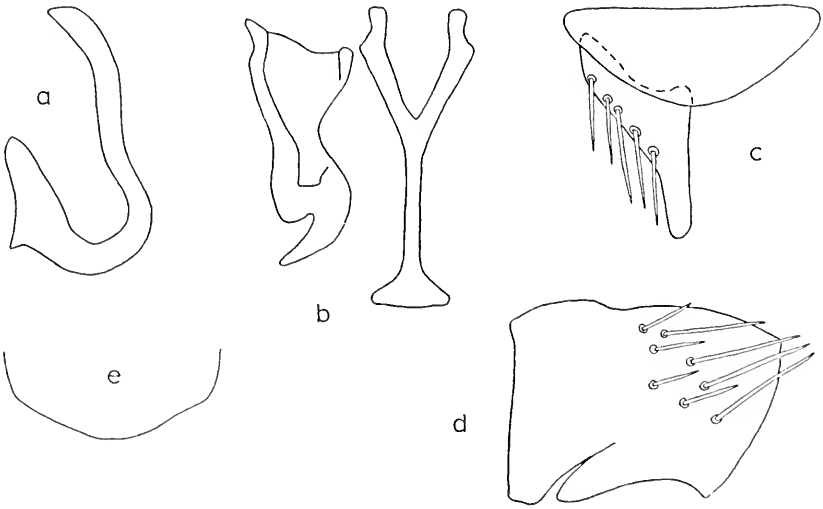

Figure 25.—*B. cochrani: a,* aedeagus, lateral view; *b,* style and connective, dorsal view; *c,* valve and plate, ventral view; *d,* male pygofer, lateral view; *e,* female abdominal sternum VII, ventral view.

Head wider than pronotum; vertex slightly longer medially than next to eye, interocular width slightly less than three times median length; ocellus located at a distance of from 1 to 1½ times its diameter from eye; anteclypeus slightly widened apically, not exceeding gena; postclypeal sutures curved mesally above antennal pits; pronotum less than 3 times as long as vertex; hind femoral chaetotaxy 2–1–1; female with posterior margin of abdominal sternum VII irregularly convex posteriorly.

Male pygofer with less than 10 setae, posteroventral margin projected ventrally; plates broadly triangular, not extending as far as pygofer apex; connective expanded apically, truncate, longer than style, stem longer than arms; style with preapical lobe rounded, apical extension slightly curved, tapered, rounded apically; aedeagus with dorsal apodeme curved anteriorly, shaft broad in lateral view, curved ventrally then dorsally.

Color stramineous; face without oblique brown lines; thoracic venter not dark, forewings hyaline with stramineous tint.

Holotype and paratype males, Pese, Panama, Oct. 22, 1952 (F. S. Blanton), in the U.S. National Museum. This species was described from these two specimens and five female specimens with the same data.

B. cochrani, new species, is apparently closely related to *B. neglecta* (DeLong and Davidson) but can be distinguished by the curvature and width of the aedeagus and its inconspicuous preatrium (see key). This species was named in honor of Dr. James H. Cochran, head of the Department of Entomology and Zoology at Clemson University, who guided the author through his early career as an entomologist and remains a faithful friend.

***Balclutha denticula*, new species**

FIGURE 26

Length of male 2.7 mm; head width .775 mm; pronotal width .750 mm; female unknown.

Head wider than pronotum; vertex as long next to eye as medially, interocular width more than three times median length; ocellus located at a distance less than its diameter from eye; anteclypeus parallel margined, slightly exceeding gena; postclypeal sutures curving mesally above antennal pits; pronotum three times as long as vertex; hind femoral chaetotaxy 2–1–1.

Male pygofer with less than 10 setae, exceeding plates in length; plates broadly triangular, apical one-fourth constricted; connective approximately equal in length to style, stem and arms equal in length; style with preapical lobe acute, apical extension slightly curved, acute apically; aedeagus with a pair of processes arising ventrally at base, curved dorsally and overlapping shaft, dentate on posterior margin, shaft slender, curving anteriorly, rounded apically.

Color tan; face with faint oblique brown lines on each side of midline; thoracic venter dark.

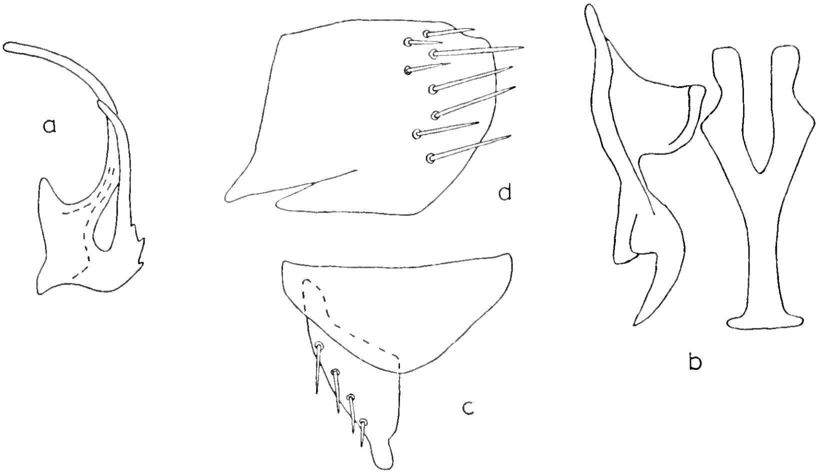

Figure 26.—*B. denticula: a,* aedeagus, lateral view; *b,* style and connective, dorsal view; *c,* valve and plate, ventral view; *d,* male pygofer, lateral view.

Holotype male, Pese, Panama, Oct. 22, 1952 (F. S. Blanton) in the U.S. National Museum. This species was described from this single specimen.

B. denticula, new species, appears to be related to *B. cochrani,* new species, but can be readily distinguished by the dentate aedeagal processes in *denticula.*

Balclutha lineata **(Osborn)**

Figure 27

Eugnathodus lineatus Osborn, 1925, Ann. Carnegie Mus., vol. 15, p. 449.
Eugnathodus flavidus Osborn, 1926, Ann. Ent. Soc. America, vol. 19, p. 351.

Length of male 2.7 to 3.2 mm, of female 3.0 to 3.6 mm; head width of male .750 to .800 mm, of female .800 to .900 mm; pronotal width of male .700 to .775 mm, of female .775 to .875 mm.

Head wider than pronotum; vertex longer medially than next to eye, interocular width from less than to approximately three times median length; ocellus located at a distance less than its diameter from eye; anteclypeus widest apically, exceeding gena; postclypeal sutures parallel above antennal pits; pronotum less than three times as long as vertex; hind femoral chaetotaxy 2–1–1 or 2–2–1; female with posterior margin of abdominal sternum VII irregularly concave.

Male pygofer with less than 15 setae; plates broadly triangular, elongate apically; connective expanded and bifid apically, equal in length to style, stem and arms nearly equal in length; style with preapical lobe rounded, apical extension tapered slightly, rounded apically; aedeagus with dorsal apodeme prominent, shaft robust, curved dorsally then anteriorly then ventrally, apical one-fourth constricted, shaft in dorsal view with apical one-fourth expanded, bifid apically.

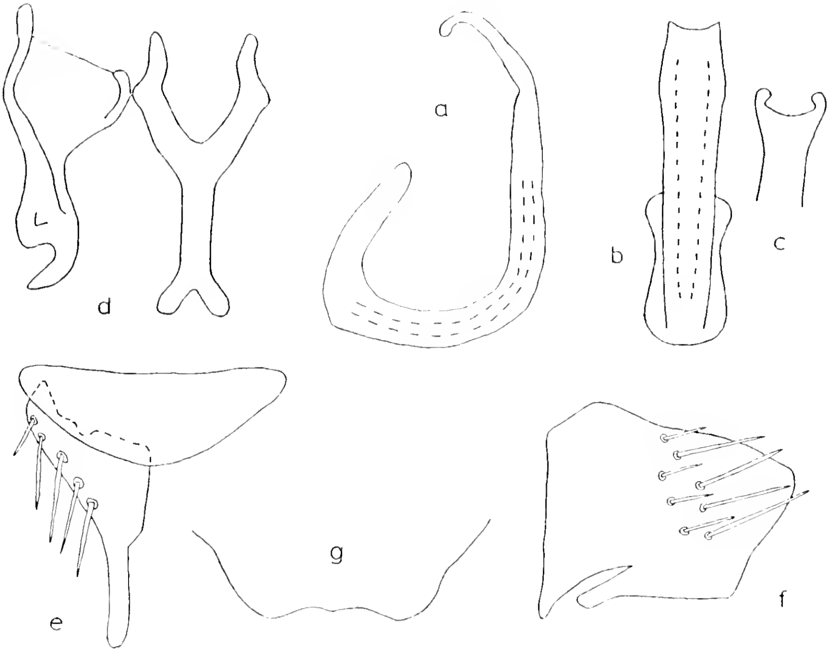

Figure 27.—*B. lineata:* *a*, aedeagus, lateral view; *b*, aedeagus, posteroventral view; *c*, aedeagal shaft apex, dorsal view; *d*, style and connective, dorsal view; *e*, valve and plate, ventral view; *f*, male pygofer, lateral view; *g*, female abdominal sternum VII, ventral view.

Color stramineous; face without oblique brown lines; vertex, pronotum, and scutellum irregularly marked with bright yellow stripes or other markings; legs brown in color; forewings subhyaline, marked irregularly with yellow bands, third apical cell with costal half marked with a heavy brown stripe which commonly extends into anteapical cell area.

The holotype has not been located. The female holotype of *E. flavidus* Osborn has been examined and is in the U.S. National Museum. A long series of specimens has been examined from Panama and British

Honduras. Specimens from Mexico and Cuba have also been examined. This species has also been reported from Bolivia (type locality) and Puerto Rico.

B. lineata (Osborn) appears to be related to *B. guajanae* (DeLong) but can be easily distinguished by the shape and curvature of the aedeagus (see key). The external color markings on the forewings and the brown color of the legs are also usually diagnostic.

***Balclutha chiasma*, new species**

FIGURE 28

Length of male 3.1 to 3.3 mm; head width .800 mm; pronotal width .775 to .800 mm; female unknown.

Head as wide as or wider than pronotum; vertex as long next to eye as medially, interocular width more than three times median length; ocellus located at a distance less than its diameter from eye; anteclypeus parallel margined or slightly wider apically, exceeding gena slightly; postclypeal sutures curving mesally above antennal pits; pronotum more than three times as long as vertex; hind femoral chaetotaxy 2–1–1.

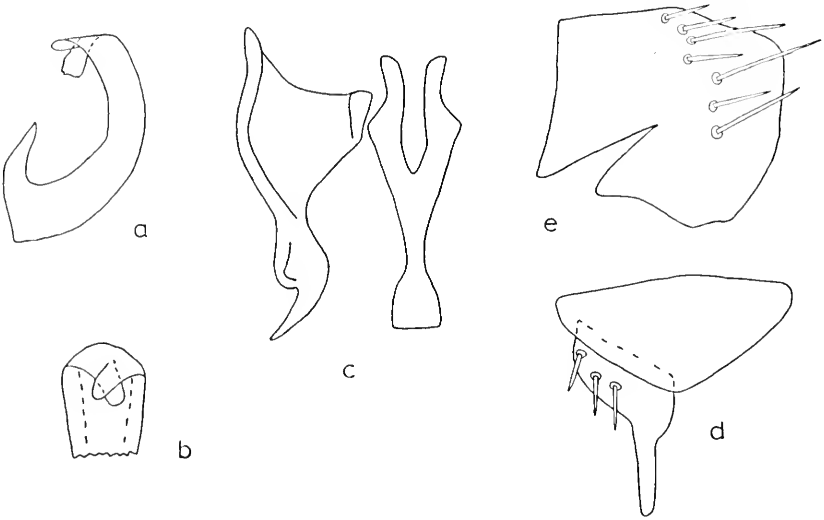

FIGURE 28.—*B. chiasma: a*, aedeagus, lateral view; *b*, aedeagus, dorsal view; *c*, style and connective, dorsal view; *d*, valve and plate, ventral view; *e*, male pygofer, lateral view.

Male pygofer with less than 10 setae; plates slender, triangular; connective expanded apically and truncate, slightly shorter than style, stem slightly longer than arms; style with preapical lobe rounded, apical extension slightly curved, acute apically; aedeagus with dorsal apodeme prominent, curved posteriorly, shaft broad in lateral view, apex forming two lobes which overlap diagonally.

Color stramineous to light brown; face with faint trace of oblique brown lines on each side of midline; thoracic venter dark; forewings hyaline with yellowish brown tint.

Holotype and paratype males from Fortin, V. C. [E. Mexico], Oct. 9, 1941 (DeLong, Good, Caldwell, and Plummer). This species was described from these two specimens. Holotype in the DeLong collection.

B. chiasma, new species, appears to be related to *B. lineata* (Osborn) but can be readily distinguished by the shorter shaft and the overlapping lobes at the apex of the aedeagus in *chiasma*.

Balclutha flavescens **(Baker)**

FIGURE 29

Eugnathodus flavescens Baker, 1903, Invert. Pacifica, vol. 1, p. 2.

Eugnathodus virescens Osborn, 1926, Ann. Ent. Soc. America, vol. 19, p. 351. [New synonymy.]

Eugnathodus abbreviata DeLong and Davidson, 1933a, Ohio Journ. Sci., vol. 33, p. 57.

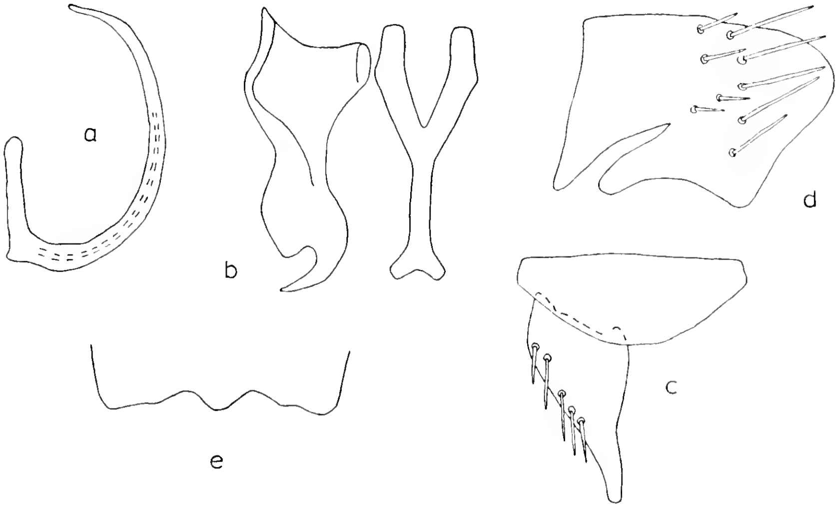

FIGURE 29.—*B. flavesciens: a*, aedeagus, lateral view; *b*, style and connective, dorsal view; *c*, valve and plate, ventral view; *d*, male pygofer, lateral view; *e*, female abdominal sternum VII, ventral view.

Length of male 2.5 to 2.8 mm, of female 2.8 to 3.2 mm; head width of male .700 to .750 mm, of female .725 to .850 mm; pronotal width of male .675 to .725 mm, of female .700 to .800 mm.

Head wider than pronotum; vertex as long next to eye as medially or slightly longer medially, interocular width more than three times median length; ocellus located at a distance equal to or slightly more than its diameter from eye; anteclypeus slightly wider apically, not exceeding gena; postclypeal sutures parallel above antennal pits; pronotum from slightly less than to three times as long as vertex; hind femoral chaetotaxy 2–1–1 or 2–2–1; female with posterior margin of abdominal sternum VII sinuate posteriorly, with a rounded median lobe.

Male pygofer not heavily setose, with a small lobe on posteroventral margin; plates broadly triangular; connective expanded apically and bifid, approximately equal in length to style, stem slightly longer than arms which diverge at approximately 30 degrees; style with preapical lobe rounded, apical extension strongly curved laterally, acute apically; aedeagus with dorsal apodeme prominent, shaft evenly curved dorsally then ventrally, gradually tapered, rounded apically.

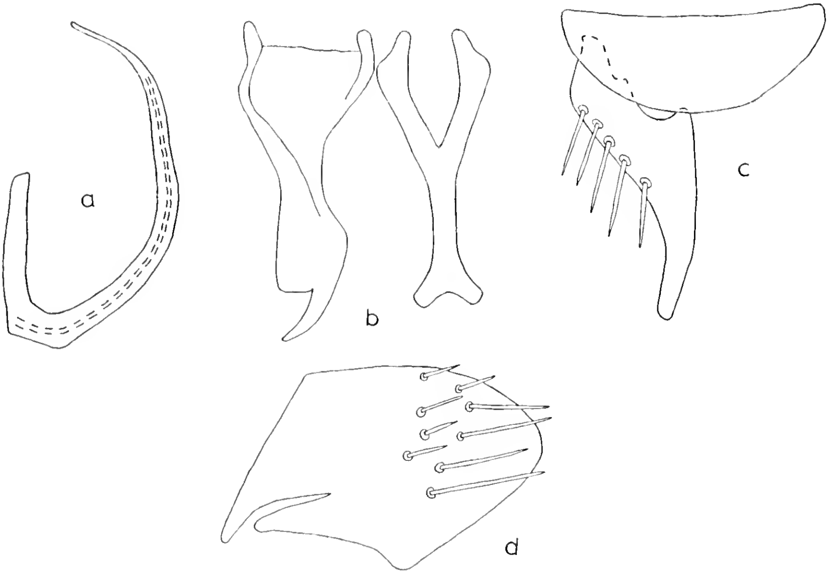

Figure 30.—*B. robusta: a,* aedeagus, lateral view; *b,* style and connective, dorsal view; *c,* valve and plate, ventral view; *d,* male pygofer, lateral view.

Color stramineous to light green; face without oblique brown lines; thoracic venter not dark; forewings hyaline to subhyaline, usually tinted as body color.

All efforts to locate the holotype of *B. flavescens* (Baker) have been unsuccessful. The descriptions of Baker (1903) and Osborn (1926) can be, in the opinion of the author, applied to several taxa. Linnavuori (1959) included an illustration of an aedeagus with his description, and his interpretation of this species is followed here. The female holotype of *E. virescens* in the U.S. National Museum and male holotype of *E. abbreviata* in the DeLong collection have been examined.

B. flavescens (Baker) is very closely related to *B. robusta* (Caldwell) and *B. curvata* Caldwell but can be distinguished by the shape of the aedeagus and less accurately by characters on the styles and connective (see key).

Balclutha robusta (Caldwell)

FIGURE 30

Nesosteles robusta Caldwell, 1952, *in* Caldwell and Martorell, Journ. Dept. Agric. Porto Rico, vol. 34, p. 85.

Length of male 2.7 to 3.7 mm; head width .750 to .850 mm; pronotal width .725 to .850 mm; female measurements not included.

Head as wide as or wider than pronotum; vertex as long next to eye as medially or slightly longer medially, interocular width approximately three times median length; ocellus located at a distance approximately equal to its diameter from eye; anteclypeus widest apically, not exceeding gena; postclypeal sutures slightly curved mesally above antennal pits; pronotum approximately three times as long as vertex; hind femoral chaetotaxy 2–2–1.

Male pygofer and plates as *B. flavescens;* connective expanded apically and bifid, slightly shorter than style, stem and arms approximately equal in length; style with preapical lobe rounded, apical extension arising from dorsum and extending ventrolaterally; aedeagus with dorsal apodeme prominent, shaft unevenly curved, tapered, rounded apically.

Color stramineous; face without oblique brown lines; thoracic venter not dark; forewings hyaline to subhyaline.

The male holotype, Puerto Rico, in the U.S. National Museum has been examined. Additional material examined was from Mexico, British Honduras, Panama, Puerto Rico, Colombia, Peru, Brazil, and Paraguay.

B. robusta (Caldwell) is very closely related to *B. flavescens* (Baker), and the differences are often subtle. The preapical lobe of the style is more evenly rounded in *robusta;* the aedeagus is less evenly curved and longer than in *flavescens*. The characters of sternum VII in the female have been described by Caldwell (1952) and Linnavuori (1959), but the author has not definitely identified females of this species.

Balclutha curvata Caldwell

FIGURE 31

Balclutha curvata Caldwell, 1952 *in* Caldwell and Martorell, Journ. Dept. Agric. Porto Rico, vol. 34, p. 81.

Length of male 2.7 to 2.9 mm; head width .750 to .850 mm; pronotal width .700 to .775 mm; female measurements not included.

Head wider than pronotum; vertex as long next to eye as medially or slightly longer medially, interocular width approximately three times median length; ocellus located at a distance approximately equal to its diameter from eye; anteclypeus slightly wider apically, not exceeding gena; postclypeal sutures parallel above antennal pits; pronotum usually less than three times as long as vertex; hind femoral chaetotaxy 2–1–1 or 2–2–1.

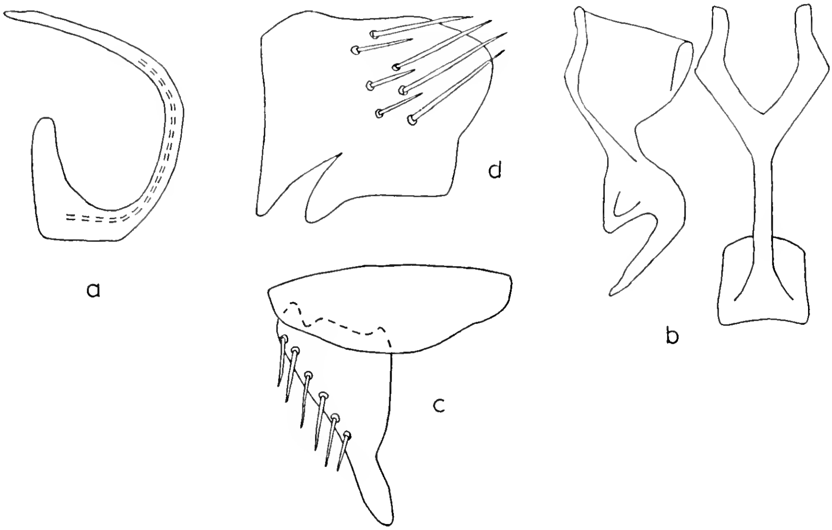

FIGURE 31.—*B. curvata: a,* aedeagus, lateral view; *b,* style and connective, dorsal view; *c,* valve and plate, ventral view; *d,* male pygofer, lateral view.

Male pygofer and plates as *B. flavescens;* connective expanded apically, truncate, apex rectangular, slightly longer than style, stem slightly longer than arms; style with preapical lobe forming approximately a 45° angle, apical extension tapered, acute apically; aedeagus with dorsal apodeme prominent, approximately one-third as long as shaft which is regularly but strongly curved anteriorly.

Color light green to stramineous; face without oblique brown lines on each side of midline or faint if present; thoracic venter not dark; forewings hyaline to subhyaline.

The male holotype, Puerto Rico, in the U.S. National Museum has been examined. Other specimens examined were from Florida, Puerto Rico, Panama, and Surinam.

B. curvata Caldwell is very closely related to *B. flavescens* (Baker) but can be distinguished by several characters. The preapical lobe of the style forms a more acute angle; the apex of the connective is rectangular and truncate; and the aedeagus is more strongly curved anteriorly in *curvata.*

Balclutha knulli (Davidson and DeLong), new combination

FIGURE 32

Agellus knulli Davidson and DeLong, 1935, Proc. Ent. Soc. Washington, vol. 37, p. 109.

Length of male 2.9 to 3.0 mm, of female 2.8 to 3.1 mm; head width of male .800 to .825 mm, of female .800 to .825 mm; pronotal width of male .725 to .775 mm, of female .750 to .800 mm.

Head wider than pronotum; vertex usually as long next to eye as medially or slightly longer medially, interocular width approximately three times median length; ocellus located at a distance aprpoximately equal to its diameter from eye; anteclypeus slightly wider apically, not exceeding gena; postclypeal sutures parallel above antennal pits; pronotum with length from slightly less to three times length of vertex;

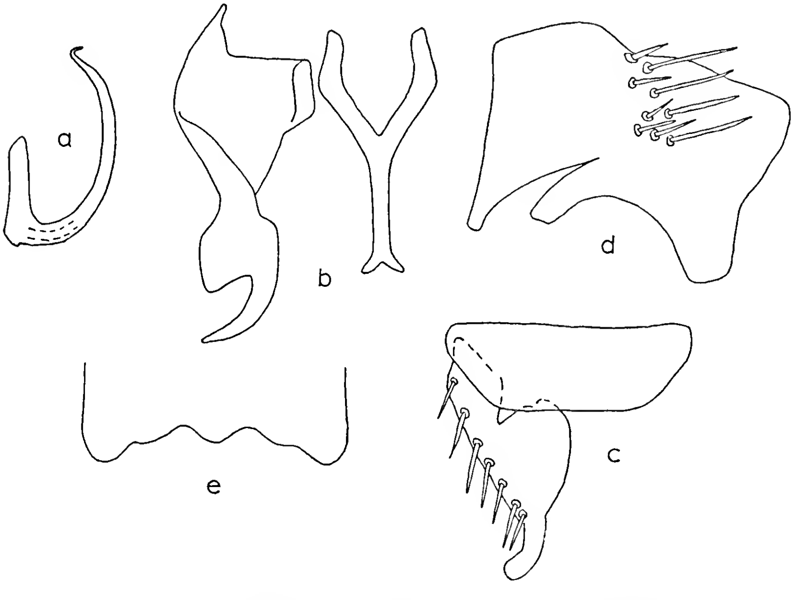

FIGURE 32.—*B. knulli:* *a,* aedeagus, lateral view; *b,* style and connective, dorsal view; *c,* valve and plate, ventral view; *d,* male pygofer, lateral view; *e,* female abdominal sternum VII, ventral view.

hind femoral chaetotaxy 2–1–1; female with posterior margin of abdominal sternum VII irregularly concave, with a rounded median lobe.

Male pygofer with posteroventral margin bearing a broad lobe which is bisected by a heavily sclerotized discal band extending obliquely almost to ventral margin, less than 15 setae present; plates broadly triangular, apical one-third curved dorsally; connective expanded apically and bifid, two-thirds length of style, stem and arms nearly equal in length, style with preapical lobe rounded, apical extension curved laterally, gradually tapered and rounded apically; aedeagus with dorsal apodeme one-half length of shaft which is regularly curved anteriorly, narrowed apically, and recurved posteriorly.

Color stramineous; face without oblique brown lines (faint trace in some females); thoracic venter not dark; forewings hyaline with tan tint.

The male holotype from Brownsville, Tex., in the DeLong collection has been examined. Additional material examined was from Texas (Mar. and June), Panama (Sept. and Oct.), and Cuba (Feb. and Mar.).

B. knulli (Davidson and DeLong) appears to be related to *B. incisa* (Matsumura) and *B. neglecta* (DeLong and Davidson) but can be readily distinguished by the recurved apex of the aedeagus and the shape of the pygofer of *knulli*.

Balclutha sandersi **(Davidson and DeLong), new combination**

FIGURE 33

Agellus sandersi Davidson and DeLong, 1935, Proc. Washington Ent. Soc., vol. 37, p. 108.

Nesosteles sandersi dubiata Caldwell, 1952, *in* Caldwell and Martorell, Journ Dept. Agric. Porto Rico, vol. 34, p. 87.

Length of male 2.7 to 3.7 mm, of female 3.2 to 3.8 mm; head width of male .650 to .825 mm, of female .750 to .825 mm; pronotal width of male .650 to .800 mm, of female .750 to .850 mm.

Head as wide as or wider than pronotum; vertex as long next to eye as medially or slightly longer medially, interocular width three times median length; ocellus located at a distance more than twice its diameter from eye; anteclypeus wider apically, exceeding gena; postclypeal sutures parallel above antennal pits; pronotum three times as long as vertex; hind femoral chaetotaxy 2–2–1; female with posterior margin of abdominal sternum VII truncate or shallowly concave.

Male pygofer with less than 15 setae, posteroventral margin with slight projection; plates extending posteriorly as far as pygofer apex, rounded apically; connective expanded apically and bifid, slightly longer than style, stem and arms approximately equal in length; style with preapical lobe rounded, apical extension slightly curved, tapered, rounded apically; aedeagus with dorsal apodeme and preatrium absent or inconspicuous, ventral margin produced basally, curved dorsally then anteriorly, shaft slender.

The male holotype, Gamboa, Canal Zone, in the DeLong collection has been examined. The holotype of *N. sandersi dubiata*, Puerto Rico, in the U.S. National Museum has also been examined. Additional specimens examined were from Mexico, Puerto Rico, British Honduras, Panama, and Chile.

B. sandersi (Davidson and DeLong) appears to be closely related to *B. incisa* (Matsumura) but can be distinguished by the connective which is bifid apically in *sandersi* and by the shape of the aedeagus (see key). Linnavuori (1959) listed *B. sandersi* and *N. sandersi dubiata* as synonyms of *B. incisa*.

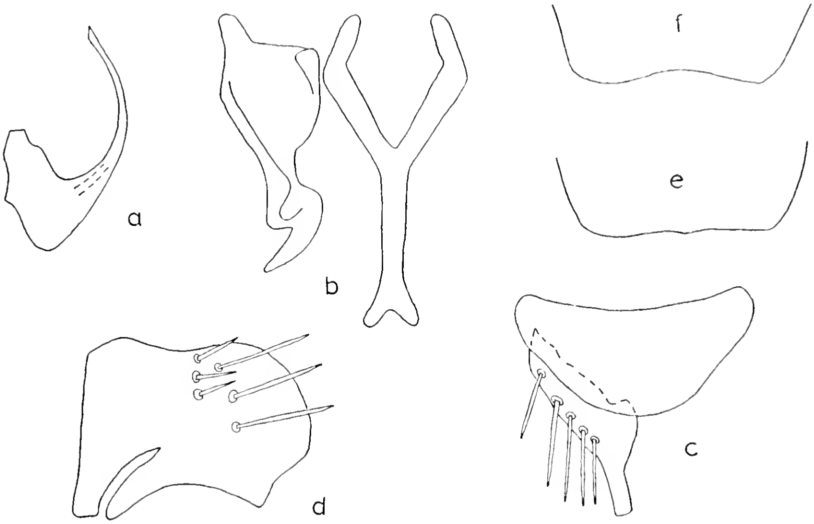

FIGURE 33.—*B. sandersi*: *a*, aedeagus, lateral view; *b*, style and connective, dorsal view; *c*, valve and plate, ventral view; *d*, male pygofer, lateral view; *e*, *f*, female abdominal sternum VII, ventral view.

Balclutha incisa (Matsumura)

FIGURE 34

Gnathodus incisus Matsumura, 1902, Természetr. Füzetek, vol. 25, p. 360.
Eugnathodus lacteus Baker, 1903, Invert. Pacifica, vol. 1, p. 2.
Eugnathodus minutus Osborn, 1929, Journ. Dept. Agric. Porto Rico, vol. 13. p. 101. [New synonymy.]
Eugnathodus neglecta var. *pallida* DeLong and Davidson, 1933a, Ohio Journ. Sci., vol. 33, p. 56. [New synonymy.]

Length of male 2.4 to 3.4 mm, of female 2.6 to 3.3 mm; head width of male .625 to .775 mm, of female .700 to .775 mm; pronotal width of male .600 to .750 mm, of female .625 to .750 mm.

Head as wide as or wider than pronotum; vertex as long next to eye as medially, interocular width more than three times median length; ocellus located at a distance approximately one-half its diameter from eye; anteclypeus parallel sided, equal to or slightly exceeding gena apically; postclypeal sutures conspicuously curved mesally above antennal pits; pronotum more than three times as long as vertex; hind femoral chaetotaxy 2–1–1; female with posterior margin of abdominal sternum VII sinuate posteriorly, with a median tooth.

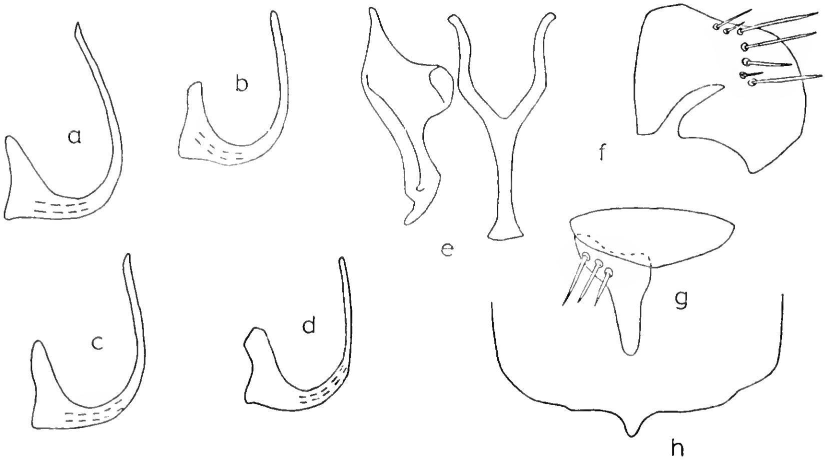

FIGURE 34.—*B. incisa: a–d*, aedeagus, lateral view; *e*, style and connective, dorsal view; *f*, male pygofer, lateral view; *g*, valve and plate, ventral view; *h*, female abdominal sternum VII, ventral view.

Male pygofer and plates as *B. neglecta;* connective expanded apically and truncate; approximately equal in length to style, stem and arms approximately equal in length; style with preapical lobe rounded, apical extension strongly curved laterally, rounded apically; aedeagus with no preatrium, shaft slender with apical two-thirds curved dorsally, rounded apically.

Color from green to stramineous to tan; face with or without oblique brown lines on each side of midline; pronotum commonly with dark longitudinal lines present; forewings usually hyaline, tinted as body color; thoracic venter commonly dark; abdomen with dorsum commonly dark.

The holotype has not been located, but it is probably in the Matsumura collection. Male paratypes of *E. minutus* Osborn and the male holotype of *E. neglecta* var. *pallida* DeLong and Davidson in the DeLong collection have been examined. Specimens have been examined from Arizona, Arkansas, Florida, Georgia, Kansas, Michigan, Mississippi, New Mexico, New York, North Carolina, Oklahoma, South Carolina, Tennessee, and Texas. Other specimens examined were from Mexico, Barbados, Puerto Rico, Trinidad Island, Panama, Guatemala, Colombia, Brazil, Ecuador, Peru, and Argentina. This species is reported from Japan and Oceania.

B. incisa (Matsumura) is closely related to *B. neglecta* (DeLong and Davidson) and to *B. diluta*, new species, but can be readily distinguished by the shape of the aedeagus (see key).

***Balclutha diluta*, new species**

FIGURE 35

Length of male 3.0 to 3.3 mm, of female 3.0 to 3.3 mm; head width of male .750 to .775 mm, of female .750 to .850 mm; pronotal width of male .725 to .800 mm, of female .750 to .800 mm.

Head as wide as or wider than pronotum; vertex no longer medially than next to eye, interocular width more than three times median length; ocellus located at a distance of from less than to equal to its diameter from eye; anteclypeus parallel sided, slightly exceeding gena; postclypeal sutures curved mesally above antennal pits; pronotum more than three times as long as vertex; hind femoral chaetotaxy 2–1–1; female with posterior margin of abdominal sternum VII sinuate posteriorly, with a slightly produced median tooth.

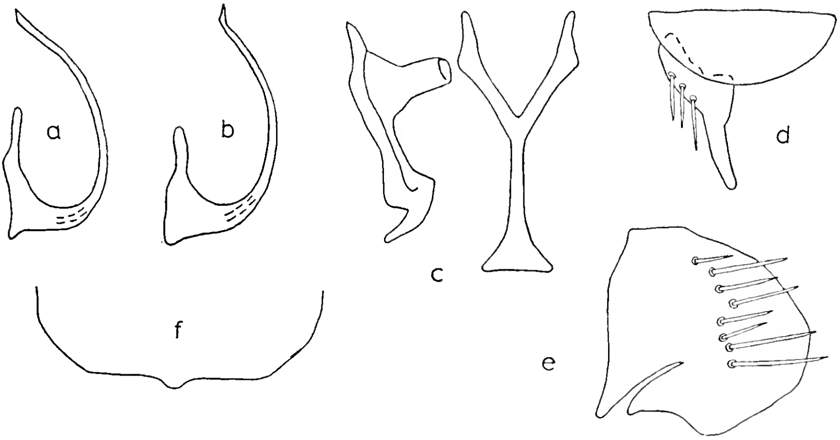

FIGURE 35.—*B. diluta: a, b*, aedeagus, lateral view; *c*, style and connective, dorsal view; *d*, valve and plate, ventral view; *e*, male pygofer, lateral view; *f*, female abdominal sternum VII, ventral view.

Male pygofer and plates as *B. neglecta;* connective expanded apically and truncate, equal to or slightly longer than style, stem slightly longer than arms; style with preapical lobe rounded, apical extension rounded and strongly curved laterally; aedeagus with preatrium inconspicuous, shaft long and slender, curving dorsally then anteriorly, acute apically.

Color tan; face without oblique brown lines; thorax with pale orange areas on dorsal surface, venter dark; forewings hyaline to subhyaline.

Holotype male, Nov. 2, 1932, Texas City, Tex. (L. D. Tuthill), at the University of Kansas. The following additional specimens have been examined: two males, Texas (Nov.), one male, Arkansas (Aug.), one male, Oklahoma (Sept.), and three males, Argentina (Mar., Jan., and Dec.).

B. diluta, new species, is closely related to *B. incisa* (Matsumura) but can be readily distinguished by the shape of the aedeagus which is curved distinctly anteroventrally in *diluta.*

Balclutha rosacea (Osborn), new combination

Eugnathodus rosaceus Osborn, 1929, Journ. Dept. Agric. Porto Rico, vol. 13, p. 102.

Length of female 3.3 to 3.6 mm; head width .850 to .900 mm; pronotal width .775 to .850 mm; male unknown.

Head wider than pronotum; vertex longer medially than next to eye, interocular width distinctly less than three times median length; ocellus located at a distance of from 1 to 1½ times its diameter from eye; anteclypeus widest apically, not exceeding gena; postclypeal sutures curved mesally above antennal pits; pronotum distinctly less than 3 times as long as vertex; hind femoral chaetotaxy 2–2–1; female with posterior margin of abdominal sternum VII broadly rounded.

Color from light to dark red; forewings hyaline to subhyaline, irregularly tinted red, veins commonly dark red.

Paratypes from Aguirre, Puerto Rico (Feb.), from the collection of Ohio State University have been examined. The species is redescribed above from these and three other specimens from Guanajibe, Puerto Rico (Feb.), in the U.S. National Museum.

B. rosacea (Osborn) appears to be closely related to *B. guajanae* (DeLong) but can be distinguished by the uniform red body color of *rosacea.* This species is known only from the female sex.

Nomina Dubia

Baker (1903) described a number of taxa with only a short description of each in the form of a key. Five of these names have not been mentioned since, or their use has been included only in a species list with no further taxonomic clarification. These names are considered to be nomina dubia until such time as type material is found and studied, if it exists. These names are: *Gnathodus delicatus*, *G. tumidus*, *G. nevadensis*, *G. vermiculatus*, and *G. abdominalis* var. *nevadensis*.

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REVISION OF THE CIRCUMTROPICAL SHOREFISH GENUS ENTOMACRODUS (BLENNIIDAE: SALARIINAE)

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Introduction

This revision is one of a series of studies on tropical blennioid fishes, a group which has engaged my attention since 1952. The purpose of these studies is to clarify the systematics, relationships, and nomenclature of the families, genera, and species included in the group.

The genus *Entomacrodus* is worldwide in distribution and occurs along the rocky and coral reef shores of primarily tropical and subtropical seas. The species are small, shallow-water, and bottom-dwelling forms. Of the 22 species included in the genus, 5 are here described as new, and 1 was recently described by me (1966) as a result of my study. If the state of our knowledge of other blenniid fishes is similar to that of *Entomacrodus*, then approximately 30 percent of the species remain to be described.

No comprehensive study of the genus *Entomacrodus* has been made, although Chapman (1951) and Schultz and Chapman (1960) revised certain of the Indo-Pacific species. My study, based on all the specimens available to Schultz and Chapman, and a large number of additional specimens resulting from increased collecting in recent years, is considerably different from previous studies. This difference is due not only to the increased amount of material, but also to a reinterpretation of the published data and my employment of additional taxonomic characters.

A large number of individuals and institutions aided me by providing specimens or laboratory space. To these I am greatly indebted, for without their consideration my study could never have progressed this far. To the following institutions and their personnel, responsible for the assistance I received, I extend my sincere appreciation (abbreviations as indicated are used throughout the text):

AMNH	American Museum of Natural History, D. E. Rosen
AMS	Australian Museum, F. H. Talbot
ANSP	Academy of Natural Sciences of Philadelphia, J. E. Böhlke
BMNH	British Museum (Natural History), P. H. Greenwood, A. C. Wheeler
BPBM	Bernice P. Bishop Museum, E. H. Bryan, Jr., J. E. Randall
CAS	California Academy of Sciences, W. I. Follett, L. P. Dempster
CNHM	Chicago Natural History Museum [now Field Museum], L. P. Woods, P. Sonoda
CU	Cornell University, E. C. Raney
IFAN	Institut Français D'Afrique Noire, J. Cadenat
IRSN	Institut Royal des Sciences Naturelle de Belgique, J. P. Gosse
LACM	Los Angeles County Museum, D. K. Caldwell
MCZ	Museum of Comparative Zoology, G. Mead, M. Dick
MNHN	Museum National D'Histoire Naturelle, M. L. Bauchot
RMNH	Rijksmuseum van Natuurlijke Historie, M. Boeseman
RU	Rhodes University, Department of Ichthyology, J. L. B. Smith
SIO	Scripps Institution of Oceanography, R. H. Rosenblatt
SU	Stanford University, Division of Systematic Biology, G. S. Myers, W. C. Freihofer
UBC	University of British Columbia, N. J. Wilimovsky, I. E. Efford
UCC	University of Corpus Christi, H. H. Hildebrand
UCLA	University of California, Los Angeles, B. W. Walker, W. J. Baldwin
UF	University of Florida, C. R. Gilbert
UH	University of Hawaii, W. A. Gosline, R. H. Snider
UMML	University of Miami, Institute of Marine Science, C. R. Robins
UMMZ	University of Michigan, Museum of Zoology, R. M. Bailey
UPR	University of Puerto Rico, J. E. Randall
USNM	United States National Museum
UW	University of Washington, R. Van Cleave
UZMK	Universitetets Zoologiske Museum (Kobenhavn), J. Nielsen
WAM	Western Australian Museum, R. McKay
ZSZM	Zoologisches Staatsinstitut und Zoologisches Museum (Hamburg), C. Kosswig

Several individuals read either early drafts or portions of the manuscript. Their suggestions materially improved the presentation and my appreciation is extended to Drs. W. R. Taylor, J. S. Stephens, Jr., R. H. Rosenblatt, R. H. Gibbs, Jr., and W. A. Gosline.

I am especially indebted to Dr. W. A. Gosline for many valuable and stimulating discussions and suggestions concerning Pacific fish distributions. He also generously arranged with his students and colleagues in Hawaii for a collecting trip which provided significant material of the new Hawaiian species described below.

A trip to Dominica, B.W.I., sponsored by the Bredin-Archbold-Smithsonian Biological Survey of Dominica, afforded me the opportunity of collecting and observing *Entomacrodus nigricans* in the field. A large number of my central Pacific specimens of *Entomacrodus* were obtained through the efforts of the Smithsonian Pacific Biological Survey Program under the direction of Dr. P. S. Humphrey.

The drawings of the fishes were made by the following illustrators: Sharon L. Lesure (pls. 1, 2, 4–6, 8, 12–16, 18, 19, 21, 22, 25–30), Fanny L. Phillips (pls. 9, 11), Carolyn B. Gast (pls. 20, 24), and Peter McCrery (pl. 23).

Many aspects of my study were financially supported by a research award from the Smithsonian Institution.

Methods

Measurements.—When possible, I made all measurements on the left side of each specimen, using a pair of needlepoint dividers that were marked off on a ruler graduated in half millimeters. I estimated to the nearest tenth millimeter. Later in the study, a set of needlepoint dial calipers measuring directly to the nearest tenth millimeter was employed. Over 100 comparisons of the two methods of measuring were made; differences ranged from 0 to ±0.4 mm, the largest involving the longest measurements. These differences were not considered significant for the purpose of this study.

Tables of routine measurements are given for each taxon treated and are to be considered part of the description. In many instances there is no discussion of tabular material although the proportions frequently indicate significant changes correlated with standard length or indicate characters that show species differences. It will occasionally be necessary to compare all or many of these tables for a particular character (for example, caudal length) in order to note meaningful key characters for a species. For some characters (e.g., eye diameter, table 3, and supraorbital cirrus length, table 4), I have made many more measurements than are included in the tables of routine measurements.

Standard length (SL): Taken from the midtip of the upper lip to the midlateral posterior margin of the hypural vertebra as indicated externally on the specimen.

Head length (HL): Taken from the midtip of the upper lip to the posteriormost point reached by the fleshy margin of the opercle, exclusive of the branchiostegal membrane.

Orbital length (OL): The horizontal diameter between the fleshy rims of the orbit. This character decreases strikingly in relative size with increase in SL. The species vary noticeably from each other. I have attempted to illustrate this variation in table 3.

Supraorbital cirrus length (OCL): The distance from the lateral point where the base of the cirrus joins the conjunctiva of the eye to the most distal point reached by the cirrus (the cirrus thus measured is the main, or longest, supraorbital cirrus; other cirri on its margins are branches). This measurement and the next are taken while the cirri are wet (the cirri shrink considerably when dried even slightly).

Nuchal cirrus length (NCL): The longest measurement from the midbase of the cirrus to the distalmost tip of the cirrus. In those specimens where the nuchal cirri arise on each side from two separate bases, the measurement was made from that base supporting the longest cirrus.

Third dorsal spine length (DS3): From the proximalmost point of the posterior axil, formed by the spine with the body contour, to the distal tip of the spine, disregarding the normal curvature of the spine.

Thirteenth dorsal spine length (DS13): Similar to DS3.

First dorsal ray length (DR1): Similar to DS3.

Pectoral fin length (PECL): The length of the longest ray.

Pelvic fin length (PELL): Taken from the internal, proximalmost point of attachment of the fin to the body to the tip of the longest ray.

Caudal fin length (CL): The length of the longest ray.

Humeral blotch length (HBL): The longest horizontal distance between the anterior and posterior margins of this marking. Where this blotch is composed of two portions, the measurement is taken of the posterior marking.

Counts.—All counts of bilaterally paired structures were made on the left side of each specimen when possible. Where population or growth differences warrant it, I have given frequency distribution tables of the variation in particular counts. For the sake of convenience of species comparison I have also given summary tables of fin ray, vertebrae, gill-raker and pseudobranchial filament counts in which all the counts for a given character for a given species have been combined (tables 1 and 2).

Dorsal fin spines: A count of the bases of the unsegmented elements. The posteriormost spine (usually the 13th) is frequently visible only in skeletal preparations or on radiographs. This element when not obvious is assumed to be present when a space exists between the spinous and rayed portions of the fin greater than that separating the 11th and 12th dorsal spines.

Dorsal fin rays: A count of the bases of the segmented rays.

Anal fin rays: Two methods of counting the segmented anal rays are employed, method A and method B. In most specimens of most species the terminal "ray" consists of two elements, the posteriormost considerably reduced, closely applied to the next element anterior and difficult to see. Radiographs or skeletal preparations show that these two elements are supported by a single proximal pterygiophore; this condition is called "S" (split through base). In another condition (typical in some species), the terminal ray is removed from the next element anterior and the terminal proximal pterygiophore supports a single segmented ray; this condition is called "N" (not split). In method A counts, the split and unsplit conditions are not differentiated. Thus the two terminal elements, if supported by a single pterygiophore, or the terminal element, if supported separately, are counted as one. In method B counts, split elements are tallied as two. Method B counts, of course, will result in higher averages than method A counts. In those species which typically exhibit the S condition, individuals with counts one ray more than the modal value (using method A) usually prove to be of the N type. What has happened, then, is that a pterygiophore has been added at the end of the fin, and where the terminal pterygiophore normally supported two elements, the posteriormost element has become associated with the added pterygiophore (or conversely, a pterygiophore was lost and the posteriormost element has become associated with the next pterygiophore anterior). Determination of the N or S condition may be difficult with some specimens. I have checked several hundred of my determinations made externally on specimens with radiographs of the same specimens and found my error to be less than one percent.

The question arises as to which of the anal fin ray counts should be used for systematic purposes—method A or method B. In other words, should one count pterygiophores or fin rays? Unless otherwise noted, anal fin ray counts reported herein refer to method A counts. Method A counts are simplest to make, are those which have generally been employed in the literature of salarine blennies, and are the ones naturally made when uninstructed individuals count anal fin rays of salarines. Investigators who try to determine ecological effects on anal fin ray counts of salarine blenniids should test their data for both method A and method B type counts.

Vertebrae: Total count of centra including that of hypural vertebra, taken from radiographs. The caudal vertebrae are those which bear a haemal spine.

Superaorbital cirri: The number of free tips, all branches included, of the cirri above the eye. The cirri generally have a common transverse base. Counts of lateral or mesial cirri exclude the tip of the main or longest cirrus (see measurements above) and include only those cirri on the lateral or mesial margins of the main cirrus.

Nuchal cirri: The number of free tips, all branches included, of cirri on the side of the nape.

In some specimens (for example all *E. macrospilus*) the nuchal cirri are absent. The normal position for nuchal cirri can be recognized by the position of a pair of pores on each side of the nape. These pores lie on a slight transverse depression (constriction) which more or less separates the head from the body dorsally. In specimens with nuchal cirri the pores are just lateral to the cirri.

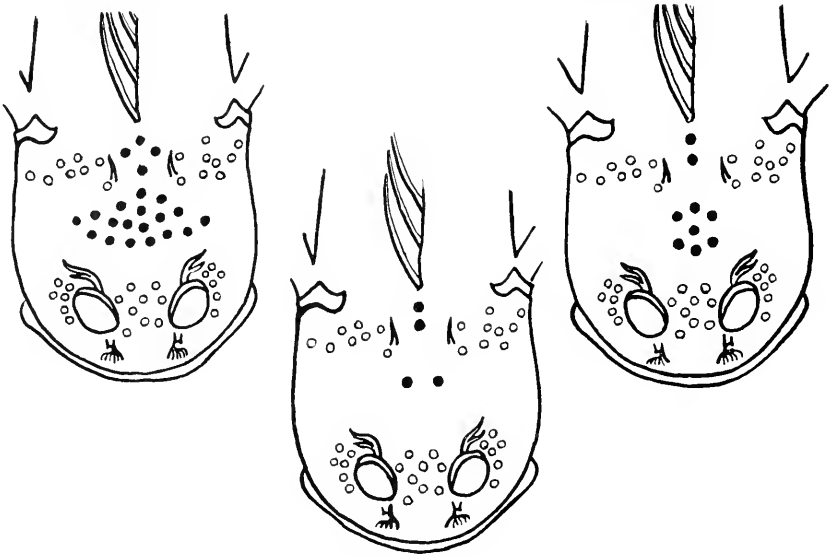

FIGURE 1.—Diagrammatic illustration of pores included in predorsal commissural group (solid dots) and other pores (open dots).

Predorsal commissural pores (fig. 1): A count of all pore openings in the region anterior to the first dorsal spine and between the bases of the nuchal cirri, extending anteriorly on top of the head a distance usually about one-half the head length or less. Anterior to the level of the nuchal cirri the area occupied by the pores frequently spreads laterally in both directions and covers an expanse broader than the internuchal cirri distance; all pores anterior to the nuchal cirri in this midregion are included in the count. In some specimens this is a difficult count to make. Overlying mucus must be removed and drying of the area is recommended. Inserting a tiny insect pin into each pore will greatly facilitate making counts.

Preopercular series of pores (fig. 2): For the purposes of this study, the first pore position is dorsalmost and occurs at about the level of the greatest horizontal distance between the posterior margins of the preopercle and opercle, excluding the branchiostegal membrane. The pore positions in most specimens number six, describing an arc between the first and last positions. The last pore position (ventral and anteriormost) is just ventral to the posterior corner where the membranous margins of the lips meet. Dorsal to the first pore position are a group of scattered pores. Some difficulty may be encountered in deciding which is the first pore position. Examination of the illustrations of the species should facilitate this decision. The pores at the various positions may be simple (one pore), paired (two pores connected more or less horizontally by a canal), or in multiples (more than two pores connected to a common canal). A count of the number of these three types of conditions at the pore positions is a useful taxonomic character.

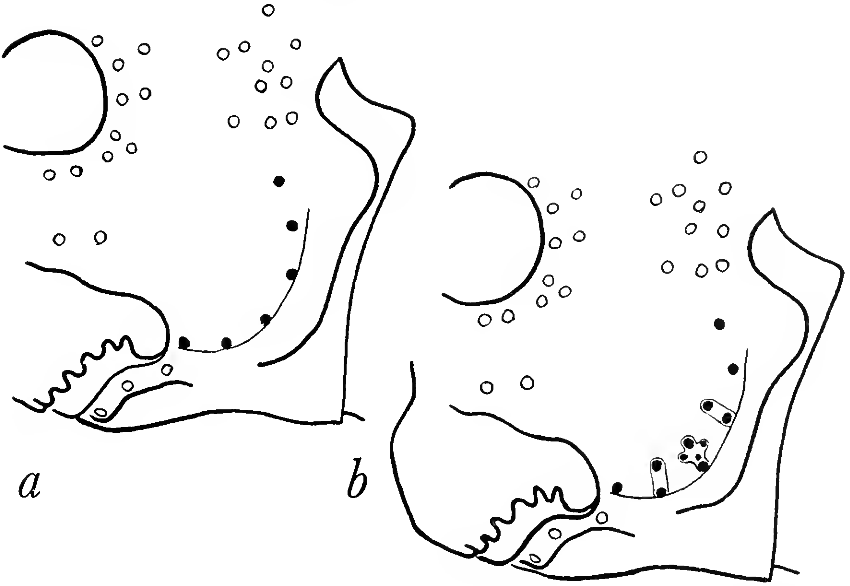

FIGURE 2.—Diagrammatic illustration of pores included in preopercular group (solid dots): *a*, all pore positions simple; *b*, first, second, and sixth positions with simple pores, third and fifth positions with paired pores, fourth position with multiple pores.

Pores before anterior nostril: A count of the number of pore openings closely adjacent and more or less anterior to the anterior nostril.

Lateral line pores: Anteriorly the lateral line pores open into a continuous canal; posteriorly, on the midside, the pores occur in more or less regular, separated pairs, the members of a pair joined by a short canal. Large or small gaps in the occurrence of some pore pairs should be ignored in determining the level of occurrence (usually below a dorsal fin element) of the posteriormost pair of pores. Frequently, the posteriormost pair of pores is well removed from the others. Posterior to the last pair of pores there usually occurs what appears to be a series of simple pores. Close examination will show that these are merely shallow depressions or pits.

Lip crenulae (table 5): The number of small lobulations on the ventral margin of the upper lip. Some crenulae are broad, others very shallowly separated and scarcely distinct. If there is a doubt, the internal surface of the lip will sometimes exhibit the mucosal lining organized into pads corresponding to crenulations, and these may be counted instead of the crenulae. Counts of crenulae are unreliable where numerous irregularities occur on the lip.

Color pattern descriptions.—The word "dusky" denotes a dark area relative to the palest surrounding areas. Usually a dusky area consists of a concentration of nonimpinging black melanophores that may not be individually recognizable to the naked eye.

Plates.—The drawings of the complete lateral views of specimens are all made to a base total length of 6½ inches and are reproduced here 1:1. The head measurements were made as projections, rather than from point to point. For this reason, measurements of the head taken from the illustration will give different relative values from those which would be obtained if actual specimens were measured point to point. All efforts were made to obtain accuracy and completeness in representing the specimens drawn. All pore openings visible from the view drawn are included except those of the anterior continuous portion of the lateral line, which were impossible to determine accurately. The inserted drawing of the upper lip on each plate portrays the lip with its laterally, posteriorly projected portions expanded anteriorly. The snout region of the head in blenniids is fleshy and relatively soft, and the shape is variable in some degree. This apparent variation is increased because of the position in which the specimens were held when the artist drew the head contours. Some allowance should thus be made when comparing actual specimens with the drawings. Finally, because only one specimen has been illustrated from a particular population, some allowance must be made for natural variation, which is particularly great in color pattern.

Entomacrodus Gill

Entomacrodus Gill, 1859, Proc. Acad. Nat. Sci. Philadelphia, vol. 11, p. 168. [Type-species: *E. nigricans* Gill, monotypy.]

Salarichthys Guichenot, 1867, Mem. Soc. Sci. Nat. Cherbourg, vol. 13, pp. 96–100. [Type-species: *Salarias vomerinus* Valenciennes, original designation.]

Giffordella Fowler, 1932, Proc. U.S. Nat. Mus., vol. 80, no. 6, pp. 14–15. [Type-species: *G. corneliae*, original designation.]

DESCRIPTION.—Dorsal fin spines 13 (rarely 12 or 14); dorsal fin rays 13–18; anal fin spines 2; anal fin rays 14–19 (see methods); segmented caudal fin rays typically 13 (7 rays on upper half of hypural vertebra, 6 on lower half), typically 2 most dorsal and 2 most ventral rays simple, central 9 rays branched; pectoral fin rays 12–15 (14 in over 90 percent of specimens of all species); pelvic fin rays I,4; total gill-rakers on first arch 9–30 (number increasing with increase in SL in some species); pseudobranchial filaments 3–17 (number increasing with increase in SL in some species); vertebrae, including hypural, 33–36; 11th vertebra always bears first haemal spine; supraorbital cirri 1–38 (number increasing with increase in SL in some species); nuchal cirri 0–20 (rarely lacking cirri on both sides except in *E. thalassinus* and *E. macrospilus;* number increasing with increase in SL in some species); cirri present on posterior margin of tube rim of anterior nostril; predorsal commissural pores 2–69 (normally 3 or more, increasing in number with increase in SL in most species, constant in only one species); preopercular series of pores occupying 6 positions (rarely 5 or 7) and varying from all positions with simple pores to all positions with pairs or multiples of pores; pores before each anterior nostril 1–7; posterior nostrils present; paired, or multiples of, pores in circumorbital series at at least one position (usually along dorsoposterior margin of orbit); lateral line pores on body side continuous (sometimes with short side branches anteriorly) and arched in area above appressed pectoral fin, composed of short disconnected bipored tubes on midside, terminating posteriorly in area below and between posterior dorsal spines and caudal fin origin; over 100 freely movable teeth supported by each pair of premaxillaries and dentaries (more on premaxillaries than dentaries), implanted in connective tissue (rather than on bones of jaws); a relatively small to large recurved canine (rarely absent) inserted posteriorly on each articular bone; 1–11 short, truncate teeth on vomer (rarely absent, frequently easily removed); 6 branchiostegals; 4 pectoral fin radials (none fused together); 2 postcleithra; posttemporal forked; basisphenoid present; 5 circumorbital bones (dorsalmost is probably the dermosphenotic); interopercle reduced, internal to preopercle, well removed from subopercle, not extending posterior to connection with epihyal; premaxillary concave ventrally (to accept dental plate); dentary concave anteriorly (to accept dental plate); ascending wing of parasphenoid reaching descending wing of frontal; pterosphenoid and prootic excluded from orbit by ascending wing of parasphenoid; no pharyngobranchials; one upper pharyngeal bone on each side, bearing several strong, pointed teeth; 2nd, 3rd, and 4th epibranchials attached to upper pharyngeal bone.

Moderately small (to 153 mm SL) fishes with a deeply incised dorsal fin between spinous and rayed portions; first spine over opercle;

posteriormost dorsal segmented ray well anterior to caudal fin base, although bound by dorsal fin membrane to caudal peduncle or proximal portion of caudal fin. Longest dorsal ray usually longer than longest dorsal spine; posteriormost dorsal spine shortest dorsal element, greatly reduced and frequently visible only on skeletal preparations and radiographs; posteriormost dorsal ray shortest. Interradial membrane not incised between dorsal spines or between rays. First anal spine inserted below level of fourth to second posteriormost dorsal spine; posteriormost segmented anal ray inserted below level of third to second posteriormost dorsal segmented ray, not bound to body. Anal spines shorter than anal rays; interradial membrane incised up to one-half distance to base between spines and between rays, except for membrane between posteriormost 1–3 rays. Pectoral fin with longest ray on lower half (usually fifth or sixth ray from bottom); interradial membrane shallowly incised between lower 4–6 rays; lower rays thicker, stronger, than upper rays. Pelvic fin spine not visible externally, second from lateralmost ray longest, medialmost ray shortest, membrane incised only between lateralmost two rays. All fin rays, except central rays of caudal, normally simple, some ray tips of the dorsal, anal or pelvics shallowly bifurcate in some large specimens of some species.

Tip of snout ventral and anterior to anteriormost margin of orbit; gill opening complete, extending from one side to the other across the ventral body surface; no thin, fleshy, well-elevated crest on top of head; ventral margin of upper lip entire to completely crenulate (entire in only two species); free dorsal margin of upper lip incomplete, absent across snout.

SEXUAL DIMORPHISM.—Males: Anal papilla small, just posterior to anus and anterior to first anal spine; both anal spines distinct, the anterior slightly shorter than the posterior; skin of anal spines and as many as four anteriormost rays becoming swollen, fleshy, rugose, or plicate in presumably mature specimens. Flesh of dorsal portion of head becoming thickened, swollen in appearance, sometimes forming a low distinct fold medianly, never very prominent. Color pattern frequently darker, frequently more uniform than that of females in same collection. Supraorbital cirri frequently relatively longer than cirri of females from same collection. Females: Anal papilla present, included posteromedianly in a fleshy, posteriorly directed swelling behind anus; swelling incorporating much reduced first anal spine (frequently visible only in skeletal preparations or on radiographs); first anal spine frequently visible in young females. Flesh of head not thickened or swollen; head without median fold.

Several of the taxa considered here (see *E. s. lighti*, *E. epalzeocheilus*, *E. strasburgi*, *E. cadenati*, *E. t. longicirrus*, and some populations of *E. decussatus*) exhibit sexual dimorphism in average numbers of segmented dorsal rays. Other taxa either do not show such differences or the data are inconclusive. In all taxa where such sexual dimorphism occurs, males tend to average more rays than females. In all species, exceptionally high dorsal counts were usually from males and low counts from females. Dimorphism in other meristic characters was not noted.

The species dwell in shallow water, in tide pools, along reefs, or rocky shores and are essentially circum- and subtropical in distribution.

In all species of *Entomacrodus*, except *E. vermiculatus*, *E. niuafoouensis*, and *E. nigricans*, for which there were sufficient data, males attained a larger size than females, and the largest specimen in any given collection was usually a male. In the first two named exceptions, females attained a larger size than males, and in the latter exception the sexes attained equal size. In general, however, males averaged larger than females. Overall sex ratios in the different species were quite variable, and generalizations cannot be made.

INTRAFAMILIAL RELATIONSHIPS.—The genus *Entomacrodus* is a member of the family Blenniidae and belongs in the subfamily Salariinae as defined by Norman (1943). (Norman's subfamily Ophioblenniinae is a synonym of the Salariinae; the former was based on specimens now known to be larval stages of salarines.) The genera of the Salariinae, with the exception of *Rhabdoblennius* Whitley and allied genera, are characterized primarily by the nature of the attachment of the teeth on the jaws. The very numerous teeth of the dentaries and premaxillaries are loosely held in each jaw in a thick band of connective tissue which is attached to the bone. The dentaries and premaxillaries have a concave surface where the connective tissue is attached. The arch of the bone encompassing the connective tissue and lying external to the bases of the teeth has been termed a "crest" by Norman. In the other subfamily of the Blenniidae (the Blenniinae), the teeth of both jaws are relatively few and firmly implanted on the bone. In *Rhabdoblennius* and allies, the premaxillary and dentary teeth are relatively few. The premaxillary teeth, while held to the jaw only by connective tissue, are tightly associated with the bone. The dentary teeth, in contrast, not only are held to the jaw by connective tissue, but some also are loosely inserted in openings in the dentary bone.

The genera and species of the Salariinae are poorly known and a meaningful discussion of relationships of the genera is not possible at present. *Entomacrodus* usually has been distinguished from all other salarine genera by the presence of teeth on the vomer; however, Smith (1959) described *Pereulixia*, which has vomerine teeth, and I have seen specimens of undescribed salarine genera with vomerine teeth. *Hirculops* Smith (1959), also with vomerine teeth, is related to *Rhabdoblennius*. The combination of characters given in the generic description above will serve to separate *Entomacrodus* from all other described blennioids.

Schultz and Chapman (1960) believed *Fallacirripectes* Schultz and Chapman to be intermediate between *Entomacrodus* and *Cirripectes* Swainson. I believe that *Fallacirripectes* is the genus most closely related to *Entomacrodus*. *Fallacirripectes* differs from *Entomacrodus* in having typically 15, rather than 14, pectoral rays, fewer dorsal spines, fewer segmented dorsal and anal rays, and no vomerine teeth. (Although I have seen no specimens of *Stanulus* Smith (1959), it appears probable that *Fallacirripectes* is a junior synonym of *Stanulus*).

INTRAGENERIC RELATIONSHIPS.—I recognize seven species groups within *Entomacrodus*. My recognition of these groups is influenced greatly by the nature (or absence) of the upper lip crenulae and secondarily by other characters. I am unable to delimit intergroup relationships as I do not know which characters are specialized or unspecialized, primitive or advanced. There is no fossil record of the Blenniidae to serve as a guide.

The species groups I recognize are characterized as follows:

1. *thalassinus* group (*E. thalassinus*, *E. macrospilus*). Smallest species, lacking crenulae on the upper lip. Indian, western and central Pacific Oceans.
2. *nigricans* group (*E. sealei*, *E. corneliae*, *E. chiostictus*, *E. caudofasciatus*, *E. nigricans*, *E. textilis*, *E. cadenati*, *E. vomerinus*). Relatively small species, the lateral thirds of the upper lip crenulate and the central portion entire. Circumtropical.
3. *stellifer* group (*E. stellifer*). Relatively large species, the middle third of the upper lip crenulate and the lateral thirds entire. Western Pacific Ocean.
4. *rofeni* group (*E. rofeni*). Relatively small species, the upper lip completely crenulate, high dorsal ray, anal ray and vertebral counts, constantly three pores in the predorsal commissural group, and the dorsal fin free from the caudal. Central Pacific Ocean.
5. *cymatobiotus* group (*E. cymatobiotus*, *E. strasburgi*, *E. chapmani*). Relatively small species, the upper lip completely crenulate, generally low meristic counts, and the dorsal fin free from the caudal. Western and central Pacific Ocean.
6. *striatus* group (*E. striatus*, *E. marmoratus*, *E. randalli*, *E. epalzeocheilus*, *E. niuafoouensis*). Relatively large species, the upper lip completely crenulate, generally high meristic counts, and the dorsal fin free from the caudal.

7. *decussatus* group (*E. decussatus*, *E. vermiculatus*). Largest species, having the upper lip completely crenulate in adults, generally high meristic counts, dorsal fin attached at, or posterior to, the caudal base. Indian, central and western Pacific Oceans.

ZOOGEOGRAPHY.—Some aspects of this topic are discussed under the individual species accounts (see especially "Relationships" under *E. chiostictus*). There is a decreasing number of species of *Entomacrodus* in the various oceans as one progresses westward from the central Pacific Ocean around the world to the eastern Pacific Ocean (table 6). If one subscribes to the hypothesis that the center of origin of a particular taxonomic group is the area where the most species of that group occur, then the central Pacific Ocean is the area of origin of *Entomacrodus*. The central Pacific is also the only area where as many as six species (fig. 3) have been taken at a single locality. Ekman (1953, p. 18) has stated that the Indo-Malayan (Indonesian) region (here comprised of portions of the Indian Ocean and western Pacific areas of table 6) is the area from which adjacent regions derived their marine shore faunas; however, Ladd (1960), on the basis of geologic evidence, fossil molluscan faunas, and present meteorological conditions, postulated that the Indonesian area received its marine shore fauna by invasion from the central Pacific Ocean. Actually, the distribution of the species of *Entomacrodus* does not support an Indonesian origin as opposed to a central Pacific origin of the genus. If one eliminates from consideration the isolated island species of *Entomacrodus*, there are eight species found in the central Pacific and probably eight occurring in Indonesia (assuming that *E. niuafoouensis*, which has been recorded from the Indian and western Pacific Oceans but not Indonesia, probably does or did occur in Indonesia). There are six species common to both areas; this leaves two species in each area which do not occur in the other.

None of the areas of table 6 have representatives of all the species groups of *Entomacrodus*. The eastern Pacific and eastern and western Atlantic are all occupied by the same group, *nigricans*. The Indian ocean has four groups, and the central and western Pacific areas each have six groups. The central and western Pacific areas together have all seven groups. In spite of the lack of definitive data to support a contention that some portion of the Old World tropical Pacific is the area of origin of *Entomacrodus*, I find it difficult to believe otherwise.

Nine of the 15 central and western Pacific Ocean species of *Entomacrodus* have their entire distribution either along or near a line circumscribing the periphery of the tropical-subtropical portions of the area (fig. 4: the basis for the construction of the line is the distribution of the Pacific coral reefs as given by Wells, 1957, except that

TABLE 1.--Frequency distributions of number of segmented dorsal and anal fin ray elements and vertebrae (data combined for all specimens of each taxon) of species and subspecies of *Entomacrodus* (for meaning of methods A, B and N or S, see methods section)

Species and subspecies	Dorsal rays						Anal rays, method A						Anal rays, method B							Percent		Vertebrae			
	13	14	15	16	17	18	14	15	16	17	18	19	14	15	16	17	18	19	20	N	S	33	34	35	36
decussatus	-	-	-	40	115	3	-	-	1	9	126	17	-	-	-	1	14	124	14	4.5	95.5	-	4	82	2
vermiculatus	-	-	1	45	10	-	-	-	1	6	52	-	-	-	-	1	19	39	-	21.4	78.6	-	2	29	-
s. stellifer	-	-	2	19	4	-	-	-	-	4	19	2	-	-	-	3	15	7	-	80.0	20.0	-	-	14	6
s. lighti	-	-	57	31	-	-	-	-	2	49	36	-	-	-	1	33	49	4	-	74.8	25.2	-	10	41	3
marmoratus	-	1	57	33	-	-	-	1	51	41	-	-	-	1	4	81	7	-	-	38.6	61.4	-	38	10	-
epalzeocheilus	-	2	49	17	-	-	-	1	35	32	-	-	-	-	5	56	7	-	-	42.6	57.4	1	32	1	-
niuafoouensis	-	-	17	17	-	-	-	-	19	15	-	-	-	-	4	26	4	-	-	44.1	55.9	-	26	1	-
randalli	-	-	4	7	-	-	-	-	2	9	-	-	-	-	1	7	3	-	-	63.4	36.6	-	8	1	-
striatus	-	6	331	384	4	-	-	3	246	467	10	-	-	-	35	533	156	2	-	49.2	50.8	2	123	2	-
rofeni	-	-	-	12	1	-	-	-	-	1	12	-	-	-	-	-	7	5	-	46.2	53.8	-	-	12	-
strasburgi	1	15	22	-	-	-	-	-	35	3	-	-	-	-	7	29	3	-	-	18.0	82.0	-	24	3	-
cymatobiotus	11	116	11	-	-	-	-	4	117	16	-	-	-	-	8	120	9	-	-	8.0	92.0	1	19	-	-
chapmani	-	12	14	-	-	-	-	6	19	1	-	-	-	-	11	15	-	-	-	23.0	77.0	-	3	-	-
sealei	1	17	91	5	-	-	-	5	97	12	-	-	-	-	8	99	7	-	-	7.0	93.0	2	21	-	-
corneliae	1	6	6	-	-	-	-	-	9	2	-	-	-	-	2	9	-	-	-	36.8	63.2	-	8	-	-
chiostictus	-	105	423	3	-	-	-	26	471	27	-	-	-	-	40	465	19	-	-	4.0	96.0	8	89	2	-
vomerinus	-	-	16	101	9	-	-	1	4	96	25	-	-	1	-	11	96	18	-	11.9	88.1	-	5	57	5
textilis	-	11	60	-	-	-	-	8	63	-	-	-	-	1	12	58	-	-	-	8.4	91.6	-	10	-	-
cadenati	-	19	71	2	-	-	-	1	58	33	-	-	-	-	3	78	11	-	-	25.0	75.0	-	42	-	-
nigricans	1	245	265	1	-	-	3	23	428	27	-	-	1	3	49	413	15	-	-	9.7	90.3	3	77	1	-
caudofasciatus	-	12	122	12	-	-	-	2	106	34	-	-	-	-	7	107	28	-	-	7.4	92.6	2	79	4	-
t. thalassinus	35	245	20	-	-	-	-	45	234	13	-	-	-	1	83	198	10	-	-	14.5	85.5	2	54	6	-
t. longicirrus	20	62	4	-	-	-	-	24	57	5	-	-	-	6	47	33	8	-	-	46.5	53.5	6	20	2	-
macraspilus	-	-	5	1	-	-	-	-	-	3	3	-	-	-	-	-	4	2	-	16.2	83.8	-	-	3	2

TABLE 2.--Frequency distribution of number of pseudobranchial filaments and gill-rakers of species and subspecies of *Entomacrodus* (changes in numbers of elements associated with size of specimens has not been taken into consideration for this table)

	Pseudobranchial filaments															Gill-rakers																					
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
decussatus	-	-	1	4	2	15	21	21	20	22	16	2	-	2	1	-	-	-	-	-	-	-	-	1	1	5	3	9	18	19	22	18	11	15	6	2	1
vermiculatus	-	-	-	-	-	9	11	15	12	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	5	13	9	5	6	6	-	-	-	-
s. stellifer	-	-	-	1	6	13	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	4	10	4	1	-	-	-	-	-	-	-	-	-	-	-
s. lighti	-	-	-	4	24	45	9	1	-	-	-	-	-	-	-	-	-	-	-	-	1	6	29	23	15	6	2	-	-	-	-	-	-	-	-	-	-
marmoratus	-	-	-	3	1	18	30	6	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	8	20	19	8	5	4	1	1	1	-
epalzeocheilus	-	-	-	1	15	31	19	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	6	12	16	18	7	1	1	1	-	-	-	-	-
niuafoouensis	-	-	-	-	7	19	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	4	6	8	7	5	1	1	-	-
randalli	-	-	-	-	2	1	4	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	3	2	-	-	-	-	-	-
striatus	-	-	5	111	209	84	7	1	-	-	-	-	-	-	-	-	-	-	-	-	7	19	92	160	140	85	58	11	2	-	-	-	-	-	-	-	-
rofeni	-	-	1	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	8	1	2	-	-	-	-	-	-	-	-	-	-	-
strasburgi	-	-	32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	7	9	7	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
cymatobiatus	-	5	71	23	-	-	-	-	-	-	-	-	-	-	-	5	3	24	26	23	10	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
chapmani	-	-	14	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	3	5	5	3	-	-	-	-	-	-	-	-	-	-	-	-
sealei	-	1	8	70	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	10	35	30	10	2	1	-	-	-	-	-	-	-	-	-
corneliae	-	-	3	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-
chaostictus	-	-	20	224	28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	70	150	152	62	14	2	-	-	-	-	-	-	-	-	-	-
vomerinus	-	-	1	59	10	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	6	23	27	30	18	6	3	1	-	-	-	-	-	-
textilis	-	3	8	41	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	3	15	18	8	[illegible]	-	1	-	-	-	-	-	-	-
cadenati	-	-	6	44	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	12	28	16	7	1	-	-	-	-	-	-	-	-
nigricans	-	-	14	98	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	31	72	72	50	24	6	-	-	-	-	-	-	-	-	-	-
caudofasciatus	-	-	4	75	31	2	-	-	-	-	-	-	-	-	-	-	-	-	-	5	20	21	24	6	1	-	-	-	-	-	-	-	-	-	-	-	-
t. thalassinus	2	10	166	6	-	-	-	-	-	-	-	-	-	-	-	1	20	76	72	18	9	3	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
t. longicirrus	-	1	48	4	-	-	-	-	-	-	-	-	-	-	-	-	6	13	29	19	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
macrospilus	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

I have included Easter Island). All the remaining species of the genus that occur in the area are distributed along and well within the area circumscribed by the coral reef line, and a few extend into the Indian Ocean as well.

Seven of the nine species that have peripheral distributions are endemics. Of these seven, all but one, *E. rofeni* from the Tuamotus, are from isolated island groups—Hawaiian, Marquesas, Easter. Isolated islands are expected to harbor relatively more endemics than centrally located islands in close proximity to other islands. Island

TABLE 3.--Changes in orbital diameter (as percent SL) with increase in SL of species and subspecies of *Entomacrodus* (average for SL class followed in parentheses by number of specimens on which average is based and range of orbital diameter percentages for SL class)

SL(mm)	*decussatus*	*vermiculatus*	*s. stellifer*	*s. lighti*	*marmoratus*
15-19.9	-(1:94)	--	--	-(1:10.2)	--
20	--	-(1:8.3)	--	-(1:8.1)	--
25	8.5(4:8.1-9.2)	--	-(1:8.7)	-(1:8.4)	-(1:7.7)
30	8.4(5:7.9-9.0)	--	-(1:8.4)	7.4(2:7.3-7.4)	-(1:7.4)
35	8.2(5:8.0-8.3)	--	-(1:8.3)	-(1:7.4)	7.3(3:7.0-7.7)
40	8.0(5:7.4-8.6)	-(1:7.2)	7.5(3:7.4-7.5)	7.2(2:6.7-7.6)	-(1:7.1)
45	8.0(2:7.4-8.5)	-(1:6.8)	6.8(4:6.5-7.1)	--	6.4(4:6.2-6.7)
50	-(1:7.5)	6.7(3:6.2-7.0)	6.8(2:6.6-7.1)	6.4(2:6.4-6.5)	6.6(3:6.3-7.1)
55	7.1(7:6.6-7.6)	-(1:7.3)	6.2(4:5.9-6.9)	-(1:6.1)	6.4(7:6.0-6.9)
60	6.9(4:6.2-7.6)	6.4(2:6.2-6.5)	6.2(2:6.1-6.2)	6.4(2:6.3-6.4)	6.0(3:5.7-6.3)
65	6.4(5:6.1-6.7)	-(1:6.3)	-(1:5.9)	6.0(2:6.0-6.1)	6.0(4:5.6-6.2)
70	6.6(6:6.2-7.0)	6.6(2:6.1-7.0)	-(1:5.6)	5.8(4:5.6-6.0)	--
75	6.2(3:6.1-6.3)	-(1:6.5)	-(1:5.2)	-(1:5.4)	--
80	6.3(5:6.1-6.9)	--	-(1:5.6)	-(1:5.7)	5.8(4:5.6-6.0)
85	6.4(2:6.2-6.5)	5.9(2:5.6-6.2)		5.5(2:5.5)	5.5(3:5.4-5.5)
90	6.0(3:5.8-6.1)	--		--	5.3(2:5.3)
95	6.0(2:5.9-6.0)	-(1:6.0)		-(1:5.3)	-(1:5.2)
100	5.9(2:5.7-6.1)	--			-(1:5.1)
105	5.2(2:5.0-5.3)	--			-(1:5.0)
110	-(1:5.6)	5.1(4:4.7-5.2)			--
115	5.5(5:5.1-5.7)	5.1(4:4.9-5.3)			--
120	5.2(3:4.8-5.5)	5.2(2:5.0-5.4)			-(1:4.8)
125	5.4(3:5.1-5.6)	--			
130	5.4(2:4.9-5.9)	-(1:4.8)			
135	-(1:5.2)	-(1:5.2)			
140	-(1:4.7)	-(1:4.5)			
145	--	4.8(2:4.6-4.9)			
150	-(1:4.9)	-(1:4.8)			

TABLE 3.--Continued

SL (mm)	*epalzeocheilus*	*niuafoouensis*	*randalli*	*striatus*	*rofeni*
15-19.9	--	--	--	--	--
20	--	--	--	8.0(3:6.4-9.1)	--
25	7.0(5:6.7-7.2)	--	--	8.0(2:7.8-8.3)	7.5(3:7.1-7.7)
30	7.1(2:6.9-7.3)	7.6(2:7.6-7.7)	—	7.4(9:7.0-8.3)	6.6(2:6.3-6.9)
35	6.3(2:6.2-6.4)	—	--	7.3(14:6.4-8.2)	6.4(4:6.0-6.8)
40	6.3(8:6.0-6.8)	-(1:6.4)	--	7.0(21:6.3-7.7)	6.4(2:6.3-6.4)
45	6.3(5:6.0-6.4)	6.4(4:6.2-7.0)	-(1:6.9)	6.8(25:6.1-7.5)	
50	6.1(6:5.1-6.9)	6.3(3:6.2-6.4)	-(1:6.6)	6.5(21:5.7-7.4)	
55	6.4(2:6.4-6.5)	6.3(7:5.9-6.4)	--	6.2(18:5.6-6.9)	
60	6.0(3:5.7-6.3)	5.8(3:5.5-6.2)	--	5.8(16:5.5-6.8)	
65	5.4(3:5.2-5.7)	6.1(4:5.9-6.2)	--	5.6(8:5.2-5.9)	
70	-(1:5.4)	-(1:6.0)	--	5.4(5:5.1-5.8)	
75	5.1(2:5.0-5.2)	-(1:5.4)	--	5.0(2:5.0-5.1)	
80	5.4(2:5.0-5.7)	5.4(2:5.1-5.7)	--	4.9(3:4.8-5.0)	
85	-(1:4.5)	—	-(1:6.3)	-(1:5.1)	
90	--	--		-(1:4.5)	
95	4.8(2:4.8-4.9)	-(1:5.2)		-(1:4.7)	
100	-(1:4.5)				

SL (mm)	*strasburgi*	*cymatobiotus*	*chapmani*	*sealei*	*corneliae*
15-19.9	8.6(3:8.5-8.6)	--	--	--	--
20	7.9(5:7.4-8.6)	-(1:7.8)	--	-(1:8.5)	--
25	7.2(11:6.7-7.7)	6.9(12:6.3-8.2)	6.9(2:6.4-7.4)	7.5(4:7.1-8.2)	--
30	6.6(7:6.2-6.9)	6.3(8:6.1-6.6)	-(1:6.4)	6.9(13:6.6-7.4)	--
35	-(1:6.3)	6.0(7:5.4-6.3)	6.1(4:5.9-6.4)	6.7(10:6.1-8.1)	-(1:6.5)
40		5.8(8:5.4-6.1)	5.6(2:5.5-5.6)	6.2(4:5.8-7.2)	
45		5.4(6:5.0-5.8)	5.2(2:4.9-5.4)	6.5(5:6.0-6.8)	
50			5.4(5:5.0-5.8)	6.1(6:5.8-6.6)	
55			--	-(1:5.4)	
60			-(1:4.9)	-(1:5.7)	
65			--		
70			-(1:4.6)		
75					
80					
85					
90					
95					

TABLE 3.--Continued

SL(mm)	*chiostictus*	*vomerinus*	*textilis*	*cadenati*	*nigricans*
15-19.9	--	--	--	--	--
20	-(1:7.0)	--	-(1:7.6)	--	8.1(2:7.6-8.6)
25	6.8(4:6.1-7.4)	--	7.3(3:7.1-7.4)	-(1:7.0)	7.6(2:7.3-8.0)
30	7.1(8:6.7-7.5)	--	6.4(2:6.2-6.7)	6.9(3:6.4-7.3)	6.7(8:6.3-7.0)
35	6.7(13:6.1-7.3)	7.2(2:6.7-7.6)	6.3(3:6.4-6.8)	6.4(4:5.7-6.8)	6.6(14:6.1-7.4)
40	6.3(10:5.1-7.1)	6.4(3:5.8-7.0)	5.9(4:5.6-6.1)	5.8(2:5.5-6.0)	6.4(11:6.0-6.7)
45	6.0(12:5.5-6.6)	6.4(2:6.2-6.5)	6.2(5:5.9-6.7)	6.2(3:5.5-6.8)	5.9(12:5.7-6.5)
50	5.8(4:5.5-6.0)	-(1:6.1)	5.8(4:5.7-6.1)	5.8(4:5.5-6.0)	5.8(10:5.6-6.0)
55	-(1:5.2)	-(1:5.6)	5.5(2:5.3-5.7)	5.5(4:5.2-6.0)	5.4(3:5.3-5.5)
60	5.2(3:5.1-5.3)	-(1:5.2)	-(1:5.0)	5.5(8:5.1-5.9)	5.3(4:5.1-5.6)
65	4.9(3:4.7-5.2)	-(1:5.1)		5.4(3:5.1-5.7)	
70		5.3(4:5.0-5.7		--	
75		-(1:5.1)		-(1:4.7)	
80		4.9(6:4.6-5.3)			
85		5.0(2:4.6-5.4)			
90		-(1:4.4)			
95		--			
100		-(1:4.5)			

SL(mm)	*caudofasciatus*	*t. thalassinus*	*t. longicirrus*	*macrospilus*
15-19.9	--	--	8.2(2:7.8-8.7)	-(1:8.0)
20	--	7.4(7:6.8-8.0)	6.8(3:6.4-7.1)	
25	7.7(5:2.1-8.8)	6.6(29:5.7-7.5)	6.8(9:6.5-7.2)	
30	6.9(11:6.0-7.8)	5.8(12:5.0-7.0)	6.6(11:6.0-7.2)	
35	6.6(7:6.3-7.4)	5.4(6:5.0-5.9)	6.1(9:5.4-6.8)	
40	6.4(6:5.8-7.1)		5.6(8:5.2-6.0)	
45	6.1(7:6.0-6.5)		5.3(2:5.2-5.4)	
50	6.0(3:5.8-6.1)			

endemism can be explained in two ways: chance isolation (with possible subsequent divergence) of a species with a former, wider distribution (relicts); and arrival of a species with subsequent establishment of breeding populations and divergence before other possible competitors have had the chance to invade and become established.

The central Pacific of the past probably was much more densely spotted with islands than it is today (see Menard, 1964, especially his discussion of the Darwin Rise). Various factors (subsidence,

TABLE 4.--Frequency distributions of main supraorbital cirrus length, as percent SL, of species and subspecies of *Entomacrodus* (Note: table does not take into account differences between populations of a single taxon, or the regressions of cirrus length on size, which occur in most species; thus differences between and within many of the species, or the different sexes within a species, are even greater than is apparent from the table)

Males	Cirrus length as percent of SL (lower limits of class)																									
	1.9	2.3	2.7	3.1	3.5	3.9	4.3	4.7	5.1	5.5	5.9	6.3	6.7	7.1	7.5	7.9	8.3	8.7	9.1	9.5	9.9	10.3	10.7	11.1	11.5	11.9
decussatus	-	-	1	1	1	4	2	3	-	2	5	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-
vermiculatus	-	-	-	-	-	-	-	2	3	-	3	4	-	-	-	1	-	1	-	-	-	-	-	-	-	-
s. stellifer	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	1	-	-	1	1	1	2	2	1	1	-
s. lighti	-	-	-	-	-	-	-	-	-	-	-	2	1	2	2	3	4	2	2	2	2	1	1	-	-	1
marmoratus	-	-	-	-	-	1	1	4	3	5	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
epalzeocheilus	-	-	-	-	-	1	1	-	1	2	1	1	1	2	3	1	1	1	2	3	1	-	-	2	1	2
niuafoouensis	-	-	-	-	-	-	-	-	-	1	1	1	2	-	-	1	-	-	-	-	-	-	-	-	-	-
randalli	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
striatus	-	-	1	6	10	14	6	25	20	8	8	6	2	2	2	-	-	-	-	-	-	-	-	-	-	-
rofeni	-	-	-	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
strasburgi	-	1	5	6	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
cymatobiotus	-	-	-	6	8	14	11	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
chapmani	-	-	-	-	1	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
sealei	-	-	-	-	-	2	7	7	2	7	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
corneliae (none)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
chiostictus	-	-	2	3	9	14	16	35	25	35	26	7	5	2	2	-	-	-	-	-	-	-	-	-	-	-
vomerinus	-	-	3	5	5	8	3	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
textilis	-	-	2	-	5	5	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
cadenati	1	5	6	2	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
nigricans	1	13	16	13	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
caudofasciatus	-	-	-	-	3	1	3	2	9	6	7	6	3	1	2	-	-	-	-	-	-	-	-	-	-	-
t. thalassinus	1	9	17	18	10	8	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
t. longicirrus	-	-	-	-	-	-	-	-	-	-	5	7	4	8	6	1	8	-	1	1	-	-	-	-	-	-
macrospilus	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

TABLE 4.--Continued

Females	Cirrus length as percent of SL (lower limits of class)																									
	1.9	2.3	2.7	3.1	3.5	3.9	4.3	4.7	5.1	5.5	5.9	6.3	6.7	7.1	7.5	7.9	8.3	8.7	9.1	9.5	9.9	10.3	10.7	11.1	11.5	11.9
decussatus	-	4	2	1	6	6	7	2	4	2	4	2	-	1	-	1	-	-	-	-	-	-	-	-	-	-
vermiculatus	-	-	-	-	1	2	4	2	-	2	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
s. stellifer	-	-	-	-	-	-	-	-	1	1	-	1	2	1	-	1	1	1	-	-	-	-	-	-	-	-
s. lighti	-	-	-	-	-	-	-	2	1	-	5	1	2	1	2	3	-	2	-	-	2	-	-	-	-	-
marmoratus	-	-	-	-	2	4	11	4	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
epalzeocheilus	-	-	-	-	-	-	1	-	5	3	4	2	1	1	2	1	-	1	1	-	-	-	-	-	-	-
niuafoouensis	-	-	-	-	-	-	3	-	2	4	5	4	2	2	-	-	-	-	-	-	-	-	-	-	-	-
randalli	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
striatus	-	-	2	12	21	14	9	4	3	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
rofeni	-	4	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
strasburgi	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
cymatobiotus	-	-	3	6	5	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
chapmani	-	-	3	1	1	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
sealei	-	-	2	5	6	8	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
corneliae	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
chiostictus	-	-	6	24	39	26	16	11	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
vomerinus	-	1	2	6	12	8	4	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
textilis	1	-	-	8	6	7	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
cadenati	1	11	14	5	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
nigricans	11	16	15	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
caudafasciatus	-	1	-	1	4	2	2	2	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
t. thalassinus	-	-	5	3	6	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
t. longicirrus	-	-	-	-	-	8	4	9	4	6	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
macraspilus (none)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

erosion) have removed many of the formerly existing islands from the ocean's surface. The Hawaiian Islands (on the periphery), for example, were probably once less isolated than presently. *Entomacrodus* species, of that island group, possibly arrived during times of decreased isolation. The species existing there now, well differentiated from their closest relatives, are either relatively unchanged relicts (of an earlier, more widely distributed species) or more recently evolved isolates. Gosline and Brock (1960) have noted the high percentage of fish species endemic to the Hawaiian Islands and have pointed out that some Hawaiian species are obvious relicts: e.g., *Chilorhinus platyrhynchus* (Norman), from the Hawaiian Islands and New Britain, both peripheral (the only other species of the genus is in the West Indies); *Acanthurus leucopareius* (Jenkins) from Hawaiian, Marcus, and Easter Islands, all peripheral; *Caranx cheilio* Snyder, from Hawaiian and Easter Islands.

The close relationship of the three endemic Marquesan species of *Entomacrodus* with nonendemic species and the probably younger age of the Marquesas (high islands), as compared with adjacent island groups (Tuamotus, low islands), tend to indicate relatively recent arrival and divergence of *Entomacrodus* species in the Marquesas.

The restriction of *E. rofeni*, *E. stellifer*, and *E. niuafoouensis* to the peripheral area is not so easily explained as are the endemics of the Hawaiian, Marquesas, and Easter Islands. I tentatively believe these three species to be relicts. The disjunct distribution of *E. niuafoouensis*, at least, would tend to support such a belief. The disjunct distribution (fig. 5) of the Pacific populations of *E. decussatus* (not peripherally limited) resulting in a group of northwestern and a group of southeastern populations, indicates that *E. decussatus*

TABLE 5.--Frequency distribution of number of crenulae on ventral margin of upper lip of certain species of *Entomacrodus*

Species	Number of crenulae 18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
cymatobiotus	-	-	-	-	-	-	-	-	3	9	14	23	23	19	9	6	4	2	-	-	-	-
strasburgi	-	1	-	3	4	3	6	4	5	-	-	1	-	-	-	-	-	-	-	-	-	-
chapmani	-	-	-	-	-	-	-	-	-	-	-	-	-	6	2	2	2	3	4	1	2	1
rofeni	-	-	-	-	-	2	2	2	2	1	1	-	-	-	-	-	-	-	-	-	-	-
striatus	1	1	3	2	12	11	31	37	40	36	35	19	7	4	1	2	1	-	-	-	-	-
niuafoouensis	-	-	-	-	-	-	-	-	-	1	4	1	4	7	6	3	2	2	1	-	-	1
epalzeocheilus	-	-	-	-	-	1	-	7	6	14	9	11	8	-	1	-	-	-	-	-	-	-
randalli	-	-	-	-	-	-	1	-	1	-	2	1	-	2	2	-	-	-	-	-	-	-
marmoratus	-	-	-	-	-	-	-	-	-	-	-	1	5	3	12	13	5	5	2	-	1	1

TABLE 6.--General distribution of the species of *Entomacrodus* (X indicates widespread occurrence; locality indicates only known distribution)

Species	Eastern Pacific Ocean	Western Atlantic Ocean	Eastern Atlantic Ocean	Indian Ocean	Western Pacific Ocean (105°E-180° longitude)	Central Pacific Ocean (180°-120°W longitude and Easter Island)
decussatus				Western Australia	X	X
vermiculatus				X		
stellifer					X	
marmoratus						Hawaii
epalzeocheilus				X		Tutuila[1]
niuafoouensis				Madagascar[1]	X	X
randalli						Marquesas
striatus				X	X	X
strasburgi						Hawaii
cymatobiotus					X	X
chapmani						Easter Island
rofeni						Raroia
sealei					X	X
corneliae						Marquesas
chiostictus	X					
caudofasciatus				Christmas, Cocos-Keeling	X	X
vomerinus		Brazil, Fernando Noronja				
nigricans		X				
cadenati			X			
textilis			Ascension, St. Helena			
thalassinus				Seychelles	X	X
macrospilus						Marquesas
Total species	1	2	2	6 or 7[1]		14 or 15[1]

[1] See geographic variation section under *E. niuafoouensis*, where the possibility is discussed that the Madagascar population of *E. niuafoouensis* may be a *niuafoouensis*-type development of *E. epalzeocheilus* and the Tutuila population of *E. epalzeocheilus* may be an *epalzeocheilus*-type development of *E. niuafoouensis*

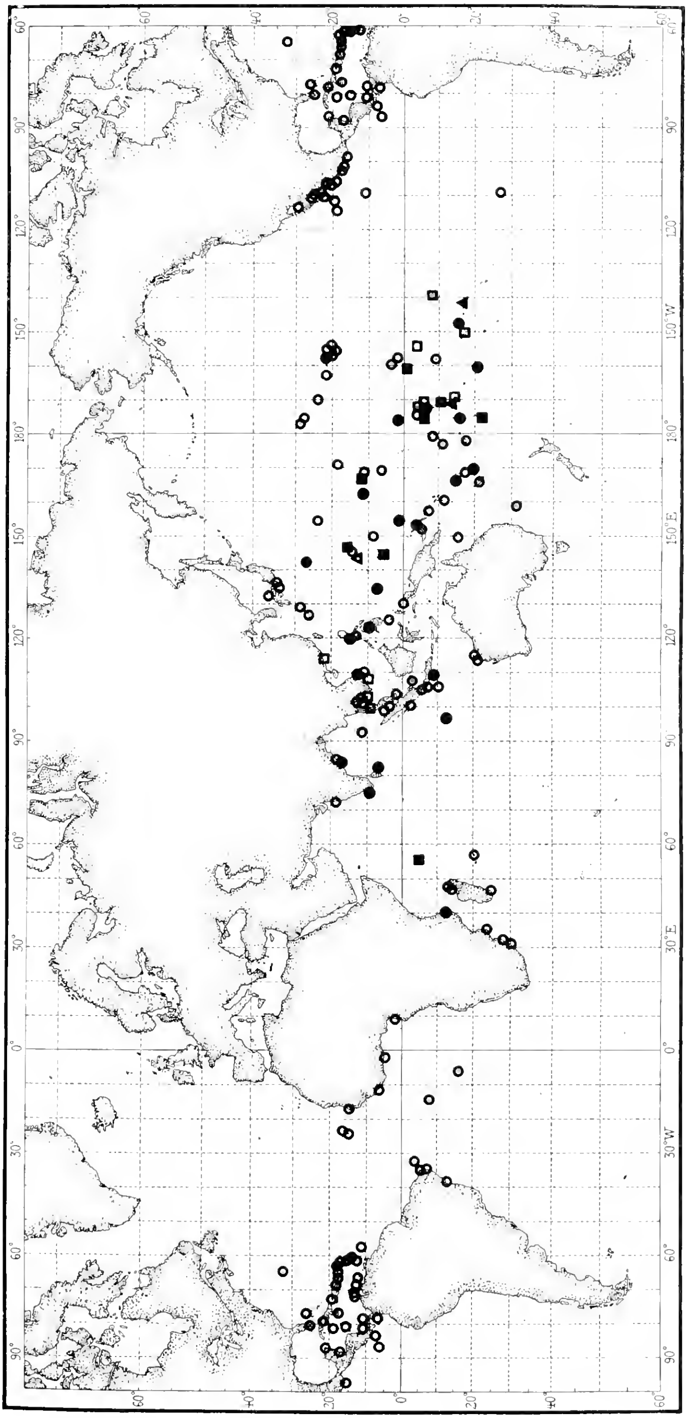

FIGURE 3.—Distribution of the genus *Entomacrodus* (symbols denote number of species at a particular locality).

○ 1 ● 2 □ 3 ■ 4 △ 5 ▲ 6

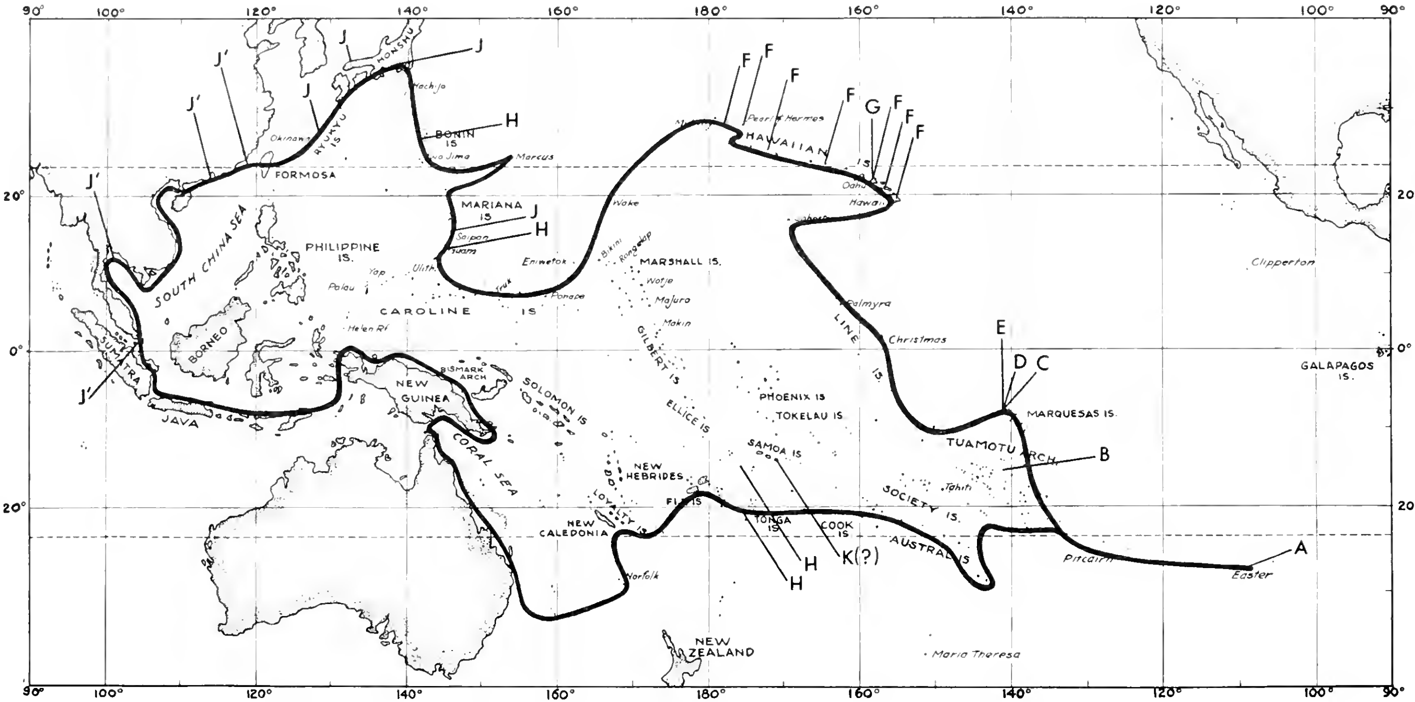

FIGURE 4.—Distribution of some species and subspecies of *Entomacrodus* in the central and western Pacific Ocean.

A	*E. chapmani*	D	*E. macrospilus*	G	*E. strasburgi*	J′	*E. s. lighti*
B	*E. rofeni*	E	*E. corneliae*	H	*E. niuafoouensis*	K	*E. epalzeocheilus*
C	*E. randalli*	F	*E. marmoratus*	J	*E. s. stellifer*		

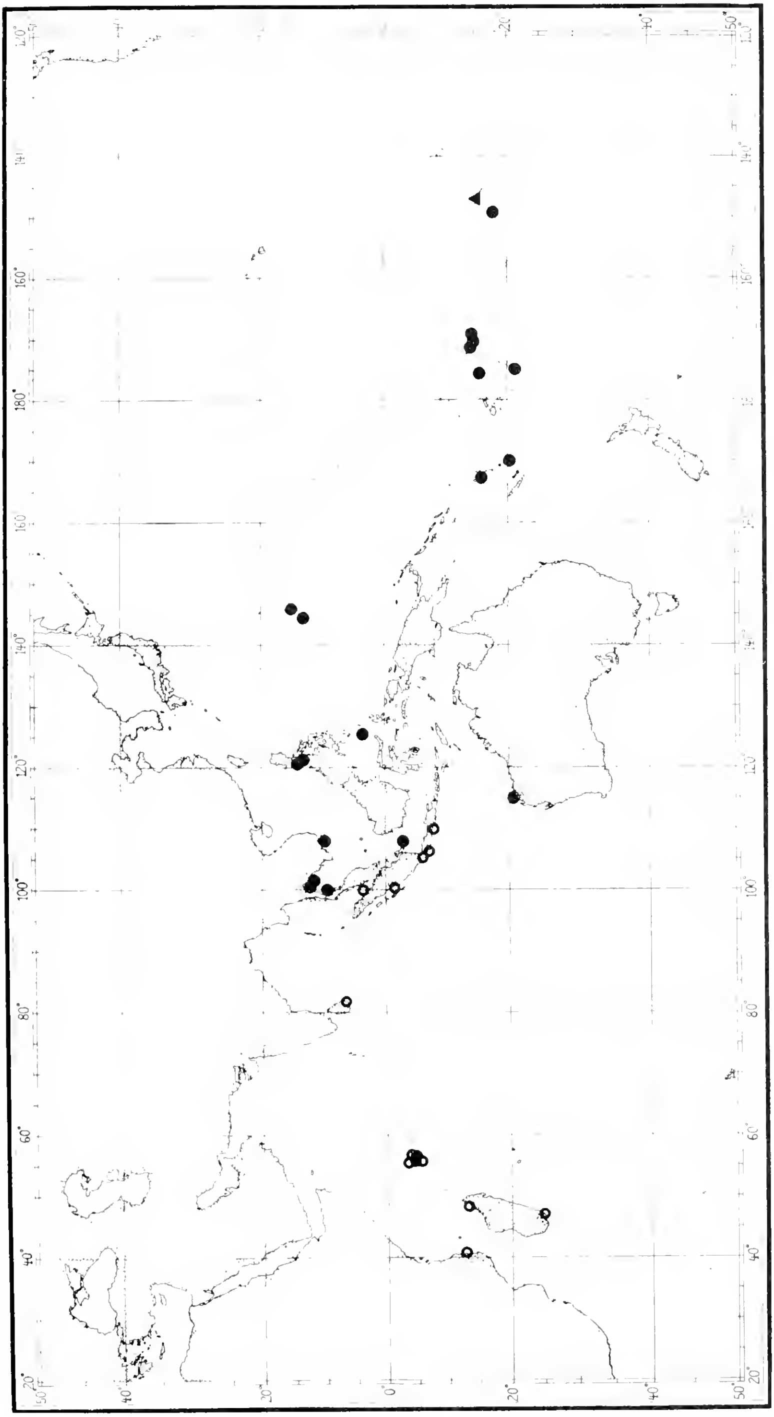

FIGURE 5.—Distribution of some species of *Entomacrodus*.
● *E. decussatus* ○ *E. vermiculatus* ▲ *E. rofeni*

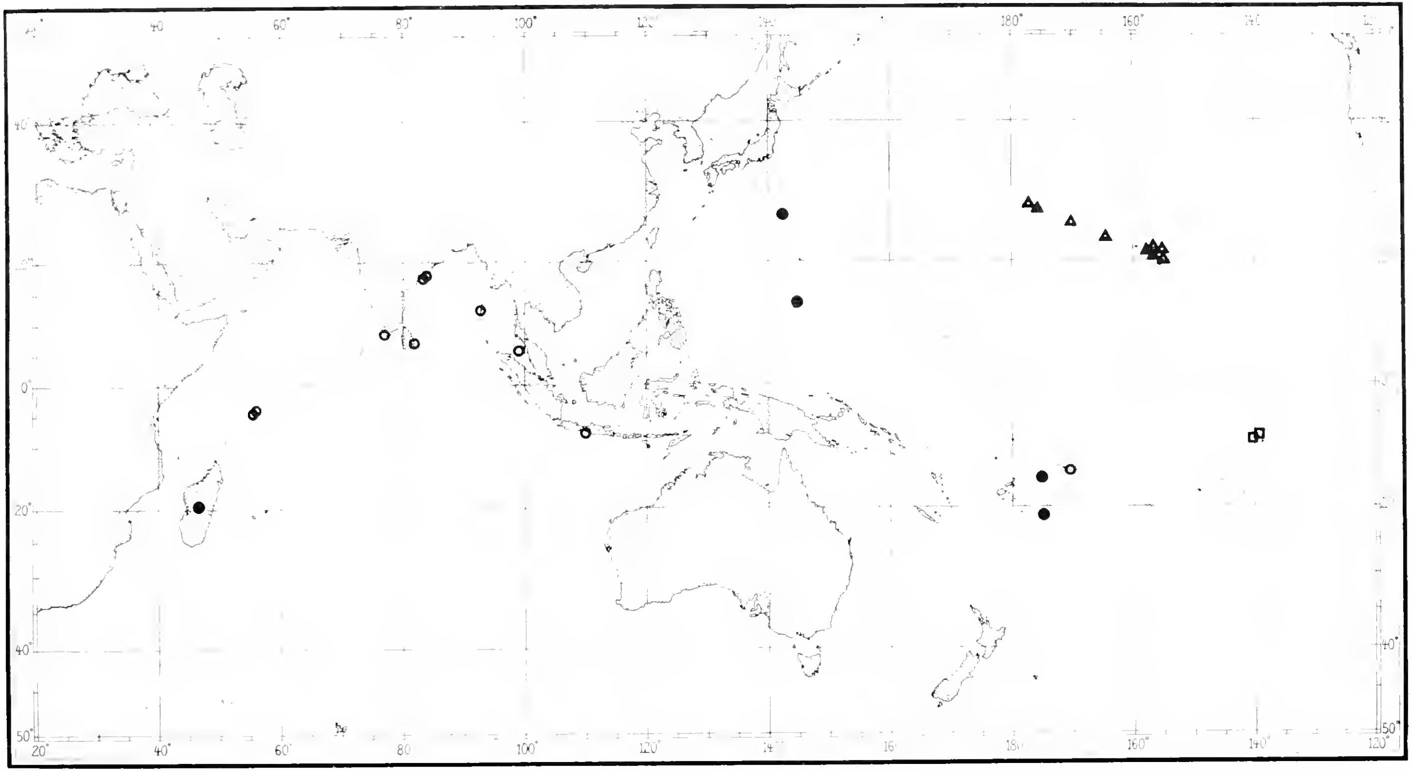

FIGURE 6.—Distribution of some species of *Entomacrodus*.

● *E. niuafoouensis* (Madagascar collection locality unavailable)

○ *E. epalzeocheilus* (Java record based on Bleeker, 1859)

☐ *E. randalli*

△ *E. marmoratus*

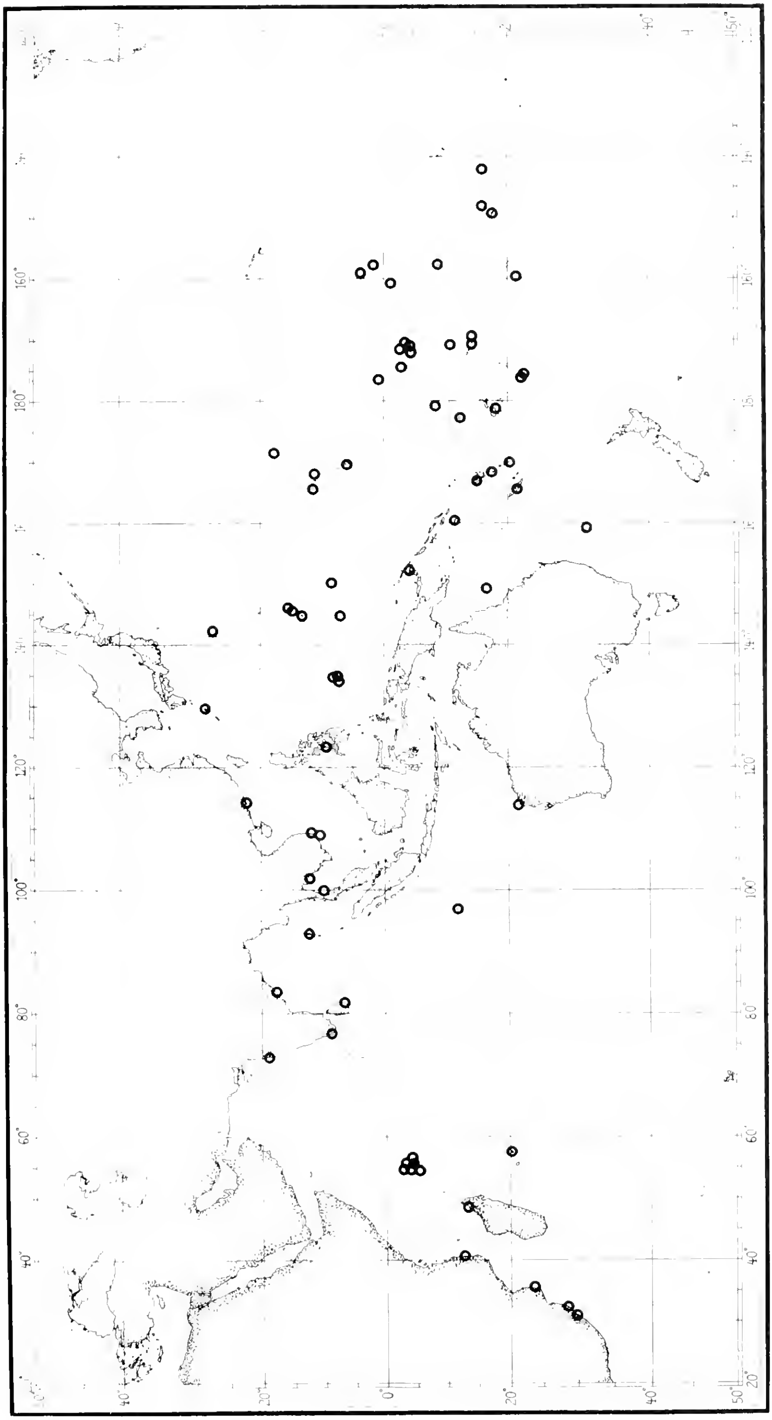

FIGURE 7.—Distribution of *Entomacrodus striatus.*

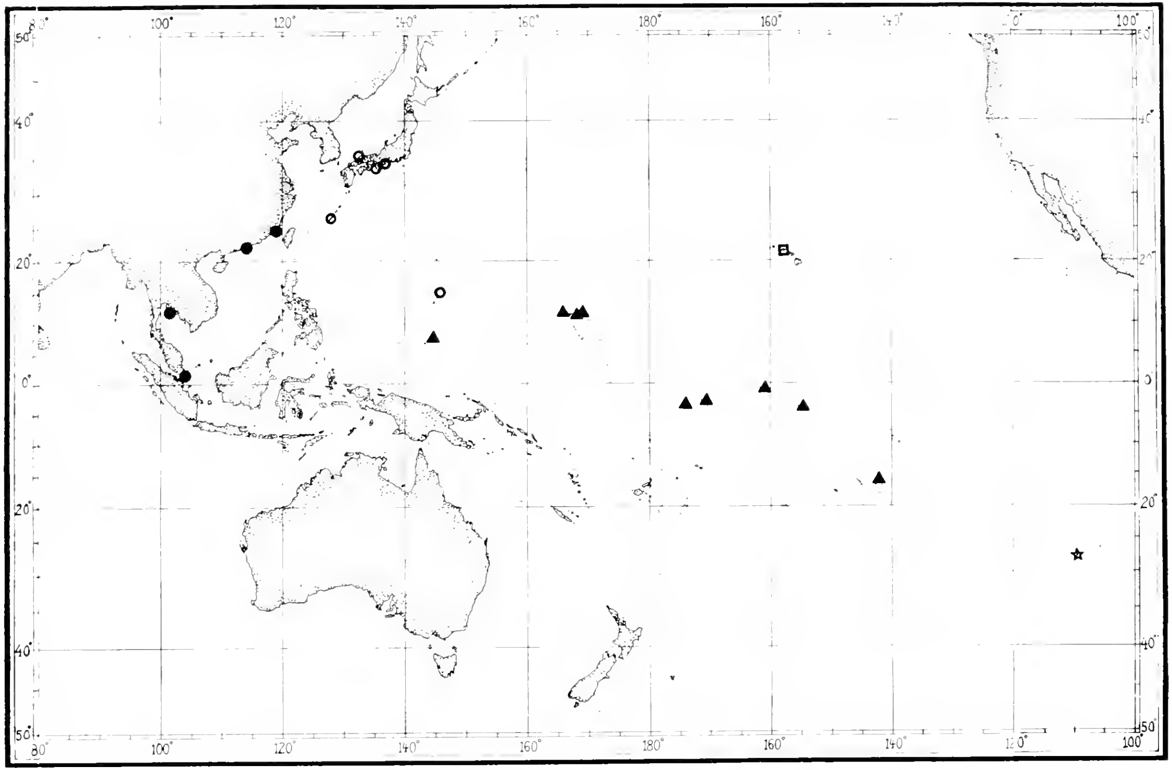

FIGURE 8.—Distribution of some species and subspecies of *Entomacrodus*.

▲ *E. cymatobiotus* ☐ *E. strasburgi* ★ *E. chapmani* ○ *E. s. stellifer* ● *E. s. lighti*

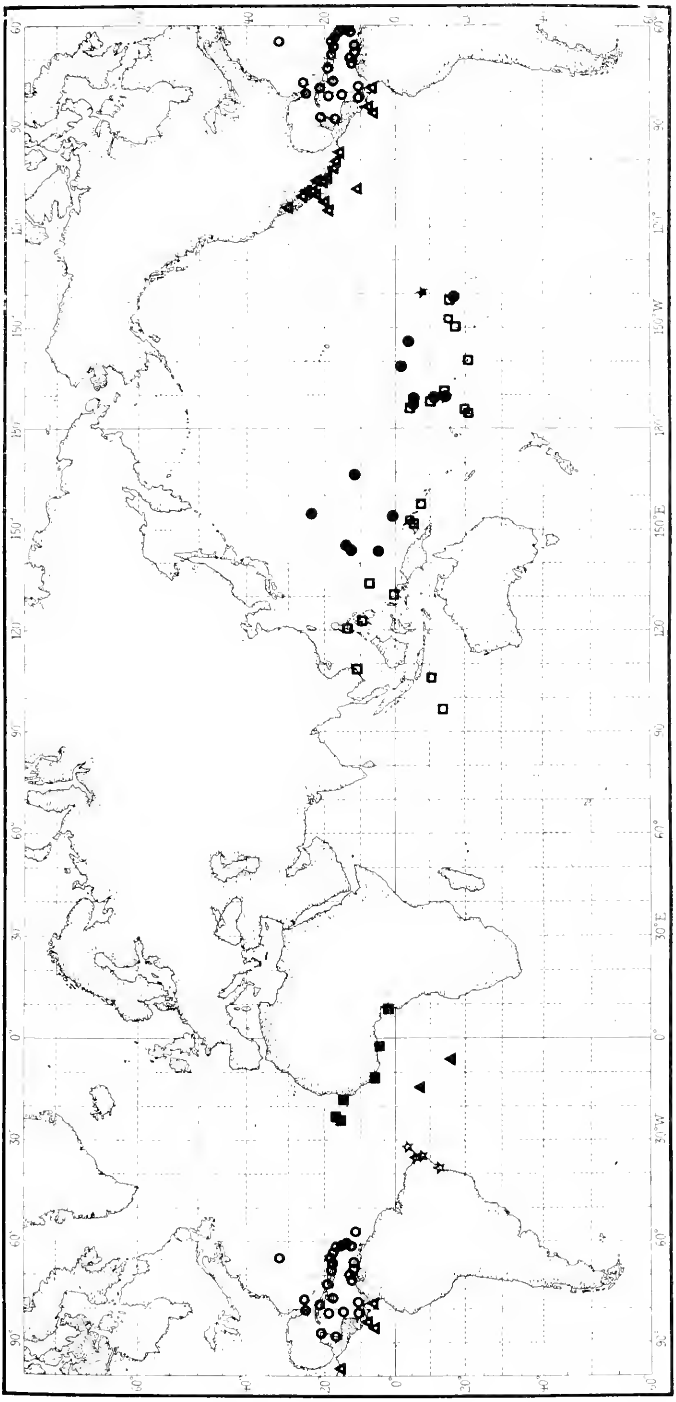

FIGURE 9.—Distribution of some species of *Entomacrodus.*

● *E. sealei*
□ *E. caudofasciatus*
○ *E. nigricans*
▲ *E. textilis*
■ *E. cadenati*
△ *E. chiostictus*
☆ *E. vomerinus*
★ *E. corneliae*

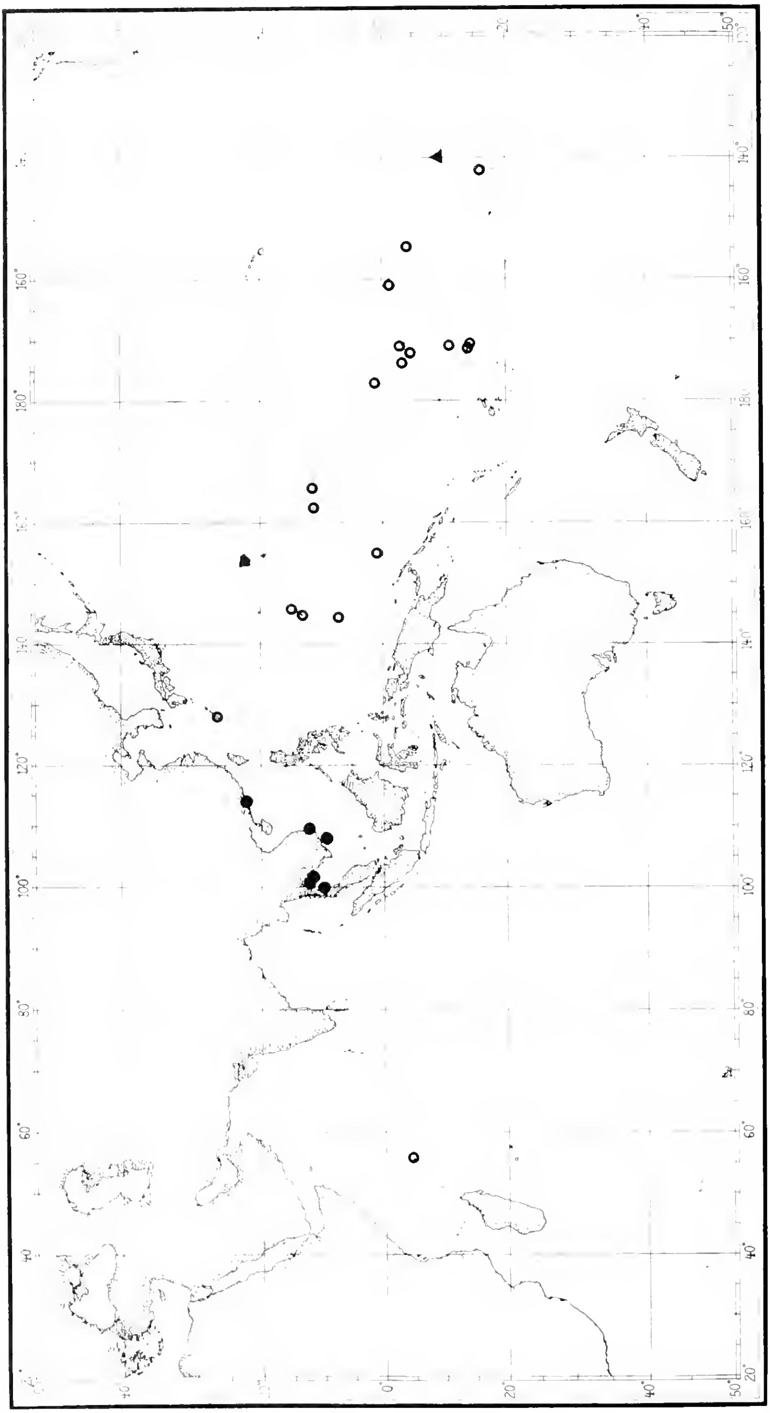

FIGURE 10.—Distribution of *Entomacrodus macrospilus* and the subspecies of *Entomacrodus thalassinus.*

○ *E. t. thalassinus* ● *E. t. longicirrus* ▲ *E. macrospilus* also has a relict type distribution. It may be that the distribution of *E. decussatus* is contracting and will become peripherally limited.

To explain how a relict species might become limited to the periphery, one can draw on the example of the fairy-ring mushroom, which starts from a central area and spreads as an ever enlarging ring around the central area that no longer harbors the species. If the suitable habitat is limited, the mushroom (or fish) will have its last stand along the periphery of the habitat. Matthews (1915) postulated the displacement of primitive forms from a central area by the development of more progressive (successful) forms in the central area.

A perusal of several recent revisions of Indo-Pacific fishes indicates to me that many species will be found whose distributions in the central and western Pacific are restricted to the periphery of the area. The reason for basing a Pacific peripheral distribution hypothesis primarily on *Entomacrodus* species is that there have been available to me more collections from more diverse localities than have been available to authors of similar ichthyological revisions.

A peripheral hypothesis for shore fish distribution in the central and western Pacific makes less perplexing such distributions as that of *Acanthurus leucopareius*. The hypothesis indicates that a species such as *Zebrasoma flavescens* (Bennett) with a known distribution (completely peripheral) of Marcus, Guam, Saipan, Bikini, Wake, Johnston, the Hawaiian Islands, and Tuamotus (Randall, 1955), need not be expected to occur throughout the central and western tropical Pacific.

Key to Species and Subspecies of *Entomacrodus*

1a. Upper lip with crenulae on all or part of ventral margin; gill-rakers usually more than 14 (13 or less only in 8 percent of specimens of *E. caudo*; *fasciatus*, 61 percent of *E. cymatobiotus*, and 50 percent of *E. strasburgi*), several species commonly exceeding 100 mm SL 4

1b. Upper lip without crenulae on ventral margin; gill-rakers 9–15 (1 of 228 specimens with 18 gill-rakers; 13 or fewer gill-rakers in 93.0 percent of specimens); largest specimen known 49.7mm 2

2a. Some circumorbital pores included in dark spot on head posterior to eye; segmented dorsal rays 13–15 (uncommonly 15); segmented anal rays 15–17 (uncommonly 17) 3

2b. No circumorbital pores included in dark spot on head posterior to eye; segmented dorsal rays 15 or 16; segmented anal rays 17 or 18.
macrospilus (Marquesas Islands)

3a. Supraorbital cirrus of males 5.9–9.5 percent of SL, females 3.9–6.5 percent SL (fig. 11) . . . . **thalassinus longicirrus** (South China Sea)

3b. Supraorbital cirrus of males 2.3–4.9 percent of SL, females 2.7–4.7 percent SL (more than 4.1 percent in only one specimen, fig. 11).
thalassinus thalassinus (Indian and Pacific Oceans)

4a. Ventral margin of upper lip with middle one-third to three-fifths crenulate (sometimes weakly and very irregularly) and lateral portions entire . 5

4b. Ventral margin of upper lip completely crenulate (sometimes weakly and irregularly), or only middle one-third to one-half of ventral margin without crenulae (or, as a rarity, left or right side of ventral margin without crenulae) 7

5a. Supraorbital cirri usually 5 or more (less than 1 percent of specimens with less than 5); gill-rakers 19–30 (rarely less than 20); nasal cirri subequal in size and shape; without a distinct dark spot distally on membrane between 1st and 2nd dorsal spines; caudal fin frequently with distinct stripes, bars, or spots; posteriormost proximal anal pterygiophore supporting 2 rays in over 80 percent of specimens; posterior canines of lower jaw rarely absent 17

5b. Supraorbital cirri 1–3 (3 in only 1 of 111 specimens); gill-rakers 14–20 (91 percent of specimens with less than 19); nasal cirri irregular in size and shape, usually 1 cirrus on each anterior nostril a broad flap from which arise smaller cirri (pls. *4c*, *5d*); males (and frequently females) with a distinct dark spot distally on membrane between 1st and 2nd dorsal spines; caudal dusky without distinct stripes, bars, or spots; posteriormost proximal anal pterygiophore supporting a single ray in over 75 percent of specimens; 1 or both posterior canines in lower jaw frequently absent . 6

6a. Color pattern (when specimen immersed in liquid) on side of body consisting of dark bands either broken up by numerous pale or dark vermiculations or reticulations, or with inclusions of fine pale spots or dashes (pl. 4). **stellifer stellifer** (Pacific)

6b. Color pattern on side of body consisting of more or less uniformly, diffusely dark dusky bands or pairs of blotches (usually darker along midsides) neither broken by vermiculations or reticulations, nor with fine pale spots or dashes (pl. 5) . . . . **stellifer lighti** (South China Sea)

7a. Ventral margin of upper lip with middle one-third to one-half entire, lateral portions crenulate (species of Atlantic, Pacific, and Indian Oceans) . . 8

7b. Ventral margin of upper lip completely, sometimes very weakly and irregularly, crenulate (or, as a rarity, one side crenulate and the other entire) (species of Indian and Pacific Oceans) 16

8a. Upper lip with many fine dark spots (occasionally obscured by a dusky overlay); spots sometimes arranged in 7–10 more or less vertical rows; infrequently 1 or 2 rows with spots fused, forming stripes; sometimes ventral 2 spots of each row fused; a dark spot, or stripe, directed dorsoposteriorly from posterodorsal margin of eye, sometimes fused across top of head with stripe from other side; a disjunct continuation of this marking occasionally extends anteroventrally from below eye; an irregular J- or U-shaped dark marking posterior to, and separated from, eye by a pale interspace; shorter arm of marking anterior to longer arm, and open end of marking directed dorsoposteriorly; arms of marking occasionally outlined as dark spots and dashes . . . . **cadenati** (eastern Atlantic)

8b. Upper lip without dark spots; its markings variable, present as solid stripes or bands of variable intensity (sometimes restricted to ventral half of lip), occasionally obscured by a dusky overlay, or upper lip often pale with a few nebulous marks or none; a dark spot, or stripe, directed dorsoposteriorly from posterodorsal region immediately behind eye present only in Brazillian specimens; J- or U-shaped dark mark behind eye absent, but 1 arm of such a mark may be present in Brazillian specimens 9

9a. Darkest and usually largest marking on body a subovate to subquadrate blotch on side below lateral line and just posterior and dorsal to level of pectoral axil 10

9b. Darkest and largest markings on body posterior to region specified in 9a, usually in form of paired vertical bands or paired midlateral blotches, several of which are of similar intensity; occasional specimens with body almost uniformly pale or with diffuse dusky markings 11

10a. Gill-rakers 15–23 (modally 18 or 19); underside of head with alternating dark stripes and pale interspaces extending posteromedially from lower lip; pectoral base with 2 slender elongate dark markings, 1 on base of pectoral rays and 1 on anterior fleshy pectoral base, separated by a pale interspace; upper lip with 7–9 distinct dark stripes, sometimes restricted to ventral half of lip; stripes narrower than pale interspaces; terminal lateral line pores below segmented dorsal fin rays 4–7; supraorbital cirrus length 2.2–4.7 percent SL (usually less than 4.4 percent), about equal in similar size males and females; predorsal commissural pores usually fewer (table 55) than in 10b . . **textilis** (Ascension and St. Helena)

10b. Gill-rakers 13–18 (modally 14–16); underside of head unmarked, diffusely dusky, or with alternating pale stripes and dusky interspaces extending posteromedially from lower lip; some specimens from New Britain with slight indications of dark stripes; pectoral base uniformly or irregularly dusky, without slender elongate dark markings separated by a pale interspace (except 1 specimen from New Britain); upper lip usually diffusely dusky, infrequently with about 9 irregular faint dusky bands (never very distinct) mostly restricted to ventral half of lip; terminal lateral line pores in area below and between dorsal fin spine 8 and dorsal ray 5 (usually anterior to dorsal ray 3); supraorbital cirrus length 2.5–7.8 percent SL (usually less than 5 percent in females and more than 5 percent in males); predorsal commissural pores usually more (table 65) than in 10a . . . . **caudofasciatus** (Indian and Pacific Oceans)

11a. Preopercular series of pores with pairs or multiples of pores at 3 or more positions (rarely at only 3 positions). 12

11b. Preopercular series of pores with simple pores at all positions, or less than 3 positions with paired pores (except *E. chiostictus* with 0–22 percent, average 8 percent, of specimens, depending on population, with 3 or 4 positions with paired pores; only 2 specimens of over 500 with 5 positions paired), positions never with multiples of pores. 13

12a. Head with 2 conspicuous dark, more or less vertical, stripes behind each eye; upper lip variably pale and dusky. . **corneliae** (Marquesas Islands)

12b. Head without conspicuous dark markings; upper lip with 7 pale stripes alternating with broader dusky bands (occasionally median and one lateral stripe on each side Y- or ( )-shaped).
sealei (western Pacific, not Marquesas)

13a. Segmented dorsal fin rays usually 16 or 17; segmented anal fin rays usually 17 or 18; gill-rakers commonly 20–24; predorsal commissural pores usually fewer at any given size (compare data in table 52 with data in tables 49, 61, 65); vertebrae usually 35 or 36.
vomerinus (Brazil and Fernando Noronja)

13b. Segmented dorsal fin rays usually 13–15; segmented anal fin rays usually 15 or 16; gill-rakers usually 13–19 (rarely 20 or 21); predorsal commissural pores usually more numerous at any given size; vertebrae usually 33 or 34 14

14a. Supraorbital cirrus length 1.9–3.9 percent SL (usually less than 3.3 percent); upper lip usually with 7–9 dark stripes (frequently present only as faint indications and restricted to lower half of lip) alternating with pale bands; dark stripe on fleshy pectoral base separated by pale area from base of pectoral rays; preopercular series of pores simple, rarely with one or two positions with paired pores.
nigricans (Caribbean Sea, Florida, Bermuda)

14b. Supraorbital cirrus length 2.7–7.9 percent SL (usually more than 3.2 percent except in specimens from Cape San Lucas where cirri appear to be malformed); color pattern of upper lip variable, dark stripes present or absent, numbering up to 14; dark stripe present or absent on fleshy pectoral base; preopercular series of pores varying from all positions simple to all positions with paired pores 15

15a. A dark spot frequently present just posterior to eye; preopercular series of pores frequently including paired pores at 1 or more positions (60 percent of specimens); upper lip color pattern frequently of 10–14 dark stripes separated by pale interspaces, occasionally of about 7 pale stripes separated by dusky interspaces, or irregularly or uniformly dusky; a dark stripe frequently present on fleshy pectoral base separated by a pale area from pectoral rays . . . . . **chiostictus** (eastern Pacific)

15b. No dark spot just posterior to eye; preopercular series of pores usually all simple (never more than 1 pair included in series); no dark stripe present on fleshy pectoral base; lip stripes, when present, fewer than 8.
caudofasciatus (Tahiti, Raroia, Makatea, Rarotonga)

16a. Pseudobranchial filaments 5–16 (commonly 10 or more); segmented anal rays 16–19 (commonly 18–19, associated with more than 3 predorsal commissural pores); segmented dorsal rays 15–18 (commonly 17 or 18); main supraorbital cirrus with rarely less than 2 lateral branches; 13th dorsal spine frequently obvious (when obvious, usually more than 2.9 percent SL); membrane of last dorsal ray frequently attached over, or posterior to, caudal origin; color pattern of sides frequently much vermiculated, reticulated, or of several irregular light to dark longitudinal stripes; eye usually larger at any given size (table 3); commonly attaining sizes of over 100 mm SL (up to 153 mm) 17

16b. Pseudobranchial filaments 4–12 (rarely more than 9); segmented anal rays 14–18 (commonly 18 in only *E. rofeni,* which has only 3 predorsal commissural pores); segmented dorsal rays 13–17 (rarely 17); main supraorbital cirrus with or without lateral branches; 13th dorsal spine usually not obvious (when obvious, usually less than 2.9 percent SL); membrane of last dorsal ray attached anterior to caudal origin; color pattern of sides never vermiculated, reticulated, or of longitudinal stripes; eye usually smaller at any given size (table 3); only 2 species (*E. marmoratus* and *E. epalzeocheilus*) attaining a size of 100 mm SL (largest specimen known 121 mm) 18

17a. Color pattern of body of specimens over 80 mm SL with large number of tiny vermiculations; pectoral fin diffusely dusky, sometimes with a reticular pattern of fine dark lines; dorsal rays 15–17 (modally 16); anal rays 16–18; pores before anterior nostril 2 or more (55 of 56 specimens).
vermiculatus (Indian Ocean other than Australia)

17b. Color pattern of body of specimens over 80 mm SL quite variable, but never consisting of tiny vermiculations; pectoral fin usually striped, spotted, or

barred; dorsal rays 16–18 (modally 17); anal rays 16–19; pores before anterior nostril varying in number with population, but typically 1.
decussatus (Pacific Ocean and western Australia)

18a. Two to 20 cirri on each side of nape (sometimes in form of single main cirrus with several branches at its distal end, the free tip of each branch here counted as a cirrus) 19

18b. One cirrus on each side of nape (only rarely, in large specimens, 2 cirri on one side of nape) 20

19a. Nuchal cirri on each side almost always arising from 2 main bases (patches), the medial cirri patch the broadest based and usually with more cirri than the lateral patch; 1 pore before each anterior nostril; main supraorbital cirrus with at least 3 cirri arising from both its medial and lateral margins; 29–39 crenulae on ventral margin of upper lip (usually more than 30); preopercular series of pores with 0–7 positions with pairs or clusters of pores (less than 4 pairs or clusters in 73 of 80 specimens).
marmoratus (Hawaiian Islands from Midway to Hawaii)

19b. Nuchal cirri on each side arising from a single base (very rarely arising from 2 main bases on 1 side only); 2 or more pores before each anterior nostril (except in some specimens smaller than 60 mm SL, where a single pore may be present); main supraorbital cirrus with cirri arising only along its mesial margin (5 specimens with 1 cirrus and 1 with 2 cirri arising from lateral margin); 23–32 crenulae on ventral margin of upper lip (usually less than 30); preopercular series of pores with 4–7 (usually more than 4) positions with pairs or clusters of pores.
epalzeocheilus (Indian Ocean and Samoa)

20a. Pairs or clusters of pores at 2–5 positions in preopercular series of pores; up to 69 predorsal commissural pores (frequently more than 20) 21

20b. No pairs or clusters of pores included in preopercular series of pores (all pores simple); up to 33 predorsal commissural pores (rarely more than 20) 24

21a. One pore before each anterior nostril; gill-rakers 15–24 22

21b. Two to 4 pores before each anterior nostril (except in one specimen which had 2 on one side and 1 on the other): gill-rakers 23–26 23

22a. Gill-rakers 15–21 (rarely more than 19); pseudobranchial filaments 4–7; upper lip color pattern uniformly dusky or consisting of 7 or 8 dusky bands separated by pale stripes; no dark humeral blotch.
sealei (western Pacific)

[Note: Almost all specimens entering key couplet 22a will be *E. randalli* as only a few unusual specimens of *E. sealei* have the upper lip completely crenulate.]

22b. Gill-rakers 21–24; pseudobranchial filaments 8–10; upper lip pattern consisting of numerous diffuse spots; a slender dark humeral blotch present.
randalli (Marquesas Islands)

23a. Seven to 9 diffusely dusky bands on lip; dark blotch in humeral region conspicuous; nuchal cirrus 4.1–4.7 percent SL. **niuafoouensis** (Madagascar)

23b. Seventeen to 23 dusky stripes on upper lip; dark blotch in humeral region, if present, diffuse, not obvious; nuchal cirrus 2.4–3.9 percent SL.
niuafoouensis (Pacific Ocean)

24a. Predorsal commissural pores 3 in specimens 26–42 mm SL (apparently remaining constant); anal rays 18 (one specimen out of 13 with 17 rays); vertebrae 35; head smaller, 21.3–23.0 percent SL in specimens 26–42 mm SL, decreasing in relative size with increasing SL.
rofeni (Raroia, Tuamotus)

24b. Predorsal commissural pores more than 3 in specimens 26–42 mm SL (except 33–80 percent of specimens of *E. striatus*, depending on SL class, table 32); number of pores usually increases with increase in SL; anal rays 14–17 (less than 1 percent of specimens of *E. striatus* with 18 rays); vertebrae 33–35 (rarely 35); head larger, 21.3–26.3 percent of SL in specimens 26–42 mm SL, decreasing in relative size with increase in SL (head lengths rarely overlapping with *E. rofeni* in similar-sized specimens: see tables 35, 39, 42, 44, 66) 25

25a. A distinct subovate to subquadrate, more or less uniformly dark spot on body in humeral region dorsal to level of pectoral axil (this mark usually much larger and darker than other body markings); no dark spot just posterior to orbit . . . . . **caudofasciatus** (Indian and Pacific Oceans)

25b. No distinct, uniformly dark spot on body in humeral region dorsal to level of pectoral axil (markings in this region, when present, are diffuse, scarcely larger or darker than other body markings and correlated with an elongate dark spot just posterior to orbit) 26

26a. Color pattern on body usually consisting of clusters of dark spots, diameter of individual spots usually smaller than half orbital diameter; predorsal commissural pores usually fewer at any given size (compare table 52 with tables 41, 43); first dorsal ray 8.5–13.5 percent SL, usually less than 12.0 percent; main or longest supraorbital cirrus frequently with more than 2 lateral cirri branches; soft dorsal fin rays frequently 16 or 17, rarely 14 . . . . **striatus** (Indian and Pacific Oceans)

26b. Color pattern on body either absent or consisting of dark blotches, usually paired, some of which equal or exceed orbital diameter; predorsal commissural pores usually more at any given size (compare tables 41 and 43 with table 32); first dorsal ray 11.7–16.8 percent SL, usually more than 13.0 percent; main or longest supraorbital cirrus usually without lateral cirri branches, never more than 1; soft dorsal fin rays 13–15, never 16 or 17 27

27a. Distinct dark spot present on head posterior to orbit at or above midorbital level (pls. 15*c*, 17*a*); greatest width of spot usually more than half orbital diameter; paired blotches on body sides always present, well marked; dorsal lip crenulae 31–39; no dusky bands separated by pale stripes on upper lip . . . . **chapmani** (Easter Island)

27b. Distinct dark spot present or absent on head posterior to orbit at or above midorbital level; when present, greatest width of spot usually less than half orbital diameter (pls. 16*c*, 17*b*); paired blotches on body sides usually faint or absent; dorsal lip crenulae 19–35; dusky bands separated by pale stripes present or absent on upper lip (not Easter Island) 28

28a. Dorsal lip crenulations 26–35 (26 in only 3 of 107 specimens); dark spot, usually elongate, just posterior to eye at or above midorbital level, followed by an elongate pale area and then a diffuse dusky blotch lighter than the spot (pls. 15*c*, 17*a*); markings on upper lip a diffuse sprinkling of melanophores; predorsal commissural pores 6–22 (usually more than 10) in specimens 5–35 mm SL; first soft dorsal ray 14.0–16.8 percent SL in specimens 25–35 mm SL . . **cymatobiotus** (Pacific Ocean, not Hawaii)

28b. Dorsal lip crenulations 19–26; no dark spot on head posterior to eye at or above midorbital level; markings on upper lip consisting of 9 or 10 dusky bands alternating with pale interspaces; predorsal commissural pores 5–11 (rarely more than 9) in specimens 25–35 mm SL; first soft dorsal ray 10.7–14.6 percent SL in specimens 25–35 mm SL.
strasburgi (Hawaiian Islands)

Entomacrodus decussatus (Bleeker)

PLATE 1

Salarias decussatus Bleeker, 1858, Nat. Tijdschr. Nederl. Indië, vol. 15, pp. 230–231 [western Biliton and Sangi (Sangir) islands].

Salarias aneitensis Gunther, 1877, Journ. Mus. Godeffroy, vol. 4, no. 13, p. 205, pl. 118A [Aneiteum].

Salarias atkinsoni Jordan and Seale, 1906, U.S. Bur. Fish. Bull. 25 (1905), p. 428 [Apia, Samoa].

DESCRIPTION.—Segmented dorsal fin rays 16–18 (rarely 18); segmented anal fin rays 16–19 (rarely 16); posteriormost anal pterygiophore supporting 1 or 2 external elements (supporting 2 in 95.5 percent of specimens); total gill-rakers on first arch 17–30, tending to increase in number with increase in SL (table 7); pseudobranchial filaments 5–17, tending to increase in number with increase in SL (table 8); vertebrae 34–36 (usually 35); supraorbital cirri 1–28, increasing in number with increase in SL (table 9); main, or longest, supraorbital cirrus with many short branches on both mesial and lateral margins; nape with 1 cirrus on each side (frequently with small side branches in specimens over 55 mm SL); predorsal commissural pores 3 to more than 50, increasing in number with increase in SL (table 10); preopercular series of pores varying from all positions with simple pores to all positions with pairs or multiples of pores (specimens less than 40 mm SL frequently with all positions with simple pores; specimens over 90 mm SL have at least 1 pair of pores included in the series); 1 or 2 (rarely 3) pores before each anterior nostril (see also geographic variation below); lateral line pores terminating on side in area below and between dorsal ray 2 and caudal base (posterior terminus somewhat determined by size; specimens less than 40 mm SL usually have last pore anterior to level of dorsal ray 11; specimens more than 70 mm SL usually have last pore posterior to level of dorsal ray 10); ventral margin of upper lip of specimens less than 80 mm SL usually partially (centrally) crenulate and partially entire (laterally); lip of specimens over 80 mm SL frequently weakly but completely crenulate (crenulae difficult to count).

Proportional measurements: See tables 3, 4, and 11.

Males develop slight modifications of the skin of the anal spines. These modifications appear in the form of fleshy distal extensions of the skin at the tip of the spine. Greatest development occurs on the second spine, which may become plicate at the tip. Only a few specimens, the smallest of which was 115 mm SL, were available with these modifications. It is presumed that these specimens represented mature males.

The largest male examined was 153 mm SL (mature), and the largest female 133 mm. Females outnumbered males in most size classes. The smallest specimen seen was approximately 15.5 mm SL and was not an ophioblennius stage. Specimens less than 20 mm SL had vomerine teeth but lacked posterior canines in the lower jaw.

COLOR PATTERN OF PRESERVED SPECIMENS.—There is considerable variation in color pattern of specimens, including individual, ontogenetic, and geographic variations. Specimens of 16–45 mm show indications of 5½ to 6½ pairs of irregular bands on the side of the body. The bands are usually broken into three portions: dorsal, middle, and ventral. The midportions of each pair of bands are usually fused (see Schultz and Chapman, 1960, plate 116 F and H) and sometimes appear ringlike. At about 50 mm SL specimens begin to exhibit indications of irregular undulating stripes that overlay, incorporate, and frequently obscure the bands. The striping is least obvious in specimens from the New Hebrides, which are marked with a sprinkling of fine dark spots and dashes covering the sides. Large specimens from all localities except the Gulf of Thailand, South China Sea, Montebello, and Tahiti (only one specimen from each of the last two localities) have less than five diffuse dark spots dorso-

TABLE 7.--Frequency distribution of number of gill-rakers of specimens of *Entomacrodus decussatus* arranged by SL classes (in mm)

Classes	Gill-rakers 17	18	19	20	21	22	23	24	25	26	27	28	29	30
15-19.9	-	-	1	-	-	-	-	-	-	-	-	-	-	-
20	1	1	-	-	-	-	-	-	-	-	-	-	-	-
25	-	-	3	1	3	3	2	-	-	-	-	-	-	-
30	-	-	-	-	1	1	-	1	2	-	-	-	-	-
35	-	-	1	-	2	1	1	2	2	-	-	-	-	-
40	-	-	-	-	-	3	4	-	-	-	1	-	-	-
45	-	-	-	1	1	-	2	1	-	1	1	-	1	-
50	-	-	-	-	-	1	1	-	-	-	-	-	-	-
55	-	-	-	-	-	1	2	3	2	4	2	-	-	-
60	-	-	-	-	-	1	1	1	1	1	2	2	-	-
65	-	-	-	1	-	-	-	-	4	1	2	-	-	-
70	-	-	-	-	1	2	2	4	-	1	1	1	-	-
75	-	-	-	-	-	2	-	-	-	-	2	-	-	-
80	-	-	-	-	1	-	1	3	-	-	1	-	-	1
85	-	-	-	-	-	-	-	1	-	-	-	-	-	-
90	-	-	-	-	-	-	-	-	-	-	1	1	1	-
95	-	-	-	-	-	2	-	-	-	-	-	-	-	-
100-109.9	-	-	-	-	-	-	2	1	1	1	-	-	-	-
110	-	-	-	-	-	1	-	2	2	1	1	-	-	-
120	-	1	-	-	-	-	2	1	3	-	-	1	-	-
130	-	-	-	-	-	-	-	-	1	1	-	1	-	-
140	-	-	-	-	-	-	-	-	-	-	1	-	-	-
150	-	-	-	-	-	-	-	1	-	-	-	-	-	-

anteriorly on the sides. Specimens from the other localities have numerous dark spots in that region.

The upper lip varies from uniformly dusky to having three broad, dark bands separated by pale interspaces.

At least the soft portion of the dorsal fin, and sometimes the caudal fin, bear a number of discrete dark pinstripes and dashes in specimens from the New Hebrides, Tau, Tutuila, Samoa, Tongatapu, and Niuafou Islands (the latter five islands are closely associated geographically). Specimens examined from the other localities have the dorsal and caudal fins marked with diffuse dark spots which may or may not appear as enlargements of portions of what might have been a basic pinstripe pattern. The spots are usually restricted to positions over the rays while the pinstripes and dashes are continuous

TABLE 8.--Frequency distribution of number of pseudobranchial filaments of specimens of *Entomacrodus decussatus* arranged by SL classes (in mm)

Classes	Pseudobranchial filaments												
	5	6	7	8	9	10	11	12	13	14	15	16	17
15-19.9	1	2	-	-	-	-	-	-	-	-	-	-	-
20	-	1	-	-	-	-	-	-	-	-	-	-	-
25	-	1	-	5	1	-	-	-	-	-	-	-	-
30	-	-	1	4	2	-	-	-	-	-	-	-	-
35	-	-	1	3	3	-	-	-	-	-	-	-	-
40	-	-	-	1	5	2	1	-	-	-	-	-	-
45	-	-	-	1	2	2	2	-	-	-	-	-	-
50	-	-	-	-	2	-	-	-	-	-	-	-	-
55	-	-	-	-	2	5	4	3	-	-	-	-	-
60	-	-	-	-	-	2	4	2	1	-	-	-	-
65	-	-	-	-	1	2	1	3	2	-	-	-	-
70	-	-	-	-	2	2	2	3	2	1	-	-	-
75	-	-	-	-	-	1	1	1	-	-	-	-	-
80	-	-	-	-	-	2	-	3	1	-	-	-	-
85	-	-	-	-	-	-	1	1	-	-	-	-	-
90	-	-	-	-	-	-	-	2	1	-	-	-	-
95	-	-	-	-	-	1	-	-	1	-	-	-	-
100-109.9	-	-	-	-	-	1	-	-	4	-	-	-	-
110	-	-	-	-	1	-	2	2	1	-	-	1	-
120	-	-	-	1	-	-	1	2	-	1	-	1	1
130	-	-	-	-	-	1	-	-	2	-	-	-	-
140	-	-	-	-	-	-	-	-	1	-	-	-	-
150	-	-	-	-	-	-	1	-	-	-	-	-	-

across the rays or are restricted to the membrane between the rays. Many specimens over 40 mm SL have two to three narrow, dark longitudinal stripes or bands on the anal fin. On close examination, all specimens are found to have these stripes but the area between the stripes is sometimes almost as dark as the stripes themselves and thus the pattern is obscured.

Geographic variation.—(See also color pattern above.) Most specimens from Tau Island and many from Tongatapu Island have two or three pores before one or both anterior nostrils. Specimens from the other localities, with rare exceptions, have only one pore before each anterior nostril.

In at least two populations of *E. decussatus*, males appear to have higher segmented dorsal fin ray averages than females. In the Tongatapu population, of 23 males examined, 2 had 16 rays, 20 had 17 rays, and 1 had 18 rays. Of 23 females examined, 10 had 16 rays and 13 had 17 rays. In the South China Sea and Gulf of Thailand population, all 6 males examined had 17 rays; 5 females had 16 rays, and 5 had 17 rays. Sexual dimorphism of other meristic characters

TABLE 9.--Frequency distribution of number of supraorbital cirri of specimens of *Entomacrodus decussatus* arranged by SL classes (in mm)

Classes	Cirri number																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
15-19.9	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	2	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	1	2	3	-	2	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30	-	1	-	1	2	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35	-	-	-	-	1	-	1	6	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
40	-	-	-	-	1	2	2	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
45	-	-	-	-	-	2	-	-	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
50	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
55	-	-	-	-	-	-	2	2	2	4	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
60	-	-	-	-	-	-	-	1	1	2	3	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
65	-	-	-	-	-	-	-	-	-	3	2	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
70	-	-	-	-	-	-	-	1	3	2	4	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
75	-	-	-	-	-	-	-	1	-	1	-	-	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-
80	-	-	-	-	-	-	-	-	1	1	3	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
85	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-
90	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
95	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
100-109.9	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	1	-	-	-	1	-	-	1	-	-	-
110	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2	-	-	1	-	-	1	-	1	-	-	-
120	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	3	1	-	-	-	-	-	-	-	-	-	1
130	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
140	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
150	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-

was not noted, nor was sexual dimorphism of dorsal fin ray counts noted in specimens from other localities, but I do not consider my data conclusive.

NOMENCLATURE.—Bleeker based his description of *Salarias decussatus* on four specimens, 51–128 mm (total length?), from Biliton and Sangir Islands. There are only four specimens, RMNH 4778, from Biliton and Sangir Islands in the Leiden museum. These specimens are approximately 40, 51, 105, and 127 mm SL, which indicates a possible discrepancy in the measurement of the largest specimen (a specimen 40 mm SL would be about 52 mm total length, 128 mm SL, about 155 mm total length). All four specimens are in poor condition. I here designate the 105 mm (approximately 128 mm total length) specimen from Sangir as lectotype. The lectotype, a male, in better condition than the other specimens, has 16 predorsal commissural pores; the paralectotypes have 10, 12, and more than 30 pores. The 127 mm paralectotype has two pores before each anterior nostril; the lectotype and other paralectotypes have one pore before each anterior nostril.

Salarias aneitensis was described by Günther from two dried specimens, seven inches long, in the British Museum. These specimens are no longer extant in the BMNH collections, apparently having been lost during World War II when the BMNH types were removed from

TABLE 10.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus decussatus* arranged by SL classes (in mm)

Classes	Number of pores																							
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	>25
15-19.9	11	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	1	1	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	-	-	-	4	5	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30	-	-	-	-	3	2	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-
35	-	-	1	-	1	1	-	1	1	1	-	-	-	1	-	1	1	-	1	-	-	-	-	-
40	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1	1	1	-	-	1	-	1	3	-
45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	1	1	-	-	3
50	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	1
55	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	2	-	-	1	10
60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	2	-	-	1	5
65	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	2	1	-	5
70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	1	6
75	-	-	-	-	-	-	-	-	1	-	-	-	-	1	1	1	-	-	-	-	-	-	-	1
80	-	-	-	-	-	-	-	-	1	-	-	-	-	1	1	-	1	-	-	-	-	-	-	3
85	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
90	-	-	-	-	-	-	-	-	-	-	.1	-	-	-	1	-	-	-	-	-	-	-	-	1
95	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
100-109.9	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	1	-	-	-	-	-	1	2
110	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-	-	1	1	1	-	1
120	-	-	-	-	1	-	-	-	-	-	1	1	-	-	1	-	-	-	1	-	1	-	-	2
130	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
140	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
150	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

the museum for safer storage. Chapman (1951, p. 279) supposedly reported on Günther's types, but the specimens he saw were too small (107 and 125 mm, much less than 7 inches) to be the types and were undoubtedly BMNH 1931.7.4.4–5, also from Aneiteum.

Chapman (1951) considered *E. aneitensis* a synonym of *E. decussatus*, but Schultz and Chapman (1960) recognized both species. The basis for this latter recognition seems concerned primarily with color pattern and the supposed fact that the nuchal tentacle of *E. decussatus* had one or two short cirri on its margin, while the nuchal tentacle of

TABLE 11.--Proportional dimensions as percent SL of specimens of *Entomacrodus decussatus* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DS13	DR1	PECL	PELL	CL
USNM 124118	Guam	-	32.1	25.5	9.0	6.2	4.1	11.8	4.7	14.0	26.0	19.6	25.5
USNM 124118	Guam	♂	35.4	26.6	8.2	6.2	3.4	12.2	3.7	13.8	22.6	19.2	-
USNM 115474	Tutuila	♀	37.8	26.0	8.3	5.2	2.6	11.7	3.4	13.5	25.7	20.0	24.9
USNM 115474	Tutuila	♂	38.5	25.1	8.2	4.5	2.6	11.9	2.6	14.6	25.4	18.5	24.1
USNM 124118	Guam	♀	42.2	24.6	8.1	7.1	2.8	12.6	4.3	15.4	23.9	19.0	26.1
USNM 115474	Tutuila	♂	44.7	25.0	8.5	4.5	3.1	12.1	3.4	11.2	24.8	19.0	24.6
USNM 115474	Tutuila	♀	55.1	24.3	7.4	4.5	2.7	12.7	3.4	14.1	24.0	17.0	25.4
USNM 115474	Tutuila	♀	55.8	24.0	7.6	3.5	2.8	12.2	3.5	14.2	24.0	17.0	23.2
USNM 115474	Tutuila	♀	62.1	24.5	7.6	3.7	2.4	12.2	3.4	13.5	23.2	16.4	22.8
USNM 124118	Guam	♀	68.2	24.2	6.7	6.0	2.2	11.9	3.8	13.3	23.6	17.7	24.0
USNM 115474	Tutuila	♀	71.4	24.2	7.0	4.3	2.1	12.0	3.5	12.6	22.8	14.7	22.4
USNM 139838	Guam	♂	72.9	23.3	6.6	6.2	2.7	-	4.1	12.9	23.0	15.1	24.7
SU 62003	S. China Sea	♂	75.5	22.5	6.1	6.4	2.0	11.9	4.0	13.8	23.3	15.2	25.2
USNM 139838	Guam	♀	79.6	23.4	6.2	6.2	3.1	11.3	3.9	12.6	23.5	15.7	24.5
USNM 139838	Guam	♀	81.8	23.2	6.4	4.4	2.3	12.2	5.4	13.2	23.6	16.1	23.8
USNM 115474	Tutuila	♂	83.2	23.6	6.9	3.0	1.9	11.0	3.6	12.5	22.5	15.2	22.1
USNM 139838	Guam	♂	84.8	23.0	6.1	5.7	2.6	12.4	4.7	13.0	22.0	15.7	23.6
SU 40641	Philippines	♀	88.7	23.1	6.5	8.1	2.4	10.9	2.6	13.0	22.9	-	23.4
SU 62003	S. China Sea	♀	90.0	23.3	5.8	5.6	2.0	11.7	3.6	13.2	24.3	16.3	24.7
USNM 139838	Guam	♀	96.0	22.4	5.9	5.4	2.4	11.7	5.3	12.5	21.8	15.3	22.9
SU 62003	S. China Sea	♀	101.6	22.5	5.7	6.6	1.9	9.5	3.7	12.0	21.6	16.2	23.8
SU 62003	S. China Sea	♂	115.2	23.4	5.6	6.2	1.6	11.7	3.6	14.1	21.4	15.4	23.8
SU 62005	Gulf of Siam	♀	125.0	23.2	5.1	5.0	1.7	11.9	3.2	13.5	23.6	15.8	23.8
SU 62003	S. China Sea	♀	125.0	23.2	5.6	5.3	1.9	12.2	4.2	12.6	20.0	16.2	22.4
USNM 139838	Guam	♀	130.6	24.5	5.9	2.4	2.1	12.2	3.5	13.0	22.7	15.5	-
SU 62003	S. China Sea	♂	144.0	22.8	4.7	6.2	1.5	11.4	3.1	12.8	21.0	14.6	22.9
SU 62003	S. China Sea	♂	153.0	22.2	4.9	6.9	1.6	9.5	2.6	11.2	19.6	13.7	20.9

E. aneitensis had none. The large number of fine small spots on the sides of *E. aneitensis* may be of specific significance, but there is so much variation in color from population to population and specimen to specimen that I prefer not to accept color pattern variation as a basis for recognizing *E. aneitensis.* Some specimens from localities other than Aneiteum are heavily spotted though not in quite the same manner as specimens from Aneiteum. The spots are relatively larger and the perimeters of the spots less sharply delimited. The character of the fringing of the nuchal cirrus in *E. decussatus* is dependent on the size of the specimen concerned. The larger specimens tend to have the nuchal cirrus margins with small branches.

Salarias atkinsoni was described from a single specimen without comparison with other species. The holotype represents the normal juvenile of *E. decussatus.*

Relationships.—*Entomacrodus decussatus* is most closely related to *E. vermiculatus* and secondarily related to *E. stellifer* (for discussion, see relationships under the latter two species).

Remarks.—*Entomacrodus decussatus* has been collected with or from the same general locality as *E. stellifer, E. thalassinus, E. sealei, E. caudofasciatus, E. striatus, E. cymatobiotus, E. epalzeocheilus* and *E. niuafoouensis.* It differs from all these species in the nature of its color pattern and from all but *E. stellifer* in having a larger eye (table 3) and typically 35 vertebrae. In addition, it differs obviously: from *E. stellifer,* in having pinnately compound supraorbital cirri and typically more gill-rakers; from *E. thalassinus,* in having a crenulate upper lip and more gill-rakers, psuedobranchial filaments, and soft dorsal rays; from *E. sealei* and *E. caudofasciatus,* in having the central portion of the ventral margin of the upper lip with crenulae and in having more pseudobranchial filaments and soft dorsal and anal rays; from *E. striatus,* in having more predorsal commissural pores and pseudobranchial filaments at comparable sizes, and in frequently having some preopercular pores paired or in multiples; from *E. cymatobiotus,* in having more soft dorsal and anal rays, gill-rakers, pseudobranchial filaments, and in frequently having some paired pores in the preopercular series; from *E. epalzeocheilus,* in having the nuchal cirri basically simple (or when branched, the branches always much smaller than the main cirrus rather than subequal), and in having the lateral margins or the supraorbital cirrus with branches; and from *E. niuafoouensis,* in having the lateral margin of the supraorbital cirrus with branches.

Distribution (fig. 5).—*Entomacrodus decussatus* is known only from islands in the Pacific Ocean and that ocean's associated gulfs and seas.

Material.—Australia (western), Montebello Island: BMNH 1961.8.16.79; Gulf of Thailand, Goh Samet Island, 12°31′38″N, 101°26′46″E: SU 62005; Goh Sak Island, 12°56′37″N, 100°47′33″E: SU 62004; Goh Tao Island, Ao Mae Hat Bay: SU 62007; South China Sea, Ilot du Sud, 10°29′15″N, 108°57′30″E: SU 62003; Biliton Island: RMNH 4778 (includes lectotype of *Salarias decussatus*); Philippine Islands, Mindoro, Puerto Galero: SU 32329; Batangas, Nasugbu: SU 14731; Samar, Mercedes: SU 40640, 40641; Sangir Island: RMNH 4778; Marianas Islands, Saipan: SU 62082, USNM 123841, 124335; Guam: USNM 123936, 124118, 139838; New Hebrides, Venui Island, Espiritu Santo: ANSP 91364; Aneiteum: BMNH 1931.7.4.4–5; Niuafou Island: USNM 91940, 91941, 91954, 91966; Tutuila Island: USNM 115474; Tau Island: USNM 115475, 143788; Samoa: BPBM 5236, USNM 51791 (holotype of *Salarias atkinsoni*); Tonga Islands, Tongatapu: UH 03082; Tahiti: BMNH 1881.10.18.12.

Entomacrodus vermiculatus (Valenciennes)

Plates 2, 3

Salarias vermiculatus Valenciennes *in* Cuvier and Valenciennes, 1836, Hist. Nat. Poissons, vol. 11, p. 301 [Seychelles].

Salarias vermiculatoides Bleeker, 1857, Nat Tijdschr. Nederl. Indië, vol. 13, p. 478 [Karangbollong, south coast Java; name only]; 1858, Act. Soc. Sci. Indo-Neerl., vol. 3, p. 40 [Trussan, western Sumatra].

?*Salarias reuteri* Lenz, 1881, Zool. Anzeig., vol. 93, p. 506 [Nossi-Bé, Madagascar].

Description.—Segmented dorsal fin rays 15–17 (rarely 15); segmented anal fin rays 16–18 (rarely 16); posteriormost anal pterygiophore supporting 1 or 2 external elements (supporting 2 in 78.6 percent of specimens); total gill-rakers on first arch 20–26 (rarely 20); pseudobranchial filaments 8–13 (usually 8–11, probably not increasing in number with increase in size beyond 65 mm SL, table 12); vertebrae 34 or 35 (usually 35); supraorbital cirri 2–38, increasing in number with increase in SL (table 13); main or longest cirrus with many short branches on both mesial and lateral margins; nape with 1 cirrus on each side (occasionally with small side branches in large specimens); predorsal commissural pores 7 to more than 50, increasing in number with increase in SL (table 14); at least first 5 preopercular pore positions with pairs or multiples of pores; 1–7 pores before each anterior nostril, (only 1 specimen with 1 pore before each anterior nostril), tending to increase in number with increase in SL; lateral line pores terminating on caudal peduncle posterior to level of last dorsal ray (in specimens over 50 mm SL; termination below segmented dorsal ray 14 in one specimen); ventral margin of upper lip completely, but weakly and irregularly, crenulate (crenulae difficult to count).

Proportional measurements: See tables 3, 4, and 15.

Males may develop slight modifications of the skin of the anal spines and rays. These modifications appear as fleshy envelopments of the fin elements. In a few specimens, larger than 114 mm SL, the skin of the anal spines and the first two anal rays was slightly rugose.

If males with rugose anal elements are considered to be mature, then both mature and immature males may occur in the same collection, and in these collections immature males may be as much as 15 mm longer than mature males.

The largest male examined was 149 mm SL, and the largest female, 153 mm. Males and females occurred with relatively equal frequency in the various size classes. The smallest specimen examined was a nonophioblennius stage juvenile, 22.9 mm, with the upper lip cremulae restricted to the middle third of the ventral lip margin.

Color pattern of preserved specimens.—This species has the most complex color pattern of all the members of its genus (see pls. 2, 3). Underlying the vermiculated pattern there seem to be $5\frac{1}{2}$ to $6\frac{1}{2}$ pairs of bands on the body (the members of a pair coalesce at their midportions). The bands are positioned on the sides somewhat similarly to the bands of other species of *Entomacrodus*.

The color pattern undergoes extreme ontogenetic change (pl. 3). At 22.9 mm, a size at which specimens of most of the other species show indications of their adult color pattern, *E. vermiculatus* is uniformly pale. One specimen, USNM 72735, about 24 mm, in poor condition, did show indications of a faded pattern. Up to about 50–70 mm, specimens exhibit a loose network of dark lines on the body that

TABLE 12.--Frequency distributions of pseudobranchial filaments and gill-rakers of specimens of *Entomacrodus vermiculatus* arranged by SL classes (in mm)

Classes	Gill-rakers							Filaments					
	20	21	22	23	24	25	26	8	9	10	11	12	13
20-24.9	-	-	-	-	-	-	-	1	-	-	-	-	-
40-44.9	1	-	-	-	-	-	-	1	-	-	-	-	-
45	-	-	1	-	-	-	-	1	-	-	-	-	-
50	1	-	1	-	1	-	-	2	1	1	-	-	-
55	-	-	1	-	-	-	-	1	1	1	-	-	-
60	-	1	-	-	1	-	-	2	-	-	-	-	-
65	-	-	1	3	-	-	-	-	1	2	1	-	-
70	1	-	-	-	-	1	-	-	-	1	1	-	-
75	-	1	-	-	-	-	-	-	1	-	-	-	1
80	-	-	-	-	-	-	-	-	-	1	-	-	-
85	-	-	1	-	-	-	-	-	-	-	1	-	-
90	-	-	1	-	1	1	-	2	2	-	-	-	-
95	-	1	1	-	-	1	1	-	-	1	2	-	-
100-109.9	-	-	2	-	-	-	-	-	-	-	-	-	2
110	1	-	1	3	-	1	2	1	3	3	-	-	-
120	-	-	-	2	1	-	-	-	-	-	3	-	-
130	-	-	3	1	-	1	-	-	1	2	-	2	-
140	-	2	-	-	1	-	2	-	1	2	2	-	-
150	-	-	-	-	-	-	1	-	-	-	1	-	-
160	-	-	-	-	-	1	-	-	-	1	-	-	-

are more or less grouped at the positions of the bands mentioned above. At larger sizes the network becomes increasingly complex until it forms tiny vermiculations, spots, and reticulations over the entire body, except for the venter of females. The upper lip may show indications of two or three dusky bands alternating with pale interspaces, or the lip may be irregularly dusky. There may be indications of a diffuse dusky band behind the eye, but there is never a distinct dark spot at that position. The vertical and pectoral fins are variously pale, dark spotted, and reticulated, depending on size.

NOMENCLATURE.—Valenciennes based his description of *Salarias vermiculatus* on a single specimen, but included comments on specimens collected by both Dussumier and Reynaud. Inferences from the description lead me to the conclusion that the description is based on Dussumier's specimen. There are two specimens from the Seychelles in the Paris museum collection, one collected by Dussumier from the "Seychelles" (MNHN A 1809) and the other from "Detroit de la Sonde" (MNHN A 2029), the locality from which Reynaud made collections (data included with this latter specimen do not mention the collector). The Dussumier specimen has 15 soft dorsal rays, the number mentioned in the description; the other specimen has 16 soft dorsal rays. I here designate Dussumier's specimen lectotype of the species. The other specimen becomes, then, a paralectotype.

TABLE 13.--Frequency distribution of number of supraorbital cirri of left eye of specimens of *Entomacrodus vermiculatus* arranged by SL classes (in mm)

Classes	Number of cirri																			
	2	5	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	>25
20-24.9	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
40-44.9	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
45	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
50	-	-	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
55	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-
60	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
65	-	-	-	-	1	1	-	1	-	1	-	-	-	-	-	-	-	-	-	-
70	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
75	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-
80	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
85	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
90	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
95	-	-	-	-	-	-	-	1	1	1	-	-	1	-	-	-	1	-	-	-
100-109.9	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-
110	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	1	2	1	-	3
120	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
130	-	-	-	-	-	1.	-	-	-	-	-	1	1	-	-	-	-	1	-	2
140	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	1	2
150	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

The syntypes of *Salarias vermiculatoides* Bleeker, from Trussan, Sumatra, are included among a number of Bleeker specimens (RMNH 4777), all conspecific with *S. vermiculatus*, and with mixed locality data, including Trussan. Since *S. vermiculatoides* is a synonym of *S. vermiculatus*, I see no reason for designating a lectotype. Bleeker (1857, see synonymy) gave no description with his first mention of *S. vermiculatoides*; the name therefore dates from 1858.

Salarias reuteri Lenz is poorly described, but mention is made that it is similar to *S. vermiculatus*. From the description it could be synonymous with *S. vermiculatus*. The holotype of *S. reuteri*, the only known specimen, was destroyed during World War II (G. von Studnitz, Director, Naturhistorisches Museum, Lübec, pers. comm.); I have, therefore, only tentatively synonymized *S. reuteri* with *S. vermiculatus*.

RELATIONSHIPS.—*Entomacrodus vermiculatus* is most closely related to *E. decussatus*. It shares many characteristics with *E. decussatus* and could be considered an Indian Ocean cognate of *E. decussatus*. The shared characters include a relatively deeper body, frequent presence of a well-developed 13th dorsal spine, a more posterior point of attachment of the dorsal fin membrane (to the caudal base or beyond in large specimens), generally larger number of gill-rakers and pseudobranchial filaments, typically 35 vertebrae, supraorbital cirrus with numerous lateral and mesial branches, numerous predorsal commissural pores, a relatively small posterior canine on each side

TABLE 14.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus vermiculatus* arranged by SL classes (in mm)

Classes	Number of pores																
	7	10	13	14	15	16	17	18	19	20	21-25	26-30	31-35	36-40	41-45	46-50	>50
20-24.9	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
40-44.9	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
45	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
50	-	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	-
55	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-
60	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-
65	-	-	-	-	-	1	-	-	-	-	2	-	1	-	-	-	-
70	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
75	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
80	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
85	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
90-99.9	-	1	-	-	-	-	-	1	-	-	1	1	-	-	-	-	-
100	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-
110	-	-	-	-	-	-	-	-	-	-	2	1	-	1	-	1	3
120	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	1
130	-	-	-	1	-	-	-	-	-	-	-	1	-	1	-	-	2
140	-	-	-	-	-	1	-	-	1	-	1	1	1	-	-	-	-
150	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
160	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

of the lower jaw, and a weakly crenulate upper lip. *Entomacrodus vermiculatus* differs from *E. decussatus* primarily in the nature of its complex color pattern which appears to be an elaboration of that of *E. decussatus.* It also differs from most specimens of *E. decussatus* in having more than one pore before each anterior nostril, and modally fewer soft dorsal rays. The posterior extension of the lateral line pores beyond the level of the last dorsal ray onto the caudal peduncle occurs with greater frequency in *E. vermiculatus* than in *E. decussatus.* It is, with *E. decussatus*, the closest relative of *E. stellifer*, but both *E. vermiculatus* and *E. decussatus* can be easily distinguished from *E. stellifer* by color pattern and the number of supraorbital cirri.

REMARKS.—*Entomacrodus vermiculatus* has been collected with or from the same general locality as *E. thalassinus*, *E. striatus*, and *E. epalzeocheilus.* It differs most obviously from all these species in the nature of its color pattern. In addition it differs: from *E. thalassinus*, in having crenulae on the upper lip, multiple pores in the preopercular series, more than one pore before each anterior nostril, and in having more gill-rakers (it also attains a maximum size of more than three times that of *E. thalassinus*); from *E. striatus*, in having multiple pores in the preopercular series, more than one pore before each anterior nostril, and more predorsal commissural pores at any particular size; and from *E. epalzeocheilus*, in the nature of its nuchal cirri, in having more supraorbital cirri, and in having lateral branches on the main supraorbital cirrus.

TABLE 15.--Proportional dimensions as percent SL of specimens of *Entomacrodus vermiculatus* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DS13	DR1	PECL	PELL	CL
USNM 199425	Malacca Str.	♀	44.6	22.8	7.2	4.5	2.7	10.3	3.6	13.2	22.8	16.1	24.2
RMNH 4777	Java	♀	57.2	25.4	7.3	6.5	2.3	11.2	3.5	12.9	23.4	16.1	23.4
USNM 197685	Mozambique	♂	61.7	22.7	6.5	6.2	3.2	11.3	-	-	21.1	16.2	25.3
RU(no number)	Seychelles	♂	64.2	22.4	6.2	5.0	2.6	-	3.9	11.8	24.6	-	23.7
USNM 178989	India?	♀	74.0	23.8	7.0	7.4	2.4	11.5	5.1	13.0	24.3	17.0	23.5
RMNH 4777	Java	♀	79.7	23.3	6.5	6.5	1.8	11.9	3.8	12.6	23.0	16.6	23.8
USNM 178989	India?	♀	89.0	23.0	6.2	6.7	2.4	11.8	4.5	13.9	23.6	16.4	23.8
USNM 197636	Seychelles	♀	89.0	22.7	5.6	4.0	2.7	9.9	3.4	11.8	23.8	14.8	21.4
RMNH 1812	Java	♀	96.6	24.3	6.0	6.2	2.2	11.8	3.1	13.2	22.8	15.5	23.3
RU(no number)	Mozambique	♂	115.0	22.0	5.2	>5.2	2.1	11.3	-	-	19.6	-	21.2
RMNH 4777	Java?	♀	116.5	22.5	5.3	5.0	1.5	10.6	2.2	12.2	20.6	15.4	21.7
RMNH 4777	Java?	♀	120.0	22.2	5.4	4.8	1.8	10.8	3.0	13.2	20.8	14.5	21.6
ANSP 102198	Seychelles	♀	134.5	22.5	4.8	4.3	1.9	12.4	-	12.8	22.7	15.5	22.2
USNM 178989	India?	♀	135.7	22.0	5.2	4.3	1.5	10.2	3.2	12.3	22.9	14.3	22.8
ANSP 102195	Seychelles	♂	148.6	23.8	4.6	8.0	2.2	10.7	-	11.3	21.3	14.3	21.4

DISTRIBUTION (fig. 5).—*Entomacrodus vermiculatus* is known only from the Indian Ocean, and is the only species of *Entomacrodus* endemic to that ocean.

MATERIAL.—Mozambique, Ibo: USNM 197685, RU uncataloged; Seychelles: BMNH 1860.3.1.18, MNHN A 1809 (lectotype of *Salarias vermiculatus*); Beacon Island: ANSP 102195; Curieuse Island: ANSP 102198; Mahé: USNM 197636; La Digue: RU uncataloged; Madagascar, Fort Dauphin: MNHN 1914–15; Nossi Be: USNM 199246; Ceylon: BMNH 1866.1.24.10–17, 1903.5.12.2–4; Java (Karangbollong) and/or Sumatra (Trussan): RNHM 4777 (includes syntypes of *Salarias vermiculatoides*); Java, locality unknown: RMNH 1812; Pelabuhan Ratu, 6°59′ S, 106°33′ E: USNM 72735; locality unknown (collected by Indian Zoological Survey): USNM 178989; Malacca Straits, Pulo Jarak (03°59′N, 100°16′E): USNM 199425; Detroit de la Sonde (Sunda Strait): MNHN A2029.

Entomacrodus stellifer (Jordan and Snyder)

(For synonymy, see subspecies)

DESCRIPTION.—Segmented dorsal fin rays 15–17 (table 16); segmented anal fin rays 16–19 (table 16); posteriormost anal pterygiophore supporting 1 or 2 external elements (supporting 2 elements in 25.2 percent of specimens of *E. s. lighti* and 20.2 percent of *E. s. stellifer*); total gill-rakers on first arch 14–20 (rarely 14 or 20); pseudobranchial filaments 6–10, increasing in number with increase in SL (table 17); vertebrae 34–36 (table 16); supraorbital cirri 1–3 (1 in over 90 percent of specimens), number not increasing with increase in SL; predorsal commissural pores 3–9, not obviously increasing in number with increase in SL (table 18); nape with 1 cirrus on each side (a flap occasionally with frayed edges); all preopercular pore positions with simple pores (rarely with 1 pair of pores at one position); 1 pore before each anterior nostril; lateral line pores terminating on side in area below and between dorsal fin ray 10 and posterior end of caudal peduncle; ventral margin of upper lip with middle one-third to three-fifths unevenly crenulate, lateral thirds or fifths entire.

Proportional measurements: See tables 3, 4, and 19.

Males do not develop noticeable modifications of the skin of the anal spines and rays and it is therefore not possible to differentiate mature from immature males externally. Males (and rarely females), presumably mature or maturing, tend to develop a low fleshy predorsal crest. Males as small as 43 mm SL may show indications of such a crest, while males as large as 60 mm may not.

The largest specimen of *E. s. stellifer* examined was a male, 82.8 mm SL, and the largest female, 67.8 mm. Too few specimens were available to determine if there was a significant difference in relative numbers of either sex at any particular size. The smallest specimen examined, 28.7 mm SL, was a juvenile male.

The largest specimen of *E. s. lighti* examined was a male, 96.6 mm SL, and the largest female was 92.0 mm. Males and females occurred with about relatively equal frequencies in any particular size class. The smallest specimen seen, 15.5 mm, was not an ophioblennily larva. At this size the ventral margin of the upper lip is almous completely entire and superficially the specimen might be mistakenlst identified as *E. thalassinus;* however, there would be more predorsa, commissural pores (table 69) in specimens of this size of *E. thalassinus*, and the number of soft dorsal and anal rays would usually be less.

Color pattern of preserved specimens.—(Specimens should be examined for color pattern while immersed in alcohol.) *E. s. stellifer:* There are most frequently 4½ pairs of dark bands on the sides. The half pair is on the caudal peduncle at the caudal base. The anteriormost pair of bands is below dorsal spines 9–11. Occasional specimens show faint indications of a half pair or pair of bands anterior to the anteriormost pair of bands just mentioned. The members of a pair of bands are separated by a narrow pale interspace. Each dark band is marked by inclusions of pale spots or dashes that increase in number in the anterior bands to the point where the pattern may appear composed of numerous small pale and dark spots and vermiculations. Dorsally the bands encroach on the bases of the dorsal fin elements. Ventrally the bands disappear just before reaching the anal fin base. The areas between the pairs of bands (or between a half pair and a pair) are variably marked with spots, which are much darker above the midline of the body than below. The sides of the head vary from almost uniformly dusky to densely marked with small dark spots, a continuation of the pattern from the anterior portion of the sides. There is frequently an indistinct dusky spot behind the midlevel of the eye, another below the eye at about its midpoint, and a third just anterior to this latter spot. These three spots are ventroposteriorly directed. The upper lip and snout vary from uniformly dusky to variegated with numerous diffuse dark and pale spots. The ventral portion of the head is variably dusky, showing adumbrations of dusky chevrons or vermiculations.

The dorsal fin bears a dark spot distally on the membrane between the anterior two spines. This spot is usually much darker in males than in females from the same collection. The remainder of the dorsal fin, except for the encroachments of the body bands, is usually light to dark dusky with indications of dark and pale dorsoposteriorly directed stripes. The anal fin is light to dark dusky in males, the pigment increasing in intensity distally. Females (and some young males) have the distal portions of the anal rays pale (without melanophores); the remainder of the fin is similar to that of males. The pectoral fin is light dusky, frequently with a broad half-moon concentration of pigment basally, which may include a number of small dark spots. The fleshy pectoral base is diffusely dusky spotted or vermiculated. The pelvic fins are pale to dark dusky. The caudal fin is dusky (without stripes or bands) with two irregular pale spots at the base which sometimes extend onto the caudal peduncle. (See also: Jordan and Snyder, 1902, fig. 10; Schultz and Chapman, 1960, pl. 115c.)

E. s. lighti: There are usually indications of about 4½ pairs of dark bands, often very irregular in shape, on the body. These are in similar position to those mentioned for *E. s. stellifer*. There may be additional bands or portions of bands anterior to these. The bands are frequently darkest and broadest in their midportions, palest and most slender ventrally. The pigment of the bands is more or less evenly distributed and no more than a few relatively large pale areas are included in them. Dorsally the bands encroach on the dorsal fin, ventrally they fail to reach the anal base. The sides of the head are variable, but at least three well-marked, posteroventrally directed bands extend from the orbit at similar positions to the marks described in this area for *E. s. stellifer* (these bands are much better defined than those found in *E. s. stellifer*). The anteriormost of these three bands may extend onto the sides of the upper lip. Occasionally a third band extends from the snout onto the upper lip between these two lateral bands. The upper lip is sometimes dusky with numerous pale spots (spots larger than those in comparably sized specimens of *E. s. stellifer*). The underside of the head bears adumbrations of dusky chevrons. The fins are similarly marked to those of *E. s. stellifer* except that the fleshy pectoral base may exhibit a distinct dark area separated by a pale area from the base of the pectoral rays.

For geographic distribution, discussion, and material, see subspecies accounts.

RELATIONSHIPS.—*Entomacrodus stellifer* is quite distinct from all other species of its genus. It is the only species in which the crenulations of the upper lip are always restricted to the middle third of the ventral margin, the nasal cirri arise from a broad flap, and there is a dark spot between the anterior two dorsal spines. Except for *E. macrospilus*, *E. stellifer* is the only species of *Entomacrodus* in which the supraorbital cirrus is typically simple. *E. stellifer* is unusual in that a large number of specimens lack one or both posterior canines in the lower jaw. This species exhibits the greatest development of any species of *Entomacrodus* of the "crest" on top of the head of males.

The restriction of the dorsal lip crenulae to the middle third of the ventral margin (present in some juveniles of *E. decussatus* and *E. vermiculatus*), the lack of rugose modifications of the skin of the anal spines and rays of males, the relatively small posterior canine in the lower jaw, the large number of vertebrae and dorsal and anal segmented rays, and the frequent occurrence of a well-developed thirteenth dorsal spine are characters that *E. stellifer* shares with *E. decussatus* and *E. vermiculatus* and which I believe relate *E. stellifer* with those species.

REMARKS.—*Entomacrodus stellifer* has been collected with or from the same restricted geographic area as *E. thalassinus* (both subspecies), *E. decussatus*, *E. striatus*, *E. niuafoouensis*, and *E. sealei*.

TABLE 16.--Frequency distribution of number of segmented dorsal and anal rays and vertebrae of subspecies of *Entomacrodus stellifer* arranged geographically

Subspecies	Dorsal rays			Anal rays				Vertebrae		
	15	16	17	16	17	18	19	34	35	36
stellifer										
Japan	2	9	-	-	4	7	-	-	8	1
Okinawa	-	9	4	-	-	11	2	-	5	5
Saipan	-	1	-	-	-	1	-	-	1	-
lighti										
Amoy, China	1	-	-	-	-	-	-	-	-	-
Hong Kong	54	30	-	2	47	35	-	10	40	3
Thailand	-	1	-	-	-	1	-	-	-	-
Singapore	2	-	-	-	2	-	-	-	1	-

TABLE 17.--Frequency distribution of number of pseudobranchial filaments of subspecies of *Entomacrodus stellifer* arranged by SL classes (in mm)

Classes	Pseudobranchial filaments								
	lighti					*stellifer*			
	6	7	8	9	10	6	7	8	9
15-15.9	1	-	-	-	-	-	-	-	-
20	-	1	-	-	-	-	-	-	-
25	-	2	-	-	-	1	-	-	-
30	-	3	-	-	-	-	2	-	-
35	1	4	3	-	-	-	1	-	-
40	1	2	6	-	-	-	-	3	-
45	-	6	6	-	-	-	2	2	-
50	-	1	7	-	-	-	-	3	-
55	-	1	4	-	-	-	-	3	1
60	-	-	5	2	-	-	-	1	1
65	-	2	4	1	-	-	-	1	-
70	1	-	6	2	-	-	-	-	-
75	-	-	1	3	-	-	1	-	-
80	-	-	1	1	-	-	-	1	-
85	-	2	1	-	-	-	-	-	-
90	-	-	1	-	-	-	-	-	-
95	-	-	-	-	1	-	-	-	-

Entomacrodus stellifer stellifer (Jordan and Snyder)

PLATE 4

Scartichthys stellifer Jordan and Snyder, 1902, Proc. U.S. Nat. Mus., vol. 25, p. 461, fig. 10 [Wakanoura, Japan].

GEOGRAPHIC VARIATION.—Though few specimens are available, it appears that Japanese specimens have lower average counts than do specimens from the other localities. The low fin ray counts of the Japanese specimens are most similar to those of specimens of *E. s. lighti* from Hong Kong (table 16). Specimens of *E. s. stellifer* from Okinawa, the locality at which *E. s. stellifer* occurs most closely to *E. s. lighti* (at Hong Kong), have higher average counts than do specimens of *E. s. lighti*.

DISCUSSION.—*E. s. stellifer* is differentiated from *E. s. lighti* by its color pattern, in which the bands on the body are punctuated with small pale dots and dashes, and the anterior portion of the sides and head frequently bear numerous dark spots and vermiculations. In *E. s. lighti* the bands are unbroken by pale spots and dashes; and dark spots and vermiculations, when present on the head and anterior portions of the sides, are not numerous.

Males and females of *E. s. stellifer*, unlike *E. s. lighti*, do not exhibit sexual dimorphism in numbers of dorsal fin rays.

TABLE 18.--Frequency distribution of number of predorsal commissural pores of subspecies of *Entomacrodus stellifer* arranged by SL classes (in mm)

Classes	Number of pores												
	lighti						*stellifer*						
	3	4	5	6	7	8	3	4	5	6	7	8	9
15-19.9	2	-	-	-	-	-	-	-	-	-	-	-	-
20	1	-	-	-	-	-	-	-	-	-	-	-	-
25	1	-	1	-	-	-	-	1	-	-	-	-	-
30	2	-	1	-	-	-	-	2	-	-	-	-	-
35	5	3	-	-	-	-	-	1	-	-	-	-	-
40	5	3	-	-	1	-	-	1	-	-	-	-	1
45	9	3	1	-	-	-	1	1	-	1	1	1	-
50	4	1	2	1	-	-	1	1	-	-	-	-	1
55	5	2	-	-	-	-	-	3	-	1	-	-	-
60	2	4	1	-	-	-	1	-	1	-	-	-	-
65	3	2	3	-	-	-	-	1	-	-	-	-	-
70	4	2	1	1	1	-	1	-	-	-	-	-	-
75	1	2	-	1	-	-	-	1	-	-	-	-	-
80	1	-	-	1	-	-	-	-	1	-	-	-	-
85	-	2	1	-	-	-	-	-	-	-	-	-	-
90	-	-	-	-	-	1	-	-	-	-	-	-	-
95	-	-	1	-	-	-	-	-	-	-	-	-	-

DISTRIBUTION (fig. 8).—*E. s. stellifer* is known only from Japan, Okinawa and Saipan.

MATERIAL.—Japan, Wakanoura: SU 7069 (holotype of *S. stellifer*), 7156, USNM 50298; Kamishima: UCLA W57-24; tide pools near Egumi, Shumane-Ken: UMMZ 144750; Okinawa, tide pool at Kimmu Wan: USNM 111605, 132795; Marianas, Saipan: USNM 132845.

TABLE 19.--Proportional dimensions as percent of SL of subspecies of *Entomacrodus stellifer* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DS13	DRI	PECL	PELL	CL
stellifer													
USNM 111605	Okinawa	♀	28.7	24.7	8.7	6.6	-	10.1	-	12.5	-	18.8	23.0
USNM 111605	Okinawa	♀	32.0	23.4	8.4	6.9	-	10.0	1.6	13.1	25.9	19.1	22.5
USNM 132795	Okinawa	♀	36.0	23.6	8.3	5.8	1.4	9.7	1.7	11.7	24.2	18.0	22.4
USNM 132845	Saipan	♂	40.0	23.5	7.5	10.0	1.8	9.3	-	11.2	22.5	16.5	21.5
USNM 132795	Okinawa	♀	41.5	22.7	7.5	8.4	1.7	10.4	1.2	12.0	24.3	17.8	21.7
USNM 132795	Okinawa	♂	43.4	23.7	7.4	7.4	1.4	10.4	2.3	11.5	23.3	15.0	21.0
UMMZ 144750	Japan	♀	47.8	22.8	6.7	8.2	2.1	10.5	2.5	13.8	23.8	17.2	22.2
USNM 132795	Okinawa	♂	48.2	22.8	7.1	9.5	-	10.4	2.1	12.0	23.9	16.8	21.8
SU 71536	Japan	♀	48.8	22.8	7.0	5.3	2.0	10.4	1.6	12.5	24.2	-	21.5
USNM 132795	Okinawa	♂	49.2	22.8	6.5	7.3	1.8	10.6	2.4	11.4	23.2	16.3	21.3
USNM 132795	Okinawa	♀	50.5	22.8	7.1	7.1	1.0	9.5	2.4	12.5	23.4	16.4	20.8
UMMZ 144750	Japan	♂	51.7	23.2	6.6	11.6	1.7	11.0	2.9	13.0	23.2	15.5	21.6
USNM 50298	Japan	♂	55.6	21.4	5.9	10.4	1.8	10.8	-	12.6	21.8	15.3	22.5
USNM 132795	Okinawa	♀	56.2	23.0	6.9	8.9	1.4	9.6	1.8	11.7	23.5	16.0	21.7
UMMZ 144750	Japan	♂	56.6	22.6	6.2	11.0	1.9	10.6	2.5	13.4	23.8	14.8	23.0
USNM 132795	Okinawa	♂	60.8	21.5	6.2	8.2	1.6	9.2	2.3	12.3	21.9	14.0	19.9
UMMZ 144750	Japan	♂	61.0	22.0	6.1	10.8	1.6	10.3	2.0	11.3	21.3	15.7	21.3
UMMZ 144750	Japan	♀	67.6	20.8	5.9	6.8	1.9	10.0	2.1	12.6	22.5	15.5	21.3
SU 7069[1]	Japan	♂	74.9	21.8	5.6	11.3	1.5	10.0	2.3	12.9	20.8	-	20.6
UMMZ 144750	Japan	♂	82.8	21.2	5.6	7.5	1.2	10.5	2.4	14.7	23.3	15.9	23.0
lighti													
SU 62071	Hong Kong	♂	24.8	24.6	8.1	6.8	2.4	10.5	-	11.7	26.2	18.1	21.8
SU 30664	Singapore	♂	28.4	25.3	8.4	5.6	2.8	12.0	-	12.3	25.7	19.4	22.5
SU 62071	Hong Kong	♂	30.0	25.0	7.3	7.3	2.0	10.7	2.0	12.3	26.6	18.7	21.7
SU 62071	Hong Kong	♂	33.6	24.4	7.4	10.1	2.1	10.7	1.8	12.2	26.8	19.3	22.6
SU 62071	Hong Kong	♀	38.0	24.0	7.4	8.2	1.8	10.5	1.6	13.2	25.6	18.7	21.3
SU 62071	Hong Kong	♀	40.5	23.7	7.6	7.7	2.5	11.1	2.5	13.6	24.7	16.6	22.0
SU 62072	Hong Kong	♂	44.9	22.7	6.7	8.9	1.3	11.6	-	13.6	22.5	-	22.3
SU 62071	Hong Kong	♀	51.5	21.8	6.4	8.7	1.9	9.7	1.7	13.2	24.5	16.7	20.4
SU 62072	Hong Kong	♀	53.7	22.2	6.5	6.0	1.7	8.2	-	11.9	21.4	-	20.1
SU 62071	Hong Kong	♀	59.0	22.2	6.1	6.9	1.7	10.0	-	11.4	22.5	15.1	19.8
SU 30664	Singapore	♂	62.8	22.3	6.4	7.3	0.8	10.3	-	12.3	21.5	14.6	20.9
SU 62072	Hong Kong	♀	63.7	22.3	6.3	5.5	1.6	10.0	-	12.2	22.9	-	20.4
SU 62071	Hong Kong	♂	65.5	22.0	6.1	9.5	1.1	11.0	-	12.4	22.8	14.5	20.6
SU 62072	Hong Kong	♀	67.0	21.5	6.0	6.0	1.5	9.0	-	11.8	20.9	-	20.2
SU 62071	Hong Kong	♂	72.0	22.1	5.6	8.5	1.4	10.8	2.5	13.3	21.8	14.7	20.3
SU 62071	Hong Kong	♀	73.0	22.7	6.0	6.8	0.7	9.2	-	12.7	23.6	17.0	20.0
SU 62072	Hong Kong	♀	73.0	20.8	5.8	5.2	1.5	9.6	-	12.0	21.6	-	20.0
SU 62071	Hong Kong	♂	73.8	22.6	5.7	9.1	1.2	11.2	-	13.3	22.4	14.9	21.1
SU 62072	Hong Kong	♂	78.0	21.2	5.4	8.3	1.4	10.2	-	13.1	20.8	-	20.5
SU 62072	Hong Kong	♂	84.8	21.8	5.7	8.0	1.4	10.6	-	13.2	20.6	-	20.6
SU 62071	Hong Kong	♂	87.4	22.1	5.5	8.7	1.1	10.5	-	12.2	20.1	13.8	19.4
SU 62071	Hong Kong	♂	87.9	21.8	5.5	8.0	1.5	11.5	2.3	14.2	22.8	15.0	21.0
SU 62071	Hong Kong	♂	96.6	21.5	5.3	6.6	1.0	10.3	-	12.9	20.2	13.4	20.2

[1] Holotype of *Scartichthys stellifer*

Entomacrodus stellifer lighti (Herre)

PLATE 5

Salarias lighti Herre, 1938, Proc. Biol. Soc. Washington, vol. 51, p. 65 [Dodd Island, Amoy, China].

REMARKS.—Males tend to have a higher average number of segmented dorsal fin rays than do females. Of 50 males examined, 25 had 15 dorsal rays and 25 had 16 dorsal rays. Of 35 females examined, 29 had 15 dorsal rays and 6 had 16 dorsal rays. Other meristic characters did not exhibit sexual dimorphism.

DISTRIBUTION (fig. 8).—This subspecies is restricted to the South China Sea and its extension, the Gulf of Thailand. The area is more or less enclosed by a chain of closely approximated islands extending from Taiwan to Sumatra. These islands probably have acted as an effective barrier, isolating populations of this taxon from populations of the nominal subspecies. The same area also defines the distribution of *E. t. longicirrus*.

MATERIAL.—China, Amoy, Dodd Island: SU 33001 (holotype of *S. lighti*); Hong Kong, Sharp Island: SU 62072; Cape D'Aguilar: SU 62071; Shelter Island: USNM 197976; Kiu Tsui Chau: USNM 197985; Thailand, Hinson Chalam, 12°30′15″N, 101°26′45″E: SU 62093; Malaya, Singapore: SU 30664.

Entomacrodus marmoratus (Bennett)

PLATES 6, 7*a–b*

Blennius marmoratus Bennett, 1828, Zool. Journ., vol. 4, pp. 35–36 [Sandwich Islands = Hawaiian Islands].

DESCRIPTION.—Segmented dorsal fin rays 14–16 (rarely 14), varying with population (table 20); segmented anal fin rays 15–17 (rarely 15), varying with population (table 20); posteriormost anal pterygiophore supporting 1 or 2 external elements (60.2 percent supporting 2); total gill-rakers on first arch 19–29 (usually 21–26); pseudobranchial filaments 8–12 (rarely 11 or 12; 6 or 7 in specimens 19–22 mm SL); vertebrae 34 or 35 (34 in 38 of 48 specimens); supraorbital cirri 1–34, number increasing with increase in SL (table 21); main or longest supraorbital cirrus with lateral and mesial branches in specimens over 25 mm SL; nape with 2–20 cirri on each side (specimens over 19 mm SL); number increasing with increase in SL (table 22); arising from 2 main bases on each side (85 of 93 specimens; on at least 1 side in 90 of 93 specimens; from 1 base on each side in 3 of 93 specimens); the medialmost nuchal cirrus on each side with the broadest base and usually the most branches; predorsal commissural pores 3–23, number increasing with increase in SL (table 23); preopercular series of pores ranging from all positions with simple pores to all positions with pairs or multiples of pores (usually including 2 or 3 positions with simple pores); 1 pore before each anterior nostril (2 before each nostril in only 1 specimen); lateral line terminating on side in area below and between segmented dorsal fin rays 4 and 16 (posterior to ray 8 in specimens over 40 mm SL); ventral margin of upper lip completely crenulate; lip crenulae number 29–39 (usually 30–36).

Proportional measurements: See tables 3, 4, and 24.

Only three males, 86, 94, and 121 mm SL, were seen with rugose fleshy modifications of the skin of the anal spines and first to third anal rays. Presumably these males, each the largest in its respective collection, were mature. The largest male examined was 121 mm SL, the largest female 114 mm. Females were about twice as numerous as males in all size classes up to that of the largest female.

The smallest metamorphosed specimen examined, 19.2 mm SL, was well marked with vertical bands on the body. This specimen had two cirri on each side of the nape and vomerine teeth, but I could not see posterior canines in the lower jaw (canines also not present in a specimen 20.5 mm, but present in a specimen 22.5 mm). The largest ophioblennius stage examined, 20 mm SL (the smallest 19.5 mm), lacked vomerine teeth and had dark pigment only on top of the head and at the tips of the pectoral rays. Three or four larval canine teeth were present laterally on each side of the lower jaw, the most anterior were the largest on each side.

A group of smaller ophioblennius larvae that might contain specimens of *E. marmoratus* was collected with the three larvae mentioned (for discussion, see *E. strasburgi*).

COLOR PATTERN OF PRESERVED SPECIMENS.—Strasburg (1956, fig. 2) has figured a specimen of *E. marmoratus* and I present three (pls. 6, 7*a*, *b*). None of these four illustrations adequately portrays color pattern, which is quite variable. There are usually 4½ pairs of dusky, irregular, vertical bands, or spots, on the body, the half pair at the caudal base. The bands, or spots, may be so poorly

TABLE 20.--Frequency distribution of number of segmented dorsal and anal rays in specimens of *Entomacrodus marmoratus* arranged geographically southeast to northwest (for meaning of N and S see methods section)

Locale	Dorsal rays			Anal rays			N	S
	14	15	16	15	16	17		
Hawaii	-	11	13	-	10	4	1	13
Maui	-	2	2	-	1	3	3	1
Molokai	-	1	-	-	-	1	1	-
Lanai	-	2	-	-	-	2	2	-
Oahu	-	24	6	-	21	10	11	20
Necker	-	-	1	-	-	1	1	-
Laysan	-	10	9	-	10	10	10	10
Pearl and Hermes	-	1	-	-	1	-	-	1
Midway	1	6	12	1	8	10	8	11

TABLE 21.--Frequency distribution of supraorbital cirri of left side of specimens of *Entomacrodus marmoratus* arranged by SL classes (in mm)

Classes	Number of cirri																																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
15-19.9	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
40	-	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
45	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
50	-	-	-	-	-	-	-	-	-	1	-	-	1	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
55	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2	1	1	-	1	-	1	-	-	1	-	-	-	-	-	-	-
60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-
65	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-
70	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
80	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
85	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	1	-	-	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
95	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	2	-	-	-	-	-	-	-
100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
105	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
110	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
115	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
120	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-

represented as to be almost unrecognizable as such. Usually the midportions of the bands are darkest; sometimes the members of a pair are fused at the midportions. Dorsally the bands usually extend onto the spinous and soft dorsal fins. Ventrally the bands are palest failing to reach the ventral body contour. Various pale spots and irregular dusky markings are scattered on the sides (usually ventrally or between the band pairs). A small faint to dark spot is frequently found in the humeral region. This spot may vary from absent to most obvious mark on the body in a single collection of specimens. In life the humeral spot is irridescent dark olive green. The most noticeable mark on the head is a dark, irregularly crescentic area just posterior to the orbit. This area may fuse ventrally with a large darkly dusky area in the preopercular region. The opercular area is usually paler than the preopercular area. The upper lip may be almost uniformly dusky, include adumbrations of up to 20 dusky stripes (rarely), or consist of about 7 dusky bands separated by pale stripes. The underside of the head varies from uniformly pale to marked with some irregularly dusky, almost indistinct, chevrons separated by fine pale stripes.

The spinous dorsal fin is irregularly dusky with darker dusky areas

TABLE 22.--Frequency distribution of total number of cirri on left side of nape of specimens of *Entomacrodus marmoratus* arranged by SL classes (in mm)

Classes	Number of cirri																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
15-19.9	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
40	-	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
45	-	1	1	1	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-
50	-	-	-	-	1	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-
55	-	1	-	2	1	1	1	-	-	1	1	-	-	-	-	-	-	-	-	-
60	-	-	-	-	1	-	2	-	2	-	-	1	-	-	-	-	-	-	-	1
65	-	-	-	1	-	1	-	-	1	1	2	-	-	-	-	1	-	-	-	-
70	-	-	-	-	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-
75	-	-	-	-	-	-	-	1	-	-	1	-	-	1	-	-	-	-	-	-
80	-	-	-	-	1	-	1	1	2	-	-	1	-	-	-	-	-	-	-	-
85	-	-	-	-	3	1	1	1	-	-	-	2	-	-	-	-	-	-	-	-
90	-	-	-	-	-	1	2	-	1	2	-	-	1	1	-	-	-	-	-	-
95	-	-	-	-	1	1	-	-	-	1	-	1	-	1	-	-	-	-	-	-
100	-	-	-	-	-	1	1	-	-	-	-	1	-	-	-	-	1	-	-	-
105	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
110	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
115	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
120	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-

overlying the bases of some spines (extensions of the body bands onto the fin). Each soft dorsal fin ray bears two or three dusky spots, so arranged that they form diagonal bands, separated by pale interspaces, across the fin. The anal fin is evenly dusky, grading darker distally and paler proximally, with the anterior surface or the tips of the rays distinctly palest. One large mature male had evenly dusky dorsal fins and the anal fin dusky, grading darker distally with the darkest areas the anterior surface of the tips of the rays. Few males were available but it seems the darker anal fin may be a male character. The caudal fin is more or less evenly dusky, frequently with one or two vertical rows of slightly darker dusky spots. The pectoral fin is evenly dusky, grading to much darker ventrally. The fleshy pectoral base is irregularly to uniformly dusky. The pelvic fins are pale dusky.

GEOGRAPHIC VARIATION.—There are indications of a cline in average number of soft dorsal and anal rays (table 20). The averages are lowest from the island of Hawaii and gradually increase as one progresses northwesterly through the island chain to Midway.

NOMENCLATURE.—Bennett (1828) described *Blennius marmoratus* from a single specimen which now appears to be lost. If *B. marmoratus* actually came from the Hawaiian Islands, the type description

TABLE 23.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus marmoratus* arranged by SL classes (in mm)

Classes	Number of pores																				
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
15-19.9	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35	-	-	-	-	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
40	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
45	-	-	-	-	-	1	3	1	1	-	-	-	-	-	-	-	-	-	-	-	-
50	-	-	-	-	1	-	1	-	-	1	1	-	1	-	-	-	-	-	-	-	-
55	-	1	-	-	-	1	2	3	-	-	-	1	-	-	-	-	-	-	-	-	-
60	-	-	-	-	2	1	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-
65	-	-	-	-	-	1	3	-	-	-	1	-	-	-	1	-	1	-	-	-	-
70	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
75	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	1
80	-	-	-	-	-	-	-	-	2	1	-	1	1	1	-	-	-	-	-	-	-
85	-	-	-	-	-	-	3	1	-	-	1	1	-	1	-	1	1	-	-	-	-
90	-	-	-	-	-	-	-	2	1	-	2	1	-	-	-	-	1	-	-	-	-
95	-	-	-	-	-	-	1	-	-	2	-	1	1	-	-	-	-	-	-	-	-
100	-	-	-	-	-	-	-	-	-	1	-	1	-	-	1	1	-	-	-	-	-
105	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-
110	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
115	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
120	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-

undoubtedly refers to the species treated here. If it did not come from the Hawaiian Islands—and there is some reason to doubt that it did—it must refer to another species, probably *E. striatus*. Under these circumstances it would be a senior synonym of *E. striatus*, and the species treated here as *E. marmoratus* would be without a name. My reason for questioning the origin of Bennett's specimen is based on the fact that *Blennius sordidus* and *Scorpaena asperella*, described in the same paper and also supposedly from Hawaii, appear not to occur in the Hawaiian Islands (Strasburg, 1956, p. 243; Gosline, 1955, p. 461). For reasons I intend to publish elsewhere, I believe *Blennius sordidus* to be an eastern Pacific species. Furthermore, in Bennett's description of *B. marmoratus*, he stated, in reference to the nuchal cirri: " . . . there is also a very short filament on each side . . . ." Since in the 4-inch long specimen of the species treated here one would expect to find several cirri on each side of the nape, the description does not seem to apply to the species I am treating. Bennett did note the branching on both margins of the supraorbital cirrus and one would have expected him to report multiple cirri on each side of the nape had they been present.

In spite of the indications to the contrary, I favor allocating Bennett's name to the Hawaiian species of *Entomacrodus*, with which it most closely agrees in description and in which sense I employ it here. The name *marmoratus* is now fairly widely employed for this

TABLE 24.--Proportional dimensions as percent SL of specimens of *Entomacrodus marmoratus* (for meaning of abbreviations see methods section)

Catalog no.		Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL
USNM	142060	Oahu	♂	32.2	24.8	7.4	4.3	3.1	10.9	12.1	24.2	14.3	23.3
USNM	142060	Oahu	♂	36.1	23.8	7.2	3.0	3.0	11.1	13.8	23.8	17.4	26.0
UH	933	Midway	♀	48.0	23.3	6.7	4.8	3.1	10.4	12.5	22.9	15.6	22.9
USNM	78053	Hawaii	♂	48.0	24.0	6.2	5.8	2.1	11.0	12.5	24.6	18.1	26.0
USNM	78053	Hawaii	♀	53.6	23.1	6.3	3.7	3.0	10.1	14.0	23.0	16.6	23.0
USNM	78053	Hawaii	♂	55.2	22.6	6.0	4.0	3.1	9.2	10.8	20.7	14.6	22.6
USNM	142060	Oahu	♂	58.8	24.0	6.1	4.8	3.4	8.8	12.7	23.6	16.1	24.0
USNM	142060	Oahu	♀	62.0	23.7	6.3	4.8	2.3	10.2	12.1	22.9	15.5	22.9
UH	933	Midway	♀	80.8	23.3	5.6	5.2	2.5	9.4	12.4	22.3	14.9	22.9
USNM	142060	Oahu	♀	85.8	23.1	5.4	4.0	2.3	8.7	10.5	23.3	15.5	23.6
UH	933	Midway	♀	93.6	22.9	5.3	5.0	3.1	9.6	13.5	21.9	14.4	23.2
USNM	142060	Oahu	♂	94.6	22.6	5.3	5.5	2.2	7.1	11.8	21.6	13.6	21.9
UH	933	Midway	♂	104.5	23.7	5.1	4.8	2.8	8.7	9.8	20.0	12.9	20.8
UH	933	Midway	♀	105.0	23.0	5.0	4.4	2.4	9.3	13.0	21.9	16.2	22.8

species of *Entomacrodus* and there is no benefit to be derived from using it otherwise. In any event, *Blennius marmoratus* is the oldest name available for any species of *Entomacrodus* and it matters not to Bennett's honor to which species it is applied. Let it therefore accrue to a Hawaiian species.

RELATIONSHIPS.—(See also "Relationships" under *E. niuafoouensis.*) *Entomacrodus marmoratus* is a member of the *E. striatus* species group. *E. marmoratus* differs: from all other members of the group most obviously, in having the nuchal cirri on each side arising from two bases; from all but *E. striatus*, in having both lateral and mesial branches on the main supraorbital cirrus (more cirri at a given size); and from *E. epalzeocheilus* and *E. niuafoouensis*, in having only one pore before each anterior nostril.

DISTRIBUTION (fig. 6).—*E. marmoratus* has been taken only from the Hawaiian Islands, where it has been collected with the only other species of *Entomacrodus* occurring there, also an endemic, *E. strasburgi*. It differs from *E. strasburgi* in having more supraorbital cirri, nuchal cirri, gill-rakers, pseudobranchial filaments, and crenulations on the upper lip. Strasburg (1956) reported that *E. marmoratus* abounds in areas of heavy surf occurring along rocky shores. It has also been taken from tide pools, and the larvae have been taken from under a light offshore.

MATERIAL.—Hawaiian Islands: Hawaii: USNM 78051, 78053, 126689; Maui: UH 2022; Molokai: USNM 164992 (in part); Lanai: USNM 164993 (in part); Oahu: USNM 7785, 78052, 142060, 149990, 197201; Necker: BPBM 4932; Laysan: BPBM 4929, 4930, CNHM 7718, 55942, USNM 55121; Pearl and Hermes Reef: USNM 92272; Midway: UH 933.

Entomacrodus epalzeocheilus (Bleeker)

PLATES 8, 10*a*–*b*

Salarias epalzeocheilus Bleeker, 1859, Nat. Tijdschr. Nederl. Ind., vol. 19, pp. 343–344 (16–17 on the separate) [Karangbollong, Java, in the sea].

Salarias epalzeorhynchus Gunther, 1861, Cat. Fish. British Mus., vol. 3, p. 240 [misspelling of *epalzeocheilus*].

DESCRIPTION.—Segmented dorsal fin rays 14–16 (usually 15 or 16); segmented anal fin rays 15–17 (usually 16 or 17); posteriormost anal pterygiophore supporting 1 or 2 external elements (57.4 percent supporting 2); total gill-rakers on first arch 16–25 (usually 16–19 in specimens less than 40 mm SL; usually 20–22 in specimens over 40 mm SL); pseudobranchial filaments 6–10 (6 or 7 in specimens less than 30 mm SL; usually 8 or 9 in specimens over 35 mm SL); vertebrae 33–35 (34 in 32 of 34 specimens); supraorbital cirri 3–9 (usually 4–7), number not increasing much, if any, with increase in SL; main, or longest supraorbital cirrus with all branches mesially (60 of 65 specimens, 4 specimens also with 1 lateral branch, and 1 with 2); nape with 1–10 cirri on each side (2 or more in specimens over 30 mm SL, rarely more than 7), usually arising on each side from common base (from 2 bases on only 1 side in 2 specimens); nuchal cirri number increasing very slightly with increase in SL; predorsal commissural pores 3–66, number increasing with increase in SL (table 25); preopercular series of pores with pairs or multiples of pores at all positions (rarely a simple pore included in series); 1–3 pores before each anterior nostril (2 or 3 in 56 of 65 specimens); lateral line terminating on side in area below and between segmented dorsal fin rays 2 and 11 (usually between rays 3 and 9); ventral margin of upper lip completely crenulate; lip crenulae number 23–32 (usually 25–30).

Proportional measurements: See tables 3, 4, and 26.

Males develop fleshy rugose modifications of the skin of the anal spines and the anterior two anal rays. If one considers males with these modifications to be mature, the smallest mature male examined was 52.8 mm SL. Mature and immature males may occur in the same collection and in these collections immature males may be as much as 37 mm longer than mature males.

The largest specimen examined was a male, 104.5 mm SL; the largest female was about 78 mm SL. Below 79 mm SL females were about as common as males in the various SL classes. The smallest specimen examined, 20.1 mm SL, was not an ophioblennius stage; however, posterior canines in the lower jaw were absent. These teeth were present in specimens 25 mm SL. Adult type color pattern was developed in the smallest specimen.

COLOR PATTERN OF PRESERVED MATERIAL.—Description of a male, USNM 199423, approximately 80 mm SL, from Malacca Strait, followed by variations encountered in other specimens: The ground color of the side of the body varies from dusky anteriorly to pale dusky posteriorly. There are 4½ pairs of vertical series of diffuse dusky spots, the half pair at the caudal peduncle. There are three spots in each member of a paired series, the ventralmost is faintest, fading completely before reaching the ventral body contour. Dorsally the spots are darkest and continuous onto the base of the spinous and soft dorsal fins. Anteriorly, in the region above the pectoral fin, the side bears a fine network of dusky lines encompassing tiny paler spots. The venter is uniformly pale. The side of the head is mostly dark dusky with a black spot posterior to the eye a distance about equal to the eye diameter. Three short dusky lines, separated by paler interspaces, extend from the ventroposterior (4 o'clock position) margin of the eye to the preopercular area, where they fuse with a deep dusky blotch (the black spot behind the eye extends ventrally and similarly fuses with the same blotch). Ventral to the dusky lines (5 o'clock position) are some irregular dusky lines, spots,

TABLE 25.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus epalzeocheilus* arranged by SL classes (in mm)

Classes	Number of pores																															
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	35	37	65
20-24.9	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	-	1	1	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30	-	1	-	-	-	1	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35	-	1	-	1	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
40	-	-	-	-	1	1	1	1	4	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
45	-	-	-	-	-	-	1	1	1	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
50	-	-	-	-	-	-	1	-	-	-	1	1	-	1	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
55	-	-	-	-	-	-	-	1	-	1	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	1	-	-
65	-	-	-	-	-	-	1	-	-	-	-	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
70	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
75	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	1	-	1	-	-	-	-	-	-	-	1	-
80	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
85	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
95	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
100	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

and dashes separated by paler interspaces that extend onto the ventral preopercular area. (The posterior margin of the preopercular area is diffusely pale and dusky, lighter than the almost uniformly dusky opercular area.) Below the eye (6 o'clock position) is a dusky band extending to the dorsal margin of the upper lip. Within the band are the pale openings of pores. The upper lip bears 20 vertical dark stripes of varying width and intensity, separated by paler interspaces. These stripes extend onto the snout, where they may take the form of spots. The underside of the head is dusky with the area just behind the lower lip darkest.

Except for the darkened area where the spots on the body enter the spinous dorsal fin, that fin is more or less uniformly dark dusky. The membrane of the soft dorsal fin is also dusky but the spines are mostly pale and there are several fine pale diagonal stripes coursing over the fin. The anal fin is uniformly dark dusky. The caudal fin is pale dusky with three darker vertical stripes on the proximal portion, the two posterior stripes not entering the dorsal third of the fin. There are two dark spots on the central caudal base. The pectoral fin is uniformly dusky. The fleshy pectoral base bears several small dusky spots. The pelvic fin is dusky, with the rays paler than the webbing.

The color patterns of specimens (Indian Ocean) in a single collection are quite variable. The body spots may be fused into solid bands (pl. 10*a*), limited only to the middle spots of each vertical series, or absent. The body may bear numerous scattered, small, dusky spots (pl. 10*b*) or may bear vertical paired series of spots and scattered small dusky spots, somewhat paler than the vertical series. No specimens were seen which had a humeral blotch, as found in some specimens of *E. niuafoouensis* and all *E. randalli*. The underside of the head may bear diffuse dark chevrons, the middle two joined to form a Y, or may be entirely pale. The side of the head may be pale with the only dark mark a black elongate spot behind the eye. The lip stripes may be pale to absent, or fused, and represented as a few diffuse, dusky and pale bands. The fins may be variably dusky spotted; the fleshy pectoral base may bear two dark stripes separated by a broader, paler interspace. Females do not appear to differ much, if any, in coloration from males, although in specimens from the same collection the females are less intensely marked than the males.

Two specimens from Tutuila, the only specimens of the species known from the Pacific Ocean, differed from the other specimens primarily in having the soft dorsal fin darkly spotted, with about three spots over each ray, and in having numerous pale spots on the ventral portion of the body sides.

REMARKS.—There is a tendency for males from the Indian Ocean to have higher numbers of segmented dorsal fin rays than females. Of 41 males examined, 1 had 14 rays, 25 had 15 rays, and 15 had 16 rays. Of 25 females examined, 1 had 14 rays and 24 had 15 rays. There was no evidence of sexual dimorphism in other meristic characters. The male and female specimens from Samoa each had 16 dorsal rays.

NOMENCLATURE.—*E. epalzeocheilus* was described by Bleeker (1859) from a single specimen, 85 mm, from Karangbollong, south coast (Indian Ocean) of Java. I have been unable to locate the holotype, but it is clear from the Latin description (especially "vertice cristis nullis sed poris valde conspicuis longitudinaliter seriatis; nucha utroque latere cirro membranaceo plurifimbriato occulo breviore"), that the specimens considered here are the same species as that described by Bleeker.

RELATIONSHIPS.—(See also relationships under *E. niuafoouensis*.) *Entomacrodus epalzeocheilus* is a member of the *E. striatus* species group. *E. epalzeocheilus* differs: from *E. niuafoouensis*, in having multiple nuchal cirri and in usually having fewer crenulae on the ventral margin of the upper lip; from *E. randalli*, in having more than one pore before each anterior nostril, in having stripes or bands on the upper lip, and in lacking a dark spot in the humeral region; from *E. marmoratus*, in usually lacking lateral branches on the main, or longest supraorbital cirrus, in having the nuchal cirri on each side arising from

TABLE 26.--Proportional dimensions as percent SL of specimens of *Entomacrodus epalzeocheilus* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DS13	DR1	PECL	PELL	CL
SU 14732	India	♂	32.0	24.4	7.3	4.2	3.0	10.6	-	12.5	25.6	17.2	25.0
ANSP 102201	Seychelles	♀	35.3	23.2	6.2	6.2	2.8	9.3	-	10.8	24.6	16.4	24.4
ANSP 102201	Seychelles	♀	41.8	23.0	6.7	6.0	2.9	9.1	-	11.5	26.3	16.5	23.4
ANSP 102201	Seychelles	♂	48.7	24.4	6.6	11.5	2.7	10.3	-	11.9	23.2	15.0	23.0
BMNH 1903.5.12.4	Ceylon	♀	52.4	23.3	6.1	6.7	3.1	10.5	1.9	12.2	25.8	17.2	24.0
USNM 195780	East of India	♀	54.8	22.6	6.7	5.1	3.1	10.0	1.8	12.0	25.5	15.5	-
USNM 112035	Andaman Is.	♀	54.8	24.6	6.9	5.1	2.2	9.8	-	10.8	25.4	16.4	23.8
SU 14734	India	♂	55.0	24.9	6.5	8.0	2.7	-	-	10.7	24.6	17.3	21.8
ANSP 102201	Seychelles	♂	55.1	24.3	6.4	9.8	2.5	10.5	-	12.3	23.6	14.9	24.0
SU 37131	Andaman Is.	♀	63.8	23.5	6.3	6.0	3.1	9.6	-	11.8	23.8	15.0	23.5
SU 37131	Andaman Is.	♂	64.4	24.1	5.9	5.6	3.0	10.1	-	11.5	24.8	15.0	22.8
ANSP 102201	Seychelles	♀	66.1	23.3	5.3	6.0	2.6	8.9	-	11.5	22.4	15.0	22.5
SU 14733	India	♀	69.8	24.4	5.7	7.7	2.1	10.6	-	11.2	24.2	16.5	23.2
ANSP 102201	Seychelles	♀	72.1	24.4	5.4	8.9	2.5	8.2	-	11.0	21.8	14.3	20.8
SU 14732	India	♀	76.2	24.3	5.2	8.0	2.4	10.0	-	11.4	25.6	17.2	25.0
USNM 195780	East of India	♂	80.5	23.6	5.7	7.0	2.4	11.0	2.5	13.9	23.2	14.4	22.8
ANSP 102201	Seychelles	♂	81.7	23.5	5.0	12.5	2.0	9.6	-	11.0	20.6	14.1	20.7
ANSP 102201	Seychelles	♂	104.5	21.5	4.5	11.1	2.3	9.1	-	11.7	19.6	14.2	19.3

a common base, in having more than one pore before each anterior nostril, in usually having numerous dark stripes on the upper lip, and in never having a dark humeral spot; from *E. striatus*, in having more than one pore before each anterior nostril, branched nuchal cirri, paired pores in the preopercular series, a different color pattern, and in lacking lateral branches on the main supraorbital cirrus.

REMARKS.—*E. epalzeocheilus* has been collected with or from the same generally restricted geographic locality as *E. striatus*, *E. vermiculatus*, *E. decussatus*, *E. t. thalassinus*, *E. sealei*, and *E. caudofasciatus*. It may be most obviously differentiated from: *E. decussatus* and *E. vermiculatus*, in having fewer vertebrae, usually fewer predorsal commissural pores, supraorbital cirri (lacking lateral branches on the main supraorbital cirrus), and in its strikingly different color pattern; from *E. t. thalassinus*, *E. sealei*, and *E. caudofasciatus*, in having the ventral margin of the upper lip completely crenulate, and in having more pseudobranchial filaments, more than one pore before each anterior nostril, and more than one cirrus on each side of the nape.

DISTRIBUTION (fig. 6).—*E. epalzeocheilus* is known from the Indian Ocean, northern Malacca Strait, and Tutuila, Pacific Ocean. The Tutuila population possibly represents a relict population of the species, which previously was more broadly distributed.

MATERIAL.—Indian Ocean: Seychelles Islands, Beacon Island: ANSP 102201, USNM 258171 F-2 (cleared and stained); Curieuse Island: ANSP 102183; East of India (only data): USNM 195780; India: Travancore, Konival, 10 miles south of Trivandrum: SU 14734; Madras, Vizagapatam, foot of Dolphin's Nose: SU 14733; Waltair: SU 14732; Andaman Islands: SU 37131, USNM 112035; Ceylon: BMNH 1903.5.12.4, MNHN A 2042; Malacca Strait: Pulo Perak, 05°41′N, 98°56′E: USNM 199423; Pacific Ocean: Samoa Islands, Tutuila: USNM 147653.

***Entomacrodus niuafoouensis* (Fowler)**

PLATES 9, 10*c–d*

Salarias niuafoouensis Fowler, 1932b, Proc. U.S. Nat. Mus., vol. 81, no. 8, pp. 7–8 [Niuafoou Island].

DESCRIPTION.—Segmented dorsal fin rays 15 or 16; segmented anal fin rays 16 or 17; posteriormost anal pterygiophore supporting 1 or 2 external elements (55.9 percent supporting 2); total gill-rakers on first arch 21–28 (usually 22–26); pseudobranchial filaments 7–9, number not increasing with increase in SL (above 32 mm SL); vertebrae 34 or 35 (rarely 35); supraorbital cirri 4–7, number not increasing with increase in SL (above 32 mm SL); main, or longest, supraorbital cirrus with all branches mesially (32 of 34 specimens; 1 specimen each also having 1 and 2 lateral branches); nape with 1 cirrus on each side (cirrus rarely with 1 branch in large specimens); predorsal commissural pores 6–69, number increasing with increase in SL (table 27); preopercular series of pores with all positions with multiples of pores;

positions occasionally including some pore pairs (usually at position number 6); 1–6 pores before each anterior nostril (2 or more in 32 of 34 specimens; total number of pores before anterior nostrils 3–9 in all specimens); lateral line terminating on side in area below and between segmented dorsal ray 4 and midcaudal peduncle (usually posterior to dorsal ray 10 in specimens over 40 mm SL); ventral margin of upper lip completely crenulate; lip crenulae number 27–39 (usually 30 to 36).

Proportional measurements: See tables 3, 4, and 28.

No males were seen with fleshy rugose modifications of the skin of the anal spines and rays. The largest male examined was approximately 81 mm SL; the largest female examined was 95.6 mm SL. The smallest specimen examined, 32.6 mm, was not an ophioblennius stage. Only 8 of the 34 specimens available were males.

Color pattern of preserved specimens.—Pacific Ocean specimens: The sides of the body vary from almost uniformly pale to bearing 4½ or four and two half pairs of somewhat vertical series of light to dark dusky spots. The half pair series of spots are on the caudal peduncle and in the humeral region. A small, diffusely dusky spot is noticeable in the humeral region of some specimens. The ventralmost spots of each paired vertical series are least intense and widely separated from each other. The most noticeable marking on the side of the head is a slender, more or less vertical, irregular stripe posterior to, and well separated from, the eye. Occasionally this stripe expands into, and joins ventrally, an irregular dark blotch (see: Schultz and Chapman, 1960, plate 114 D; Fowler, 1932b, fig. 3). There may be other dusky markings with included pale vermiculations, usually, but not always, between the eye and the upper lip. The posterodorsal portion of the opercle is occasionally dark margined or completely dusky. The top of the head is irregularly dusky. The ventral portion of the head always bears indications of dark or dusky chevrons, each sometimes with a distinct pale margin (see Schultz and Chapman, 1960, plate 114 D). The upper lip is marked by up to 22 dusky, sometimes irregular, stripes of varying intensity, separated by narrower pale stripes, and arranged in groups of equal intensity. Frequently the darkest stripes on each side of the lip are in the area below the eye.

The spinous dorsal fin usually bears a narrow dusky distal band followed proximally by irregular, diffuse, dusky, and pale stripings. There are up to five darkly dusky areas at the base of the fin which are extensions onto the fin of the spots on the body. The soft dorsal rays each bear two or three light to dark dusky spots arranged in diagonal series across the fin. The tips of the anal fin rays are pale, especially anteriorly on the rays. The remainder of the rays are dusky. The interradial membrane is pale to dusky, darker distally. The caudal fin bears up to five irregular vertical dusky bands or stripes separated by paler interspaces. The pectoral fins are more or less uniformly pale or light dusky except for an occasional cresentic darker area at the base of the rays. The fleshy pectoral base is pale distally and usually has a dusky cresentic area proximally. The pelvic rays are usually pale; the interradial membrane dusky.

Indian Ocean specimens: Two female specimens are available from Madagascar. These two specimens differ in color pattern from Pacific specimens primarily in two features. They have well-developed subquadrate dark blotches in the humeral region above the pectoral axil as the darkest markings on the body, and the markings on the upper lip consist of about six broad dusky bands separated by fine pale stripes.

GEOGRAPHIC VARIATION.—Pacific Ocean populations appear to be very similar, but the two specimens from Madagascar are somewhat different from Pacific specimens. Aside from color pattern (see above) these two specimens have longer nuchal cirri (table 28) and possibly more predorsal commissural pores (table 27) than Pacific specimens of equal size. Their segmented anal fin ray counts of 16, with the last anal pterygiophore supporting only a single element, occurred in only 2 of the 32 Pacific specimens available. Possibly, this indicates lower average counts for the Madagascar population.

RELATIONSHIPS.—*Entomacrodus niuafoouensis* is a member of the *E. striatus* species group. Of this group, *E. niuafoouensis* differs: from *E. epalzeocheilus*, in having the nuchal cirri simple (with one branch in a few of the larger specimens) and in usually having more crenulae on the ventral margin of the upper lip; from *E. randalli*, in having more than one pore before each anterior nostril and in having stripes or bands on the upper lip; from *E. marmoratus*, in usually having no lateral branches on the main supraorbital cirrus (almost always fewer supraorbital cirri at any given SL), simple nuchal cirri, more than one pore before each anterior nostril, and in having more stripes, when present, on the upper lip; from *E. striatus*, in having more than one pore before each anterior nostril, paired pores in the preopercular series, lacking lateral branches on the main supraorbital cirrus, and in having a distinctly different color pattern.

Members of the *E. striatus* group are quite closely related. With the exception of *E. striatus* (collected with *E. epalzeocheilus* and *E. niuafoouensis*), no two of them have been collected from the same locality. Because of the existence of a Madagascar population of *E. niuafoouensis* (otherwise known only from the Pacific Ocean) and a Samoa Islands population of *E. epalzeocheilus* (otherwise known only from the Indian Ocean), there is general overlap in the range of these

TABLE 27.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus niuafoouensis* arranged by SL classes (in mm)

Classes	Number of pores																														
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	33	38	41	48	51	63	69
30-34.9	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
40	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
45	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
50	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
55	-	-	-	-	-	-	-	-	-	2	-	-	2	-	2	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	1[1]	-	-	-
65	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	1[1]	-	-
70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-
75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
80	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	1	-	-	-	-
85	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
95	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-

[1] Madagascar specimens

two species, and they might be expected to occur in the same locality. It is conceivable, however, that the Samoan Island population is only a parallel *epalzeocheilus*-type offshoot of *E. niuafoouensis*, and the Madagascar population is a comparable *niuafoouensis*-type offshoot of *E. epalzeocheilus*, and no true overlap in the ranges of these two species really occurs. The two species are quite closely related and only slight convergent modifications would be needed to make proper identification difficult. Another possibility is that the distantly removed population of each species is a relict, indicating an early wide distribution of the species. The other two species of the related complex, *E. randalli* and *E. marmoratus*, are endemics in the Marquesas and Hawaiian Islands, respectively, and their distributions lend some support to the idea that *E. epalzeocheilus* and *E. niuafoouensis* are restricted in distribution also.

REMARKS.—*Entomacrodus niuafoouensis* has been collected with or from the same restricted geographic locality as *E. striatus*, *E. decussatus*, *E. vermiculatus*, *E. t. thalassinus*, *E. sealei*, and *E. caudofasciatus*. It may be most obviously differentiated: from *E. decussatus* and *E. vermiculatus*, in usually having fewer vertebrae, pseudobranchial filaments, supraorbital cirri (lacking lateral branches), and in having

TABLE 28.--Proportional dimensions as percent SL of specimens of *Entomacrodus niuafoouensis* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL
UH 03084	Tongatapu	♂	34.4	23.0	7.6	4.4	2.6	10.2	13.1	25.0	16.6	25.9
UH 03083	Tongatapu	♂	45.2	24.6	6.2	6.2	3.1	10.6	13.3	24.3	17.7	24.3
UMMZ 144749	Bonin Is.	♂	45.8	23.1	7.0	5.7	3.1	11.1	12.0	26.2	17.9	24.5
UMMZ 144749	Bonin Is.	♂	49.6	23.8	6.2	8.1	2.4	9.5	12.1	26.0	17.5	25.4
UH 03083	Tongatapu	♀	51.4	24.9	6.4	5.8	3.9	10.1	14.8	24.7	18.5	23.5
USNM 124117	Guam	♀	58.5	24.1	6.3	6.5	3.4	9.7	12.3	22.9	16.6	23.6
UH 03084	Tongatapu	♀	61.5	24.4	5.8	5.4	2.6	9.8	11.0	23.9	17.4	23.9
MNHN A2042	Madagascar	♀	64.1	24.2	6.2	7.2	4.7	10.9	13.7	27.8	18.7	22.2
MNHN A2042	Madagascar	♀	65.5	25.0	6.1	6.7	4.1	11.1	11.4	27.6	18.3	22.4
UMMZ 144749	Bonin Is.	♀	66.3	24.1	6.2	6.2	3.3	10.0	13.0	25.6	16.6	24.9
UMMZ 144749	Bonin Is.	♀	68.3	24.3	6.1	6.4	3.1	10.2	12.4	25.3	17.6	23.4
UMMZ 144749	Bonin Is.	♀	73.2	23.0	6.0	5.9	2.7	9.7	12.8	24.6	16.5	24.2
UH 03084	Tongatapu	♀	75.4	23.7	5.4	6.2	3.2	9.7	11.9	22.9	15.2	21.5
UH 03084	Tongatapu	♀	80.9	24.6	5.1	6.2	2.5	11.9	13.6	26.0	16.3	23.9
UMMZ 144749	Bonin Is.	♀	83.5	23.7	5.7	6.3	2.4	10.7	12.5	25.1	16.5	23.5
UH 03083	Tongatapu	♀	95.6	24.3	5.2	5.6	2.5	11.5	12.6	23.2	15.7	23.1

a strikingly different color pattern; from *E. t. thalassinus*, *E. sealei*, and *E. caudofasciatus*, in having the entire ventral margin of the upper lip crenulate, and in having more gill-rakers, usually more pseudobranchial filaments, and more than one pore before each anterior nostril.

Distribution (fig. 6).—*E. niuafoouensis* is known from Madagascar, Bonin, Marianas, Tonga and Niuafou Islands.

Material.—Madagascar: MNHN A 6924; Bonin Islands (Ogasawara), Ototoshima: UMMZ 144749; Mariana Islands, Guam: USNM 124117; Tonga Islands, Tongatapu: UH 03083, 03084; Niuafou: USNM 91932 (holotype of *Salarias niuafoouensis*), 137821, 138298.

Entomacrodus randalli, new species

Plate 11

Description.—(Characters for holotype given in parentheses.) Segmented dorsal fin rays 15 or 16 (16); segmented anal fin rays 16 or 17 (17); posteriormost anal pterygiophore supporting 1 or 2 external elements (supporting 1 element in 7 of 11 specimens; supporting 1 in holotype); total gill-rakers on first arch 21–24 (23); pseudobranchial filaments 7–10 (7); vertebrae 34 or 35 (34 in 8 of 9 specimens; holotype with 34); supraorbital cirri 4–8 (5, too few specimens available to determine if cirri or predorsal commissural pores increase in number with increase in size); main, or longest, supraorbital cirrus with all branches mesially; nape with 1 cirrus on each side; predorsal commissural pores 9–42 (21 in holotype; 9–21 in 9 specimens 39–72 mm SL; 42 in specimen 87.5 mm SL); preopercular series of pores with at least 4 positions with pairs or multiples of pores (6); 1 pore before each anterior nostril; lateral line terminating on side of body in area below and between dorsal fin ray 10 and point just posterior to level of posteriormost dorsal fin ray (below dorsal ray 10); ventral margin of upper lip completely crenulate; lip crenulae number 24–32 (28).

Proportional measurements: See tables 3, 4, and 29.

Of the 11 specimens available, the largest, 87.5 mm SL, was a male with the anal spines and first two anal rays covered with fleshy rugose modifications of the skin, indicating probable sexual maturity.

Color pattern of holotype.—(None of the specimens available were in good condition and for the most part color pattern was indiscernible. As far as could be recognized, the color pattern of all the paratypes appeared to agree in all essentials with that of the holotype.) There are six areas on the side of the body bearing irregular bandlike dusky marks. The area on the caudal peduncle consists of a pair of spots arranged one over the other. The next four areas anterior are each dusky X-like markings, darkest midlaterally, palest ventrally. These marks do not reach the ventral body contour.

Dorsally, these marks extend onto the dorsal fin taking a dorsoposterior direction. The anteriormost bandlike area is restricted to the side below the anterior dorsal fin spines. In the region of the pectoral axil this marking forms a dark (humeral) blotch.

As its darkest mark, the head bears an elongate stripe posterior to the eye. This stripe extends ventrally into a larger, paler, irregular area on the cheek. The snout and upper lip bear numerous small dusky spots arranged in somewhat vertical series. There are faint indications of a dusky Y-shaped chevron midventrally on the head.

The anal fin membranes are evenly dusky, grading darker distally, darker than the anal elements. The pectoral fin is pale dusky with a darker, diffuse, elongate spot at the bases of the central rays. Another such spot, separated by a pale area, is on the fleshy pectoral base. The pelvic fins are pale dusky. The caudal fin is pale dusky, darker along the rays, with indications of some irregular marks on its proximal half.

Relationships and comparisons.—*Entomacrodus randalli* is a member of the *E. striatus* species group. It differs from other members of the group in the following: from *E. niuafoouensis* and *E. epalzeocheilus*, in having a single pore before each anterior nostril, and spots, instead of stripes, on the upper lip; from *E. epalzeocheilus* and *E. marmoratus*, in having a single cirrus on each side of the nape; from *E. marmoratus* and *E. striatus*, in having branches of the supraorbital cirrus only on the mesial margin of the cirrus; from *E. striatus*, in having paired pores in the preopercular series and a strikingly different color pattern. *E. randalli* is quite similar to *E. niuafoouensis* and is probably a relatively recent derivative of the same species which gave rise to *E. niuafoouensis*.

Remarks.—*Entomacrodus randalli* is endemic to the Marquesas Islands and has been taken in the same collection with the other two species (fig. 6) of Marquesan *Entomacrodus*, *E. corneliae* and *E. macrospilus*, also endemics. *E. randalli* differs from these two species most prominently in having the ventral margin of the upper lip completely crenulate, more gill-rakers, and more pseudobranchial filaments.

TABLE 29.--Proportional dimensions as percent SL of specimens of *Entomacrodus randalli* (specimens in poor condition; proportions approximate; for meaning of abbreviations see methods section)

Catalog No.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL
BPBM 2333-2334	Marquesas	♀	49.0	24.5	6.9	6.5	3.7	10.8	12.8	26.1	17.3	25.5
USNM 199985 Holotype	Marquesas	♀	51.2	24.0	6.6	4.9	3.5	10.9	12.3	25.8	18.2	25.4
BPBM 2333-2334	Marquesas	♂	87.5	24.2	6.3	11.4	2.3	10.3	11.0	22.9	15.2	21.8

Holotype.—USNM 199985, female, 51.2 mm SL, east side of Anaho Bay near cliffs at shore, Nuku Hiva, Marquesas, July 17, 1957, collected by J. E. Randall.

Paratypes.—USNM 199986, two females, same data as holotype; ANSP 82148 (3 specimens), BPBM 2333 and 2334 (2 specimens), CHNM 25140 and 25141 (2 specimens), and SU 24522 (1 specimen), all from Nuku Hiva.

Etymology.—Named for John E. Randall, whose collections of Marquesan fishes were of great importance for my study.

***Entomacrodus striatus* (Quoy and Gaimard)**

Plates 5, 7*b–c*, 12

Salarias striatus Quoy and Gaimard, 1836, *in* Cuvier and Valenciennes, Hist. Nat. Poissons, vol. 11, pp. 309–310 [le rivage près du Masson, Isle de France].

Salarias fraenatus Valenciennes, 1836, *in* Cuvier and Valenciennes, Hist. Nat. Poissons, vol. 11, pp. 342–344 [Côte Malabre].

?*Salarias arenatus* Bleeker, 1855, Nat. Tijdschr. Nederl. Indië, vol. 8, pp. 173–174 [Cocos Islands].

Salarias penotus Sauvage, 1891, Hist. Phys. Nat. Polit. Madagascar, vol. 14, p. 389 [misspelling of *fraenatus;* Madagascar].

Entomaerodus wolffi Rofen, 1958, Mar. Fish. Rennell Is., *in* Nat. Hist. Rennell Is., pp. 202–204 [Rennell Island].

Entomacrodus plurifilis plurifilis Schultz and Chapman, 1960, U.S. Nat. Mus. Bull. 202, pt. 2, pp. 338–340 [Tau Island, reef at Siulagi Point].

Entomacrodus plurifilis marshallensis Schultz and Chapman, 1960, U.S. Nat. Mus. Bull. 202, pt. 2, pp. 341–343 [Bikini Atoll, Enyu Island].

Description.—Segmented dorsal fin rays 14–17 (rarely 14 or 17, table 1); segmented anal fin rays 15–18 (rarely 15 or 18, table 1); posteriormost anal pterygiophore supporting 1 or 2 external elements (50.8 percent supporting 2); total gill-rakers on first arch 14–22 (16–20 in 93 percent of specimens); pseudobranchial filaments 5–10 (usually 6–8), increasing in number only slightly with increase in SL (table 30); vertebrae 33–35 (34 in 97 percent of specimens); supraorbital cirri 1–20, number increasing with increase in SL (table 31); main, or longest supraorbital cirrus with branches mesially and usually laterally (depending on population, see variation below); nape with 1 cirrus on each side (occasionally absent); predorsal commissural pores 2–10, increasing in number slightly with increase in SL up to 49 mm SL (table 32); preopercular series of pores with all positions with simple pores; 1 pore before each anterior nostril; lateral line pores terminating on side in area below and between dorsal fin spine 11 and dorsal ray 10 (usually between dorsal spine 13 and dorsal ray 6); ventral margin of upper lip usually completely crenulate, sometimes weakly; lip crenulae numbering 18–34 (22–29 in 91 percent of specimens).

Proportional measurements: See tables 2, 3, and 35.

Males develop fleshy rugose modifications of the skin of the anal spines and the anterior first to fourth anal rays. If one considers males with these modifications to be mature, the smallest mature male examined was 44.7 mm SL. Mature and immature males may occur in the same collection and in these collections immature males may be as much as 27 mm longer than mature males.

The largest specimen examined was a male 95.5 mm SL; the largest female was 72.3 mm SL. Only 4 (1.5 percent) of 259 females (30–72 mm SL) measured were over 69 mm SL, whereas 38 (9.9 percent) of 384 males (30 mm SL and larger) were over 69 mm. In general, males outnumbered females in all size classes over 49 mm SL, but the sexes were about equal in number in the 30–49 mm size classes; thus, the proportionate number of females at these smaller sizes was greater than the proportionate number of males. The smallest specimen examined, 15.8 mm SL, was not an ophioblennius stage and no such stages were seen. Vomerine teeth and one posterior canine were visible.

COLOR PATTERN OF PRESERVED MATERIAL.—There is considerable variation in color pattern even among specimens within a single collection. The following description is based on specimens from Jarvis Island. Some variations are discussed following this description.

In specimens with the most developed pattern the sides of the body are conspicuously marked with numerous dark spots, none of which

TABLE 30.--Frequency distribution of number of pseudobranchial filaments of specimens of *Entomacrodus striatus* arranged by SL classes (in mm)

Classes	Pseudobranchial filaments 5	6	7	8	9	10	Average
20-24.9	1	3	2	-	-	-	6.2
25	1	7	11	-	-	-	6.5
30	-	12	13	-	-	-	6.5
35	1	19	21	6	-	-	6.7
40	1	15	40	8	1	-	6.9
45	-	19	24	17	-	-	7.0
50	1	8	39	13	-	-	7.0
55	-	14	20	14	-	-	7.0
60	-	8	20	9	2	-	7.1
65	-	2	6	7	1	-	7.4
70	-	3	5	4	3	-	7.5
75	-	-	2	3	-	-	7.6
80	-	1	4	2	-	1	7.5
85	-	1	-	-	-	-	-
90	-	-	1	-	-	-	-
95	-	-	1	-	-	-	-

are larger than about half the area of the orbit; most are smaller. The spots are darkest along the midline of the side and largest in the area between and under the posterior half of the spinous and anterior half of the soft dorsal fin. From this area the spots decrease in size and increase in number anteriorly to the pectoral axil, where they are smallest. The spots decrease in size and number posteriorly to the caudal peduncle. The spots also decrease in size and intensity both dorsally and ventrally to the dorsal and ventral body contours. The darkest spots cluster in about five areas on the body, which may indicate that the spots are derived from a bandlike pattern (evident in specimens from other collections). The venter is pale.

The side of the head is variably dusky with an irregular, slender, somewhat vertical dark stripe posterior to the orbit, and separated from the orbit by a distance half the orbital diameter. A faint second stripe extends from the ventral midmargin of the orbit to the upper lip. The top of the head is not noticeably marked. The underside of the head in males varies from almost uniformly dusky to having a pattern of dusky chevrons separated by pale stripes; the underside of the head infrequently has a pattern of numerous dusky spots. In females the underside of the head is marked as in males but the pale stripes are more obvious and the dusky chevrons are intruded by small pale spots. The upper lip is faintly dusky.

The spinous dorsal fin of males is dusky with two or three rows of pale spots coursing through it; that of females marked with diffuse dusky and pale spots, a pattern which can be derived from that of the males. The soft dorsal fin of both sexes bears dusky stripes coursing

TABLE 31.--Frequency distribution of number of supraorbital cirri of left eye of specimens of *Entomacrodus striatus* arranged by SL classes (in mm)

Classes	Number of cirri																				Average
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
15-19.9	8	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.2
20	1	3	3	6	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	3.8
25	-	-	3	4	9	2	4	1	-	1	-	-	-	-	-	-	-	-	-	-	5.3
30	-	1	3	3	10	11	10	6	2	2	1	-	1	-	-	-	-	-	-	-	6.4
35	-	-	-	8	12	14	11	13	17	10	3	-	-	-	1	-	-	-	-	-	7.4
40	-	-	-	1	8	18	12	21	20	9	4	1	1	1	1	-	-	-	-	-	8.0
45	-	-	-	5	6	11	12	18	21	15	9	7	2	1	-	-	-	-	-	-	8.5
50	-	-	-	1	7	8	14	18	11	6	15	10	3	4	-	-	-	1	-	-	9.0
55	-	-	-	2	2	6	7	9	13	9	12	4	5	4	2	-	1	-	1	-	9.7
60	-	-	1	-	1	1	6	8	6	6	11	11	5	2	2	1	-	-	-	-	10.3
65	-	-	-	-	-	1	2	2	3	3	1	4	1	2	1	3	1	1	-	-	11.6
70	-	-	-	-	-	1	-	2	1	1	1	3	3	-	3	3	1	-	1	-	12.8
75	-	-	-	-	-	-	-	-	-	2	-	1	1	-	-	1	-	2	-	1	14.6
80	-	-	-	-	-	-	-	1	-	-	1	1	2	-	-	2	-	-	-	-	12.7
85	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-	-	-	12.3
90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	17.0
95	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-

diagonally (ventroanteriorly to dorsoposteriorly) across the fin, and separated by pale areas. The stripes are so arranged that about three or four pass over each ray, but the same stripes do not pass over all the rays. The anal fin membrane (between each ray) is variably dusky, becoming more intense distally, generally much darker in males than females. The anal rays are paler than the interradial membrane. The caudal fin is marked by a variable number of alternating, irregularly vertical dark and pale stripes (increasing in number with increase in SL, up to about 10 or 11 dark stripes). Most of the dark pigment of the stripes is restricted to the caudal fin membrane. The pectoral fins are very faintly dusky with a concentration of pigment sometimes at the base of the rays. The fleshy pectoral base is diffusely dusky but may show evidence of a diffusely dusky band anteriorly. The pelvic fins are pale to dusky, darker in males than females.

In Marshall Islands specimens, the pale striping on the underside of the head may be very conspicuous. Pale spots and dashes may extend onto the upper lip, snout, and sides of the head. In specimens from many diverse localities, the only distinct markings are the large

TABLE 32.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus striatus* arranged by SL classes (in mm)

Classes	Number of pores 2	3	4	5	6	7	8	9	10	Average
15-19.9	-	9	-	-	-	-	-	-	-	3.0
20	1	15	1	-	-	-	-	-	-	3.0
25	-	22	3	3	-	-	-	-	-	3.3
30	2	28	22	3	1	-	-	-	-	3.5
35	1	27	32	17	1	2	-	-	-	4.0
40	1	36	36	25	4	2	-	-	-	4.0
45	-	26	41	24	12	1	5	1	-	4.4
50	2	22	41	24	8	-	1	-	1	4.2
55	1	22	25	15	5	4	2	-	-	4.3
60	-	15	21	10	5	6	2	-	2	4.7
65	1	7	10	3	1	2	1	-	-	4.2
70	1	5	6	-	4	1	-	-	1	4.6
75	-	4	3	2	-	-	-	-	-	3.8
80	-	1	5	1	1	-	-	-	-	4.2
85	-	-	1	2	-	-	-	-	-	4.7
90	-	-	2	-	-	-	-	-	-	4.0
95	-	1	-	-	-	-	-	-	-	3.0

dark spots along the midlateral length of the body. Some specimens from the South China Sea have strong indications of diffuse, dark, bandlike extensions dorsally from the concentrated areas of body spots, and some specimens exhibit three diffuse vertical bands on the upper lip.

TABLE 33.—Frequency distributions of number of segmented dorsal and anal fin rays of specimens of *Entomacrodus striatus* from the Pacific Ocean arranged north to south by latitude (for definition of method A, method B, S and N, see methods section)

Locale	Approximate latitude	Segmented dorsal rays					Segmented anal rays method A					Segmented anal rays method B					
		14	15	16	17	Average	15	16	17	18	Average	16	17	18	Average	S	N
Amami Oshima	28° 30' N	-	-	2	-	16.00	-	-	2	-	17.00	-	1	1	17.50	1	1
Ototoshima	27° 10' N	-	1	2	-	15.67	-	2	1	-	16.33	1	2	-	16.67	1	2
Wake	19° 20' N	-	1	1	-	15.50	-	2	-	-	16.00	-	2	-	17.00	2	-
Saipan	15° 15' N	1	21	25	-	15.51	-	22	26	-	16.54	-	34	14	17.29	36	12
Tinian	15° 00' N	-	1	3	-	15.75	-	2	2	-	16.50	-	3	1	17.25	3	1
Guam	13° 20' N	-	9	11	-	15.55	-	8	14	-	16.64	3	15	4	17.04	9	13
Bikini	11° 40' N	-	22	24	-	15.52	-	19	27	-	16.59	3	37	6	17.06	22	24
Rongerik	11° 20' N	-	11	7	-	15.39	-	9	9	-	16.50	3	12	3	17.00	4	4
Duamaguete, P.I.	09° 30' N	-	-	1	-	-	-	-	1	-	-	-	-	1	-	1	-
Ngarungl, Palaus	08° 10' N	-	15	10	-	15.40	-	10	14	-	16.58	-	20	4	17.17	14	10
Koror, Palaus	07° 25' N	-	1	1	-	15.50	-	1	1	-	16.50	-	2	-	17.00	1	1
Ifaluk	07° 15' N	-	4	4	-	15.50	-	2	6	-	16.75	-	8	-	17.00	2	6
Peleliu, Palaus	07° 00' N	-	-	1	-	-	-	-	1	-	-	-	1	-	-	-	1
Jaluit	05° 50' N	-	4	11	-	15.73	-	3	12	-	16.80	1	12	2	17.07	4	11
Fanning	04° 00' N	-	1	3	-	15.75	-	1	3	-	16.75	-	4	-	17.00	1	3
Christmas	02° 00' N	-	-	2	-	16.00	-	-	2	-	17.00	-	2	-	17.00	-	2
Howland	00° 50' N	-	6	7	-	15.54	-	4	9	-	16.69	1	9	3	17.15	6	7
Jarvis	00° 25' N	-	21	29	-	15.58	-	8	42	-	16.84	2	44	4	17.04	10	40
Enderbury	02° 50' S	-	14	6	-	15.30	-	11	9	-	16.45	1	16	3	17.10	13	7
Canton	02° 50' S	-	13	14	-	15.52	-	8	19	-	16.70	1	18	8	17.26	15	12
Phoenix	03° 00' S	-	6	4	-	15.40	-	1	9	-	16.90	-	9	1	17.10	2	8
McKean	03° 00' S	-	1	-	-	-	-	1	-	-	-	-	1	-	-	1	-
Hull	04° 00' S	1	2	2	-	15.20	-	1	4	-	16.80	-	2	3	17.60	4	1
New Britain	04° 15' S	-	-	2	-	16.00	-	-	2	-	17.00	-	1	1	17.50	1	1
Funafuti	08° 30' S	-	1	4	-	15.80	-	1	4	-	16.80	-	4	1	17.20	2	3
Penrhyn	09° 00' S	-	1	2	-	15.67	-	-	3	-	17.00	-	-	3	18.00	3	-
Swains	11° 05' S	-	7	6	-	15.46	-	3	10	-	16.77	-	10	3	17.23	6	7
Rennell	11° 40' S	-	-	1	-	-	-	-	1	-	-	-	1	-	-	-	1
Rotuma	12° 30' S	-	1	1	-	15.50	-	1	1	-	16.50	-	1	1	17.50	2	-
Tau	14° 15' S	1	13	36	1	15.72	-	15	36	-	16.70	3	36	12	17.18	24	27
Tutuila	14° 15' S	-	1	12	-	15.92	1	1	11	-	16.77	1	10	2	17.08	4	9
Santo, New Hebrides	15° 20' S	-	-	2	-	16.00	-	-	2	-	17.00	-	1	1	17.50	1	1
Makatea	15° 40' S	-	-	1	-	-	-	-	1	-	-	-	1	-	-	-	1
Raroia	16° 00' S	-	2	5	-	15.71	-	1	5	1	17.00	-	3	5	17.71	5	2
Herald Cay	17° 00' S	-	-	2	-	16.00	-	-	1	1	17.50	-	-	1	18.50	2	-
Tahiti	17° 40' S	-	7	13	1	15.71	-	3	16	2	16.95	-	10	11	17.52	12	9
Efate, New Hebrides	18° 10' S	-	3	6	-	15.67	-	1	7	1	17.00	1	4	4	17.33	3	6
Fiji	18° 10' S	-	2	9	-	15.81	-	3	8	-	16.73	-	9	2	17.18	6	5
Aneityum, New Hebrides	20° 10' S	-	-	1	-	-	-	-	1	-	-	-	1	-	-	-	1
Tongatapu	21° 10' S	-	-	10	1	16.09	-	-	10	1	17.09	-	8	3	17.27	2	4
Rarotonga	21° 30' S	-	1	8	1	16.00	-	-	8	2	17.20	-	3	7	17.70	5	5
New Caledonia	22° 30' S	-	2	1	-	15.33	-	1	2	-	16.67	-	3	-	17.00	1	2
Lord Howe	31° 30' S	-	-	5	-	16.00	-	-	5	-	17.00	-	3	2	17.40	2	3

In general, specimens from the western and northern Indian Ocean appear to have fewer spots on the sides than do Pacific Ocean specimens, but this characteı is difficult to evaluate. One collection of Seychelles Island specimens (ANSP 102188) as opposed to others, contained specimens with very large spots, over half the orbital diameter in size. Other specimens in the same collection exhibited paired broken bands on the sides, and alternating pale and diffusely dusky stripes on the lips. Specimens from the Seychelles, Mauritius, Madagascar, and East Africa tend to have a fusion of the spots in the humeral area which gives the appearance of a noticeable blotch, but this fusion is by no means a consistent feature. Among other Indian Ocean populations, specimens from India may or may not have a humeral blotch, and specimens from the Cocos Islands (with the possible exception of the holotype of *Salarias arenatus*) do not. Dark humeral blotches or slender spots appeared variably on specimens from Pacific Ocean and South China Sea localities but were common only in collections from Rarotonga and Fiji.

Meristic and proportional variation.—Variation in the number of lateral (as opposed to mesial) cirri branches on the main supraorbital cirrus appears to occur in certain populations. Since the number of cirri is also dependent on size (table 31), one must select specimens of about 40 mm SL or longer to insure that some lateral cirri, if they are to be developed, will be present. Under these circumstances it was found that specimens from the coast of India usually lack lateral branches (24 of 42 specimens) whereas specimens from the various Pacific populations almost always have at least one laterally placed cirrus (exception: 2 of 24 specimens from the Palaus) and frequently as many as three or four (up to seven). Seychelles Islands specimens all had lateral cirri; however, specimens from the South China Sea commonly lacked lateral cirri (the 2 specimens from Hong Kong; 10 of 44 specimens from the Viet Nam coast; 2 of 12 specimens from the Thailand coast). Specimens from Western Australia may lack lateral cirri but the supraorbital cirri of specimens from this area appeared to have been abnormally reduced or aborted, and the lack of lateral cirri may be teratological. There does not appear to be a relationship between the mesial cirri branches and the presence or absence of lateral cirri branches; thus, populations with lateral branches have more cirri at a given SL interval than do those without such branches. Presence or absence of lateral cirri branches was not considered in the construction of table 31, where data for all populations were combined (exclusive of the Western Australia specimens).

There is considerable variation also in the relative length of the main supraorbital cirrus. A selected sample of the populations indi-

TABLE 34.--Frequency distributions of number of segmented dorsal and anal fin rays of specimens of *Entomacrodus striatus* from the South China Sea (including the Gulf of Thailand) and the Indian Ocean arranged north to south by latitude (for definition of method A, method B, and S and N, see methods section)

Locale	Approximate latitude	Segmented dorsal rays			Average	Segmented anal rays, method A				Average	Segmented anal rays, method B			Average	S	N
		14	15	16		15	16	17	18		16	17	18			
SOUTH CHINA SEA																
Hong Kong	22° 13' N	-	3	-	15.00	-	2	1	-	16.33	-	3	-	17.00	2	1
Goh Samet	12° 32' N	-	5	6	15.54	-	1	10	-	16.91	-	9	2	17.18	3	8
Nhatrang	12° 22' N	-	5	11	15.69	-	5	11	-	16.69	1	11	4	17.19	8	8
Ilot du Sud	10° 29' N	-	13	29	15.69	-	8	32	1	16.83	1	28	12	17.27	18	23
Goh Tao	06° 00' N	-	1	-	-	-	1	-	-	-	1	-	-	-	-	1
INDIAN OCEAN																
Bombay, India	18° 15' N	-	8	-	15.00	-	7	1	-	16.12	1	6	1	17.00	7	1
Vizagapatam, India	17° 30' N	1	16	8	15.28	2	9	14	-	16.48	4	16	5	17.04	13	12
Andaman Is.	12° 15' N	-	3	3	15.50	-	2	4	-	16.67	-	4	2	17.33	4	2
Konival, India	07° 50' N	-	9	4	15.31	-	4	9	-	16.69	1	11	1	17.00	4	9
Ceylon	07° 00' N	-	2	-	15.00	-	2	-	-	16.00	-	2	-	17.00	2	-
Praslin, Seychelles	04° 20' S	-	-	1	-	-	-	1	-	-	-	1	-	-	-	1
Curieuse, Seychelles	04° 20' S	-	16	2	15.11	-	15	3	-	16.17	1	16	1	17.00	15	3
La Digue, Seychelles	04° 20' S	-	1	-	-	-	1	-	-	-	-	1	-	-	1	-
Anonyme, Seychelles	04° 50' S	-	4	-	15.00	-	3	1	-	16.25	-	4	-	17.00	3	1
Mahé, Seychelles	05° 00' S	-	22	7	15.24	-	18	11	-	16.38	1	22	6	17.17	23	6
St. Pierre	09° 00' S	-	-	1	-	-	1	-	-	-	-	1	-	-	1	-
Cocos-Keeling	12° 20' S	-	9	7	15.44	-	7	9	-	16.56	1	13	2	17.06	9	7
Ibo, Mozambique	12° 30' S	-	1	-	-	-	1	-	-	-	-	1	-	-	1	-
Tanikely, Madagascar	13° 30' S	-	1	-	-	-	1	-	-	-	-	1	-	-	1	-
Mauritius	20° 30' S	-	2	2	15.50	-	1	2	1	17.00	-	2	2	17.50	2	2
NW Cape, Australia	22° 00' S	1	11	8	15.35	-	9	11	-	16.55	1	15	4	17.15	12	8
Inhambane, Mozambique	23° 30' S	-	1	-	-	-	1	-	-	-	-	1	-	-	1	-
St. Lucia, So. Africa	28° 00' S	1	3	-	15.00	-	1	2	-	16.67	1	2	-	16.67	-	3
Durban, So. Africa	30° 00' S	1	-	-	-	-	1	-	-	-	-	1	-	-	1	-

cated that this variation was geographically, sexually, and ontogenetically correlated. Different samples from a relatively limited geographical area (i.e., Phoenix Islands) may have quite different relative cirrus lengths. Within most populations males tend to have relatively longer cirri than females. Relative cirrus lengths of specimens from India do not overlap with cirrus lengths of specimens from Samoa; however, plotting lengths for other populations of the species show that the cirri lengths of some populations overlap both the Indian and Samoan populations. No clinal change (east to west, north to south) in relative cirrus lengths was noted. In conclusion, it appears that the character of main supraorbital cirrus length is affected by a complex of factors and can be expected to vary considerably from one locality to the next.

Variation in average number of segmented dorsal or anal fin rays occurs among the various populations of *E. striatus*. Such variation prompted Schultz and Chapman (1960) to recognize subspecies within this species. In an attempt to determine if the variation followed any geographic pattern, I arranged frequency distributions of the counts on a latitudinal north to south basis (regardless of longitude) within the three major areas where the species occurs (tables 33, 34): Pacific Ocean, South China Sea, Indian Ocean. Inasmuch as the method of counting anal rays generally employed in the present study (method A) might obscure significant counts of the anal fin, I have also given frequency distributions of the total segmented anal elements (method B).

In the Pacific Ocean the highest average fin ray counts were obtained for populations south of the equator. A trend of increasing averages for anal rays, both methods, from north to south is particularly noticeable if averages are taken of the counts grouped by 10 degree latitude intervals; dorsal rays appear to increase in both directions from the equator:

latitude class	*dorsal ray average*	*no.*	*anal rays*		*no.*
			method A average	*method B average*	
29°–20° N	15.80	5	16.60	17.00	5
19°–10° N	15.51	137	16.56	17.14	140
09°–00° N	15.57	121	16.76	17.08	120
00°–09° S	15.43	73	16.68	17.24	73
10°–19° S	15.73	132	16.81	17.30	132
20°–29° S	15.96	25	17.08	17.40	25
30°–39° S	16.00	5	17.00	17.40	5

The validity of grouping the data in the above manner is not known, but perhaps it is suspect because the fin ray counts grouped north to south by 10 degree longitude intervals present no clear-cut trend within a particular interval. The difficulty is perhaps due to the fact that there is insufficient material from within the intervals

TABLE 35.--Proportional dimensions as percent SL of specimens of *Entomacrodus striatus* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DS13	DR1	PECL	PELL	CL
USNM 197907	Phoenix Is.	♀	30.0	23.6	7.0	5.0	2.7	10.7	1.7	11.7	24.0	16.0	25.6
USNM 115452	Samoa	♂	32.5	24.6	8.3	3.1	2.8	9.5	-	9.2	24.6	16.3	26.1
SU 14735	India	♂	37.7	23.9	6.6	6.1	2.1	9.3	-	10.9	23.8	15.1	24.1
USNM 115449	Phoenix Is.	♀	37.7	23.9	7.4	3.2	2.1	9.5	-	12.5	25.2	17.0	26.0
USNM 142165	Bikini	♀	40.0	24.5	7.5	4.5	2.2	9.0	2.0	13.5	23.0	14.5	25.0
SU 14735	India	♂	42.0	23.3	6.9	7.6	-	8.3	-	11.7	23.3	17.3	25.2
USNM 115452	Samoa	♂	42.1	25.2	7.1	2.8	2.4	9.5	1.2	10.9	22.3	15.4	25.2
USNM 142159	Bikini	♂	42.2	23.2	7.1	4.7	2.8	9.5	-	11.8	22.7	15.9	24.9
USNM 115449	Phoenix Is.	♀	42.4	23.8	6.8	4.5	2.1	9.9	-	11.8	23.6	15.1	23.6
USNM 142162	Bikini	♀	43.0	23.7	7.4	3.7	2.3	9.8	-	12.8	23.7	15.6	24.7
SU 14735	India	♀	44.0	22.7	6.6	5.0	1.8	8.9	-	11.3	22.5	15.0	25.0
USNM 115452	Samoa	♂	45.2	24.6	7.5	4.2	2.2	9.1	-	13.3	23.2	15.2	23.9
USNM 115452	Samoa	♂	45.5	24.4	6.6	4.0	2.4	9.0	1.8	12.7	22.6	15.8	24.4
USNM 142165	Bikini	♂	46.0	22.2	6.7	4.3	1.7	9.8	2.2	11.7	22.8	15.2	23.9
USNM 142158	Bikini	♂	47.4	23.2	6.3	3.6	2.5	9.3	-		22.8	16.2	25.3
SU 14735	India	♀	49.2	22.8	6.1	6.1	2.4	8.9	2.0	8.5	23.1	15.6	23.6
USNM 123855	Saipan	♀	49.2	24.0	6.9	4.5	2.2	8.7	-	12.1	22.8	13.6	23.6
USNM 115449	Phoenix Is.	♂	49.5	22.2	6.5	4.4	2.4	10.9	2.0	11.7	23.6	14.7	22.4
USNM 115449	Phoenix Is.	♀	50.0	22.4	6.0	3.8	2.4	9.2	-	11.0	22.2	14.4	23.4
USNM 142162	Bikini	♂	50.4	24.2	6.5	4.4	2.6	8.9	-	12.3	23.0	14.3	23.8
USNM 115452	Samoa	♀	51.0	23.5	6.7	3.9	1.8	8.8	0.8	11.0	22.7	14.7	24.5
USNM 123855	Saipan	♂	52.2	24.1	6.7	5.0	-	8.6	-	11.5	21.1	13.4	22.2
SU 14735	India	♂	52.8	22.9	5.7	7.2	2.6	8.5	-	10.4	22.9	15.1	23.5
USNM 115452	Samoa	♀	53.0	23.8	7.0	3.0	2.1	9.8	-	11.3	24.0	15.8	24.9
USNM 115449	Phoenix Is.	♂	53.5	22.4	6.0	5.2	2.2	11.0	-	10.8	20.7	14.0	22.4
USNM 123855	Saipan	♂	55.4	23.8	6.3	5.6	2.0	9.0	-	10.8	20.7	13.3	22.0
USNM 142165	Bikini	♂	55.5	24.5	6.5	4.5	2.0	9.9	1.8	11.0	-	13.5	23.8
USNM 142163	Bikini	♂	55.6	23.4	6.3	7.0	2.2	9.9	1.4	11.9	21.8	13.7	24.8
USNM 115452	Samoa	♂	56.2	23.1	6.6	3.6	2.7	9.2	-	12.4	21.4	13.9	23.8
USNM 123855	Saipan	♂	56.8	23.2	6.3	4.6	2.3	8.6	-	12.1	20.8	13.0	22.4
USNM 115449	Phoenix Is.	♂	59.2	22.1	5.9	4.2	-	9.3	-	10.1	20.8	12.5	22.8
SU 14735	India	♀	60.0	21.8	5.7	5.7	1.8	9.0	-	10.0	21.7	14.0	23.0
USNM 144720	Samoa[1]	♂	61.3	22.8	6.2	3.6	2.1	9.0	2.0	12.1	20.3	13.8	22.8
USNM 123855	Saipan	♂	62.2	23.5	6.4	6.4	2.4	9.5	-	12.2	21.0	12.5	22.5
USNM 115452	Samoa	♀	62.6	23.8	6.2	3.2	2.1	8.8	1.6	11.2	22.4	13.6	22.4
USNM 115449	Phoenix Is.	♂	63.6	22.3	5.5	4.7	1.7	9.9	1.6	11.0	20.4	13.4	22.2
UZMK P75354	Solomon Is.[2]	♀	64.6	23.2	6.2	3.6	-	8.8	1.7	11.6	22.2	-	23.2
USNM 142155	Bikini[3]	♂	65.7	22.7	5.8	4.6	1.8	10.0	-	-	20.6	13.7	23.2
USNM 115449	Phoenix Is.	♂	65.7	21.6	5.5	4.3	2.4	10.5	2.4	11.4	21.3	13.1	22.8
SU 14735	India	♂	66.2	21.9	5.7	6.8	1.0	10.4	-	12.2	21.1	13.3	23.4
RU(no number)	Seychelles	♂	67.0	23.0	5.2	4.8	1.8	-	-	12.2	21.5	-	22.4
SU 14735	India	♂	67.3	22.3	5.5	7.7	0.9	9.9	1.9	10.4	20.8	13.5	22.7
SU 14735	India	♂	67.9	22.8	5.9	5.3	1.3	9.7	-	11.5	22.1	11.3	22.7
SU 14735	India	♂	69.0	23.6	5.6	6.2	1.4	9.1	-	10.4	21.4	-	23.5
USNM 115449	Phoenix Is.	♂	72.6	21.9	5.2	4.7	1.6	10.6	-	11.7	20.6	13.1	22.8
USNM 115452	Samoa	♂	74.5	22.5	5.4	5.1	1.9	8.7	1.6	11.7	20.5	12.3	24.2
USNM 198141	Phoenix Is.	♂	79.4	21.5	5.0	5.0	1.8	8.8	-	10.1	21.0	12.5	22.7
USNM 198141	Phoenix Is.	♂	85.9	22.1	5.1	5.2	2.3	9.9	-	-	21.0	12.7	21.9
USNM 198141	Phoenix Is.	♂	95.5	22.4	4.7	4.7	1.6	9.5	-	10.7	21.5	12.5	22.8

[1] Holotype *Entomacrodus plurifilis plurifilis*

[2] Holotype *Entomacrodus wolffi*

[3] Holotype *Entomacrodus plurifilis marshallensis*

on which to base a meaningful study of north-south trends.

I have entered the fin ray averages of Pacific Ocean populations at their geographic locations on a map in a search for more complex trends. I could observe only that similar averages tended to group in certain locations, but there was no obvious relationship of widely separated areas with similar averages (e.g., the Line Islands and the Marshall Islands) or with averages of populations along island groups radiating out from them.

Fin ray counts and averages of populations (table 34) from the South China Sea (SCS) and Indian Ocean (IO) indicate no trends, nor are these averages similar to those of Pacific Ocean specimens from similar latitudes:

latitude class	*dorsal ray average*				*anal ray average method A*				*anal ray average method B*			
	SCS	*no.*	*IO*	*no.*	*SCS*	*no.*	*IO*	*no.*	*SCS*	*no.*	*IO*	*no.*
29°–20° N	15.00	3			16.33	3			17.00	3		
19°–10° N	15.67	69	15.26	39	16.81	68	16.44	9	17.24	68	17.08	39
09°–00° N	15.00	1	15.27	15	16.00	1	16.60	15	16.00	1	17.00	15
00°–09° S			15.20	54			16.30	54			17.09	54
10°–19° S			15.39	18			16.50	18			17.06	18
20°–29° S			15.32	28			16.61	28			17.14	28
30°–39° S			14.00	1			16.00	1			17.00	1

Strasburg (1955) reported that north-south differentiation in number of soft dorsal and anal rays occurred in the western Pacific salarine blenniid, *Istiblennius edentulus* (which has much the same distribution in the Pacific Ocean as does *E. striatus*). The average number of rays, he reported, tended to decrease from the northern latitudes to the equator and then to increase from the equator south as one progressed southeasterly along what Strasburg called the "main band" of islands (Wake, Marianas, Marshalls, Gilberts, Samoa, Tuamotus, Fijis, Societies, Gambiers). Strasburg gave no reasons to support his choice of the main band of islands upon which he based his evaluation.

Strasburg calculated regression lines for fin ray counts for the main band of islands based on average annual temperatures (which are generally correlated with latitude, decreasing north and south from the equator). He then set confidence limits at p .01 level and calculated the expected range of fin ray averages based on average annual temperatures for populations of *I. edentulus* from island groups outside the main band and demonstrated that almost all the averages fell within the range of those expected, inferring, thus, that there is some relationship between temperature and average fin ray count. Here it should be noted that if one were to eliminate the single high dorsal ray average for the Gambier specimens from Strasburg's calculations, his regression for dorsal fin rays would be hardly different from a straight line.

The temperatures Strasburg used were obtained by averaging the surface temperatures for the months of February and August as obtained from Charts II and III of Sverdrup, et al (1946). These charts were obviously redrawn from Schott (1935, pls. XX and XXII). Schott also gave temperatures for May and November (pls. XXI and XXIII). The temperatures that Strasburg has recorded to the nearest 0.1 degree centigrade were taken from the charts, which are only general plots of whole-degree centigrade isothermal lines on a map of the Pacific. The total temperature range forming the basis of Strasburg's regression, 25.5–28.0° C, covers only 2.5°. It is not unlikely that actual average temperatures for any of Strasburg's localities might differ as much as a degree from those he selected. Such differences might well alter Strasburg's conclusions. For this reason I am hesitant to test my counts against similarly derived temperature data.

Another point bearing on Strasburg's findings is the fact that he has used method A anal fin counts. Method B counts (indeterminable from his data) might have produced different results.

NOMENCLATURE.—The description of *Salarias striatus* Quoy and Gaimard was based on more than one specimen (exact number not mentioned) from Mauritius. There are three specimens (approximately 41, 44, and 58 mm SL) in the type series (MNHN A1796) in the Paris Museum. All are in poor condition. I here designate the largest of these three specimens lectotype. Aside from its greater length, the lectotype, a female, can be distinguished from the other two specimens (male and female) in having the dorsal fin rays XIV, 16 (the 14th spine is not clearly visible) as opposed to XIII, 15 or 16 (13th spine not visible) for the paralectotypes, and the soft anal rays 18 (the last not split to the base) as opposed to 17 (the last not split to the base) or 17 (the last split to the base) in the paralectotypes. The lectotype and female paralectotype have well-developed, dark humeral blotches. The male paralectotype has no humeral blotch.

Salarias fraenatus Valenciennes was based on several specimens from Bombay and although the description appears in the same work as that including the original description of *Salarias striatus*, *S. fraenatus* was compared only with the distantly related *S. textilis.* The Bombay specimens differ from the types of *S. striatus* primarily in having only a faint blotch in the humeral region, much smaller than the blotch found in the types of *S. striatus*. *S. striatus* has page priority over *S. fraenatus*.

Salarias arenatus Bleeker was described from a single specimen, 62 mm, from the Cocos Islands (Indian Ocean). Chapman (1951, p. 285) stated that Bleeker (1879, p. 20) synonymized *S. arenatus* Bleeker with *S. striatus*. Actually, Bleeker (1875, p. 74) first gave his synonymy in a paper on Madagascar fishes in which he noted the synonymy as "*Salarias arenatus* Blkr?=Salarias striatus Q&G CV," which denotes Bleeker questioned his action. In the 1878 paper Bleeker repeated this same questioned synonymy. I have been unable to locate the holotype of *S. arenatus* and it seems quite possible that it was lost even in Bleeker's day. From the description it is not possible to positively place *S. arenatus* in the synonymy of *E. striatus*. The main discrepancy I find is that Bleeker stated that his specimen had a black humeral spot "regione suprascapulari macula nigricante," whereas none of the 16 specimens I have examined from the Cocos Islands had such a mark. This may be a minor matter as occasional specimens with humeral blotches have been found in collections of specimens of *E. striatus*, where specimens with such blotches were uncommon. The only other species from the Indian Ocean with which *S. arenatus* might be identified is *Entomacrodus epalzeocheilus* (Bleeker, 1859). The described presence of a humeral spot on the body of *S. fraenatus* probably excludes it from synonymy with *E. epalzeocheilus*, which lacks such a mark.

Entomacrodus wolffi was described from a single specimen and differentiated from *E. striatus* by lacking nuchal cirri, by lacking canines in the lower jaw, in having filaments on both sides of the main supraorbital cirrus, and in having a black pectoral fin axilla. I have examined the holotype and have no reservations about including *E. wolffi* in the synonymy of *E. striatus*. Nuchal cirri are occasionally lacking in specimens of *Entomacrodus striatus* as are also canines in the lower jaw. The disposition of the lateral and mesial cirri on the main supraorbital cirrus is quite variable within a population (see discussion of variation above). The pectoral axilla of the holotype is not actually black. The blackness is due to the transparency of the skin of the axilla. Below the skin is a hollow which appears dark through the skin. This condition prevails in many specimens of *E. striatus* and depends to some extent on preservation.

Entomacrodus plurifilis was differentiated from *E. striatus* and *E. arenatus* by lacking cirri on the lateral margin of the main supraorbital cirrus and by lacking a humeral blotch. The invalidity of these two characters for species recognition within *E. striatus*, as considered here, has been discussed above. *Entomacrodus p. plurifilis* was separated from *E. p. marshallensis* because "about 71 percent of the specimens of *E. p. marshallensis* have 15 soft dorsal rays and about 51 percent have 16 soft anal rays, whereas *E. p. plurifilis*, respectively, have 70 percent with 16 soft dorsal and 83⅓ percent with 17 soft anal rays" (Schultz and Chapman, 1960). The variability of dorsal and anal fin ray counts that I have found in populations of *E. striatus* convinces me that the differences noted are insufficient for subspecies recognition.

RELATIONSHIPS.—*Entomacrodus striatus* is most closely related to a group of Indo-Pacific species (*E. striatus* species group): *E.*

epalzeocheilus, *E. niuafoouensis*, *E. randalli*, and *E. marmoratus*. The latter species are trenchantly different from *E. striatus* but are similar in having the ventral margin of the upper lip completely crenulate. In body form all these species attain a rather large size (over 85 mm SL) and have a rather robust body form, possibly a function of size. In addition, all have a well-developed, slender, elongate, dark mark just posterior to the orbit. *E. striatus* differs from all of the related forms except possibly *E. randalli* in having fewer predorsal commissural pores at any given size. It also differs from the other members of its group in always having the preopercular pore positions with simple pores. In addition, if differs: from *E. epalzeocheilus* and *E. niuafoouensis*, in usually having cirri on the lateral margin of the main supraorbital cirrus and in having a single pore before each anterior nostril; from *E. epalzeocheilus* and *E. marmoratus*, in having simple nuchal cirri; from *E. niuafoouensis* and *E. randalli*, in having fewer gill-rakers; and from *E. randalli*, in having cirri on the lateral margin of the main supraorbital cirrus.

REMARKS.—*Entomacrodus striatus* has been collected with or from the same restricted geographical area as all the other species and subspecies of Indo-Pacific *Entomacrodus*, except *E. strasburgi*, *E. marmoratus*, *E. randalli*, *E. macrospilus*, and *E. chapmani*, all of which have very limited distributions. Differentiations of *E. striatus* from the species not mentioned above can be made from the key and by referring to the various tables.

DISTRIBUTION (fig. 7).—*E. striatus* is the most widely distributed species of *Entomacrodus*, occurring from the eastern Indian Ocean to Raroia, Tuamotus, in the Pacific Ocean. It ranges from 28°30′N to 31°30′S latitude. It is primarily found in shallow tide pools and near shallow reefs.

MATERIAL.—INDIAN OCEAN: India, Konival: SU 14737; Bombay: MNHN 996 (syntypes of *Salarias fraenatus*); Vizagapatam: SU 14735, 14736; Ceylon: BMNH 1903.5.12.3, SU 22855; Andaman Islands: SU 16449, USNM 195781; Seychelles Islands: BMNH 1912.5.3.23–4; Praslin: BMNH 1908.5.14.27; Curieuse: ANSP 102186; La Digue: RU (no number); Anonyme: ANSP 102182; Mahé: ANSP 102188, 102192, RU (no number); St. Pierre: RU (no number); Mauritius: MNHN A1796 (lectotype of *Salarias striatus*), B2525, 997; Madagascar, Tanikely: USNM 199424; Cocos-Keeling Islands: BMNH 1949.11.29.604–618; Western Australia, Northwest Cape: WAM P.4654; Mozambique, Ibo: RU (no number); Inhambane: RU (no number); South Africa, St. Lucia coast, North Zululand: ANSP 54995–97; Durban, Natal: ANSP 55161.

SOUTH CHINA SEA: Hong Kong: SU 62069; Viet Nam, Nhatrang: SU 62047; Ilot du Sud (near Poulo Cécir de Mer): SU 62002; Gulf of Thailand, Goh Tao Island: SU 62008; Goh Samet Island: SU 62006.

PACIFIC OCEAN: Japan, Amami-Oshima: USNM 199816; Bonin Islands, Ototoshima: UMMZ 144748; Wake Island: SU 50164; Marianas Islands, Guam: USNM 123953, 137770, 139839; Saipan: SU 62078, 62079, 62080, USNM 123855; Tinian: USNM 124275; Marshall Islands, Rongerik Atoll, Bock Island: USNM 142176, 142177; Bikini Atoll, Enyu Island: USNM 142155 (holotype of *Entomacrodus plurifilis marshallensis*), 142164; Cherry Island: USNM 142162, 142163; Namm Island: USNM 142159; Erik Island: USNM 142157; Druk Island: USNM 142165; Boby Island: USNM 142158; Romuk Island: USNM 142161; Philippine Islands, Duamaguete: SU 28428; Palau Islands, 8 mi. northwest of Koror Island: SU 62049; Peleliu Island: USNM 123811; Ngarungl Island: SU 62056; Caroline Islands, Ifaluk Atoll: SU 62027, 62037, 62041, 62042, 62053, 62054; Jaluit (Bonham Island): BMNH 1873.4.3.190, ZSZM 20229; Christmas Island: BMNH 1964.2.14.1–2; Fanning Island: ANSP 64288–89, BPBM 4934; Howland Island: USNM 197905, 197907; Jarvis Island: USNM 198655; Phoenix Islands, Canton Island: USNM 115453; Hull Island: USNM 115454; Enderbury Island: USNM 115449; McKean Island: USNM 197906; Phoenix Island: USNM 198141; Ellice Islands Funafuti: AMS I3566, I3567, I3568, I3571, I3573; Penrhyn Island: ANSP 64352, BPBM 4935, 4936; Swains Island: USNM 115450; New Britain, Rabaul: USNM 200099; Solomon Islands, Rennell Island: UZMK P.75354 (holotype of *Entomacrodus wolffi*); Rotuma Island: BMNH 1897.8.23.108–109; Fiji Islands, Rat-tail Passage Reef, Suva, Viti Levu: UH 03079; Tonga Islands, Monotapu Beach, Tongatapu: UH 03073; near Houma Beach, Tongatapu: UH 03074, 03075; Samoan Islands, Tau Island: USNM 115452, 144720 (holotype of *Entomacrodus plurifilis plurifilis*); Tutuila Island: USNM 52264, 115456, 115457, 115459; New Hebrides: AMS I14264; Santo Island: AMS I6497, BMNH 1926.3.6.22; Efate: UH 03076, 03077; Aneiteum: BMNH 1871.4.16.6; New Caledonia, La Roche Perce, Borial: UH 03078; Australia, Coral Sea, Herald Cay: AMS IB5031, IB5032; Lord Howe Island: AMS I1864, I1865, I1866, I1867, I5903; Cook Islands, near Nikau Village, Rarotonga: UH 03072; Society Islands, Tahiti: BMNH 1873.4.2.88, UH 03080, 03081, USNM 87621, ZSZM 8205; Tuamotu Archipelago, Raroia: SU 62030, 62043; Makatea: USNM 200282.

***Entomacrodus rofeni*, new species**

PLATE 13

DESCRIPTION.—(Figures in parentheses for holotype.) Segmented dorsal fin rays 16 or 17 (17), usually 16; segmented anal fin rays 17 or 18 (18), usually 18; posteriormost anal pterygiophore supporting 1 or 2 (2) external elements (2 in 53.8 percent of specimens); total gill-rakers on first arch 16–19 (17); pseudobranchial filaments 5 or 6 (6); vertebrae 35; supraorbital cirri 5–8 (8); supraorbital cirri variable, sometimes arising from a common base, sometimes from both mesial and lateral edges of main, or longest cirrus; nape with 1 cirrus on each side; predorsal commissural pores 3, apparently unvarying; preopercular series of pores with all positions with simple pores; 1 pore before each anterior nostril; lateral line terminating on side in area below and between dorsal spines 10 and 11 (11); ventral margin of upper lip completely crenulate; lip crenulae numbering 23–28 (28).

Proportional measurements: See tables 3, 4, and 36.

Males ranged from 26.0 to 39.7 mm SL. No males were seen with rugose fleshy modifications of the skin of the anal spines and rays. Females ranged from 28.2 to 42.2 mm SL. The smallest specimen was not an ophioblennius stage.

COLOR PATTERN OF HOLOTYPE.—Male. The sides of the body are delicately marked with scattered melanophores. There are a few loose concentrations of melanophores on the sides which give the appearance of spots. The head is more or less uniformly covered with scattered melanophores. The upper lip has indications of five dark stripes separated by dusky interspaces. The spinous dorsal fin is irregularly dusky. The soft dorsal fin bears about three dusky spots are over each ray arranged in diagonal series from ray to ray. The anal fin is irregularly dusky distally, unmarked basally, on its anterior half, and completely unmarked on its posterior half. The caudal fin bears four or five rows of irregularly vertically arranged spots concentrated at the rays. The pectoral fin, its fleshy base and the pelvic fin are lightly covered with scattered melanophores.

The paratypic males are similarly marked to the holotype. The females are also similar but the dorsal fin bears fewer marks, the anal fin is immaculate, and the lateral stripe on either side of the upper lip is broader and more bandlike than the stripes in the same position on the lips of the males.

All in all, this is an inconspicuously marked species.

RELATIONSHIPS.—In spite of the fact that it shares certain characters with various other species of *Entomacrodus*, I find it difficult to relate *E. rofeni* closely to any of the other species. Its rather high vertebral number (35) is found commonly only in: *E. vomerinus*, *E. stellifer* (from both of which it obviously differs in disposition of dorsal lip crenulae and nature of supraorbital cirri), *E. marmoratus* (from which

TABLE 36.--Proportional dimensions as percent SL of specimens of *Entomacrodus rofeni* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL
SU 62031	Raroia	♂	26.0	23.0	7.7	3.5	3.5	7.7	-	23.1	15.4	26.9
SU 62031	Raroia	♂	26.1	22.2	7.7	3.4	3.1	9.6	9.2	23.1	15.3	26.0
SU 62031	Raroia	♀	28.2	22.0	7.1	2.8	3.5	9.9	10.3	23.8	16.0	26.6
SU 62031	Raroia	♂	32.0	22.5	6.9	3.1	2.4	9.4	10.0	20.6	14.8	24.2
SU 62035[1]	Raroia	♂	34.7	22.4	6.3	3.7	2.9	9.2	9.5	21.0	13.5	25.1
SU 62038	Raroia	♀	36.4	22.0	6.0	2.7	2.7	9.6	11.3	23.0	14.3	26.2
USNM 199402	Raroia	♀	37.0	21.6	6.8	2.7	3.2	9.7	10.3	21.0	13.5	25.1
USNM 199402	Raroia	♀	37.4	21.4	6.4	2.4	2.7	9.6	10.7	21.4	15.5	25.4
SU 62031	Raroia	♂	39.7	21.4	6.3	3.8	2.5	9.3	10.1	20.7	13.6	23.9
SU 62031	Raroia	♀	41.5	21.5	6.3	2.4	2.4	9.4	9.2	20.5	14.9	24.6
SU 62031	Raroia	♀	42.5	21.3	6.4	2.6	2.4	9.2	9.5	22.7	14.2	-

[1] Holotype of *Entomacrodus rofeni*

it obviously differs in number of predorsal commissural pores, anal rays and nuchal cirri), and *E. decussatus* and *E. vermiculatus* (from both of which it obviously differs in number of gill-rakers and predorsal commissural pores, eye size, and robustness of body). *E. rofeni* has a consistently lower number of predorsal commissural pores than any other species of *Entomacrodus*. *E. striatus* has relatively few such pores, but here there is a range of variation (up to 10 pores). *E. rofeni* commonly lacks vomerine teeth (4 of 13 known specimens), a lacking found in only very large specimens of *E. vermiculatus*.

Remarks.—*E. rofeni* has been collected with or from the same restricted geographic locality as *E. striatus*, *E. thalassinus*, *E. sealei*, and *E. caudofasciatus*. It can be differentiated from *E. striatus* by the characters given in key couplet 22; it differs most obviously from the other three species in having the upper lip completely crenulate and in having more vertebrae and dorsal and anal fin rays.

Distribution (fig. 5).—*E. rofeni* is known only from Raroia, Tuamotu Archipelago.

Holotype.—SU 62035, an immature male, 34.7 mm SL, from outer reef flat near Garumaoa village, west side of atoll, Raroia, Tuamotu Archipelago, July 11, 1952.

Paratypes (Collected with holotype).—USNM 199402 (4 specimens); channel between Geogeo and Kukina Islets, near Garumaoa village, west side of atoll: SU 62038 (1 specimen); outer reef near Garumaoa village on west side of atoll on shallow tidal flat next to shore: SU 62031 (7 specimens).

Etymology.—Named for Robert R. Rofen, who collected all the known specimens.

***Entomacrodus strasburgi*, new species**

Plate 14

Description.—(Character for holotype in parentheses.) Segmented dorsal fin rays 13–15 (14); segmented anal fin rays 16 or 17 (16); posteriormost anal pterygiophore supporting 1 or 2 (2) external elements (supporting 2 in 82 percent of specimens); total gill-rakers on first arch 11–15 (14); pseudobranchial filaments 5, unvarying with increase in size; vertebrae 34 or 35 (34); supraorbital cirri 1–4 (3), number increasing with increase in SL (table 37); main, or longest supraorbital cirrus with all branches mesially; nape with 1 cirrus on each side; predorsal commissural pores 3–12 (9), increasing slightly with increase in SL (table 38); preopercular series of pores with all positions with simple pores; 1 pore before each anterior nostril; lateral line pores terminating on side in area below and between dorsal fin spine 11 and dorsal ray 4 (dorsal ray 4), usually posterior to dorsal ray 1; ventral margin of upper lip completely crenulate; lip crenulae number 19–26 (25) (see table 5). (The left pectoral fin of the holotype has 13 rays, the right 14; the pectorals of 13 paratypes counted had 14 on each side.)

Proportional measurements: See tables 3, 4, and 39.

No males with fleshy rugose modifications of the anal spines were seen, although in the largest males the anal spines and anterior rays were noticeably more fleshy than the remaining rays.

The largest specimen examined was a male, 35.0 mm SL, the holotype. The largest female examined was 27.1 mm SL. Males and females were about equally common in the single large collection made. The smallest specimen examined (see also material list) was about 14.5 mm SL, not an ophioblennius stage, although posterior canines in the lower jaw and vomerine teeth were absent. These teeth were present in specimens 16.2 mm and larger.

Twenty-six ophioblennius larvae, 15.0–19.5 mm SL (see material below) from Oahu, Lanai, and Molokai, include 23 specimens which could be *E. strasburgi* (the remaining 3 are *E. marmoratus*, as evidenced by paired nuchal cirri on each side). These 23 specimens have the following counts: segmented dorsal rays 14 in 12 specimens, 15 in 11 specimens; segmented anal fin rays 16 in 20 specimens, 17 in 3 specimens; last anal pterygiophore supporting a single element in 5 specimens, 2 elements in 18 specimens. My reason for believing that these larvae are not all *E. marmoratus* is based on the fact that only 1 of 92 recognizable specimens of *E. marmoratus* had a segmented dorsal ray count of 14.

COLOR PATTERN OF HOLOTYPE (preserved).—The ground color of the sides of the body is pale. On the side below the soft dorsal fin there are several groups of diffuse, dusky spots formed by loose aggregations of melanophores. The side of the head is light dusky, darker below the level of the orbit. There are faint indications of two diffuse, dark, posteroventrally directed spokes from the ventral

TABLE 37.--Frequency distribution of number of supraorbital cirri of left eye of specimens of *Entomacrodus strasburgi* arranged by SL classes (in mm)

Classes	Number of cirri				
	1	2	3	4	Average
15-19.9	9	1	-	-	1.1
20	-	7	2	-	2.2
25	-	5	7	-	2.6
30	-	3	3	1	2.7
35	-	-	1	-	-

margin of the orbit. The top of the head is light dusky; the bottom of the head is dusky, darker than the top (the prepelvic area of the body is even darker). There is faint indication of a dusky chevron pattern on the bottom of the head, and pale stripes between the chevrons. The upper lip bears indications of 9 or 10 dusky bands separated by pale stripes.

The spinous dorsal fin bears a broad, immaculate band distally; basally there is a narrow, dusky band; the soft dorsal is irregularly dusky except for a narrow, immaculate distal margin. The anal fin is dark dusky, grading darker distally. The caudal fin bears about four irregular dusky bands punctuated by pale spots. The pectoral fin is almost entirely dusky, darker ventrally. The fleshy pectoral base is irregularly light dusky. The pelvic fin is pale with sparsely scattered melanophores over the fin membrane.

The paratypes are generally similar in color pattern to the holotype; however, the lower half of the preopercular area may bear a dark blotch or irregular vertical stripes. Females are paler than males and have the anal fin immaculate, the lip markings more diffuse.

TABLE 38.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus strasburgi* arranged by SL classes (in mm)

Classes	Number of pores										Average
	3	4	5	6	7	8	9	10	11	12	
15-19.9	3	-	1	-	4	3	-	-	-	-	6.0
20	1	-	1	2	1	1	2	-	-	1	7.2
25	-	-	1	2	2	4	2	-	-	-	7.4
30	-	-	-	2	4	-	-	-	1	-	7.3
35	-	-	-	-	-	-	1	-	-	-	-

TABLE 39.--Proportional dimensions in percent SL of specimens of *Entomacrodus strasburgi* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PECT	CL
USNM 200283	Hawaii	♀	27.1	23.6	7.4	3.0	2.6	11.4	10.7	22.1	15.1	18.1
USNM 199272	Hawaii	♂	28.0	23.9	7.1	3.2	1.8	-	14.6	24.3	15.7	21.4
USNM 199272	Hawaii	♂	29.0	23.4	7.5	3.6	2.4	11.4	12.4	21.4	15.9	20.0
USNM 200283	Hawaii	♂	29.5	22.7	6.8	3.4	0.7	13.9	13.9	23.7	15.3	19.0
USNM 199272	Hawaii	♂	29.8	23.1	6.7	3.4	2.7	13.1	12.8	-	15.8	19.5
USNM 200283	Hawaii	♂	30.8	24.4	6.8	2.9	1.6	11.4	13.6	19.8	14.6	18.8
USNM 200283	Hawaii	♂	31.5	23.8	6.7	4.4	2.2	11.7	12.1	21.6	16.5	19.4
USNM 200283	Hawaii	♂	32.0	24.0	6.2	2.8	1.9	12.2	13.4	19.4	14.7	18.8
USNM 200283	Hawaii	♂	32.1	23.7	6.2	2.8	2.2	13.1	12.5	20.6	14.0	18.7
USNM 179202 (holotype)	Hawaii	♂	35.0	23.4	6.3	3.4	1.7	13.2	11.2	21.1	14.0	18.3

Freshly caught specimens bear about 5½ pairs of vertical reddish-brown bands on the body, the half pair at the caudal peduncle. The preopercular area exhibits several reddish-brown vertical stripes. These markings are lost in preservation.

RELATIONSHIPS.—*Entomacrodus strasburgi* is a member of the *E. cymatobiotus* species group. For differentiation, see key couplets 27 and 28. In addition, *E. strasburgi* appears to differ from the other two members of the group in having a shorter caudal fin.

Entomacrodus strasburgi (fig. 8) has been collected with only one other species of *Entomacrodus*, *E. marmoratus*. Both species are endemic to the Hawaiian Islands and are the only species of *Entomacrodus* known from these islands. Both occur in the surge zone on rocky shores at depths not exceeding two meters.

REMARKS.—There is indication of sexual dimorphism in segmented dorsal ray numbers. Of those specimens sexed (20.0 mm SL and larger) 4 males had 14 rays and 13 males had 15 rays; 1 female had 13, 9 had 14, and 1 had 15 rays. There was no other apparent sexual dimorphism of meristic characters, except that of all the specimens, only 3 males had a B condition anal ray count as high as 18.

HOLOTYPE.—USNM 179202, an immature male, 35.0 mm SL, Makapuu Point, Oahu, Hawaii, Feb. 21, 1963, W. A. Gosline and class.

PARATYPES.—USNM 199272, three immature males, 28.0–29.8 mm SL, collected with the holotype; USNM 200283, 36 specimens, 14.5–32.1 mm SL, including 13 males, 11 females, and 12 sex indeterminates, same locality as holotype, Feb. 19, 1966.

Other possible material (23 ophioblennius larvae, 15.0–19.5 mm SL), not included in tables: Oahu: USNM 149991; Lanai: USNM 164993; Molokai: USNM 118063, 133913, 133918, 164992 (note: an additional three larvae, the largest two included in USNM 164993 and the largest in USNM 164992, are *E. marmoratus*).

ETYMOLOGY.—Named for Donald W. Strasburg in recognition of his studies on Hawaiian Blenniidae.

Entomacrodus cymatobiotus Schultz and Chapman

PLATES 15, 17*a*

Entomacrodus cymatobiotus Schultz and Chapman, 1960, U.S. Nat. Mus. Bull. 202, pt. 2, pp. 335–337 [Eman Island, Bikini Atoll, Marshall Islands].

DESCRIPTION.—Segmented dorsal fin rays 13–15 (14 in 84 percent of specimens); segmented anal fin rays 14–16 (15 in 85 percent of specimens); posteriormost anal pterygiophore supporting 1 or 2 external elements (supporting 2 in 92 percent of specimens); total gill-rakers on first arch 10–16 (12–14 in 75 percent of specimens); pseudobranchial filaments 4–7 (5 in 71 percent of specimens), number not increasing much, if any, with increase in SL; vertebrae 33–34 (34 in 19 of 20 specimens); supraorbital cirri 2–6, number increasing with increase in SL (table 40); main or longest supraorbital cirrus with all branches mesially, or all cirri arising from a common base; nape with 1 cirrus on each side; predorsal commissural pores 4–32 (rarely more than 20), number increasing with increase in SL (table 41); preopercular series of pores with all positions with simple pores; single pore before each anterior nostril; lateral line pores terminating on side in area below and between dorsal fin spine 11 and dorsal ray 6 (usually anterior to dorsal ray 3); ventral margin of upper lip completely crenulate; lip crenulae number 26–35 (27–33 in 92 percent of specimens).

Proportional measurements: See tables 3, 4, and 42.

Males develop fleshy rugose modifications of the skin of the anal spines and the anterior first to fourth anal rays. If one considers males with these modifications to be mature, the smallest mature male examined was 26.6 mm SL. Mature and immature males may occur in the same collection and in these collections immature males may be as much as 6 mm longer than mature males.

The largest specimen examined was a mature male 48.2 mm SL; the largest female was 41.1 mm SL. Males were more than twice as common as females in collections, but in relative numbers the sexes were about equal at sizes up to 35 mm SL. Above 35 mm SL males were relatively more common. About 22 percent of the males achieved a size of more than 40 mm SL, whereas only 1 (2.8 percent) female attained such a size. The smallest specimen examined, 16.4 mm SL, was not an ophioblennius stage. Vomerine teeth were present in this specimen, but the posterior canines of the lower jaw

TABLE 40.—Frequency distribution of number of supraorbital cirri of left eye of specimens of *Entomacrodus cymatobiotus* arranged by SL classes (in mm)

Classes	Number of cirri					Average
	2	3	4	5	6	
15-19.9	5	14	2	-	-	2.8
20	-	13	22	-	1	3.7
25	-	7	19	4	1	4.0
30	-	-	14	4	-	4.2
35	-	1	6	-	2	4.3
40	-	-	8	2	2	4.5
45	-	-	-	5	1	5.2

were undeveloped, as were the crenulations on the lateral portions of the ventral margin of the upper lip.

Color pattern of preserved material.—In male specimens over about 30 mm SL the sides of the body are usually uniformly pale. Some specimens have diffusely dusky markings on the sides in the form of 3–5 pairs of midlateral spots. The remainder of the body in these specimens may be uniformly pale or marked with scattered fine, light dusky spots and dashes. One mature male from Jarvis Island (pl. 15) was unique in having a better developed color pattern than was found in the other specimens. In this specimen there were six pairs of midlateral bars (in the drawing, the anterior pair hidden by the pectoral fin). The bands were variously interrupted, but the posterior four pairs tended to diminish in intensity dorsally and ventrally as they extended to the body contours. Diffusely dusky marks were scattered over the sides of this specimen. In males below 30 mm SL the paired markings on the sides of the body appeared much more frequently than among larger males.

On most males, the most intense mark on the side of the head is a dark elongate spot about half an eye diameter posterior to the eye. This spot is followed by an irregular pale stripe, then a broad irregularly dusky area, another pale stripe, and sometimes another broad dusky area. In some males there were several additional pale dusky stripes directed ventrally and ventroposteriorly from the orbit.

The top of the head is irregularly dusky and the ventral portion pale and unmarked. The upper lip bears scattered dusky spots.

The spinous dorsal of males is either uniformly light dusky with a narrow pale distal margin or irregularly dark dusky with indications of light or dark spots and a pale distal margin. The soft dorsal bears up to four rows of dusky spots over each ray, with the distal portion of the fin uniformly pale dusky. The anal fin is pale proximally, grading into dark dusky distally. The caudal fin bears up to about nine irregular vertical rows of dusky spots, usually overlying the rays; the number of rows is greater in large than in small specimens. The pectoral fin is light dusky, increasing slightly in intensity

TABLE 41.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus cymatobiotus* arranged by SL classes (in mm)

Classes	Number of pores																			
	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	33(sic)
15-19.9	1	2	-	4	1	1	4	2	-	-	-	-	-	-	-	-	-	-	-	-
20	-	-	2	4	6	5	9	7	5	-	1	1	-	-	-	-	-	-	-	-
25	-	-	1	1	1	5	3	6	1	5	2	2	1	3	-	2	-	-	-	-
30	-	-	-	-	-	-	3	3	2	3	2	1	1	1	1	-	-	-	-	-
35	-	-	-	-	-	-	-	1	1	1	-	3	2	-	-	-	-	-	1	-
40	-	-	-	-	-	-	2	-	2	-	1	2	2	1	1	-	1	-	-	1
45	-	-	-	-	-	-	-	-	1	-	-	1	1	-	-	1	2	-	-	-

ventrally. The fleshy pectoral base is irregularly marked with dusky. The pelvic fins are dusky.

Females differ from males in bearing almost no marks on the head and body except for very faint adumbrations of the marks behind the eye. The dorsal, anal, and caudal fins are delicately spotted with dusky. The pectorals and pelvics are paler than in males from the same collection.

RELATIONSHIPS.—*Entomacrodus cymatobiotus* is very closely related to *E. strasburgi* and *E. chapmani* (for differentiation, see key couplets 25 and 26). It appears to be closer to *E. chapmani* than to *E. strasburgi* as evidenced by general color pattern. Some males of *E. chapmani* (pl. 17*b*) exhibit adumbrations of the head color pattern of *E. cymatobiotus* (pl. 17*a*), though lacking the spot behind the eye of the latter species. The spot on the head of each of the latter two species results from intensification of the color pattern in the areas where the spots occur. In *E. strasburgi* it appears that both the areas where the spots occur in the other two species have been de-

TABLE 42.--Proportional dimensions as percent SL of specimens of *Entomacrodus cymatobiotus* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL
USNM 142182	Marshall Is.	♂	24.4	25.4	7.8	3.3	3.3	12.3	14.8	22.5	15.6	22.5
USNM 178999	Phoenix Is.	♀	25.2	26.2	8.2	3.6	4.5	11.9	16.7	25.4	17.9	23.4
USNM 142183[1]	Marshall Is.	♂	26.0	24.6	6.9	3.8	2.7	11.5	15.4	21.5	15.5	22.7
SU 62011	Raroia	♀	26.2	26.3	7.6	3.8	3.0	11.4	16.0	22.9	-	22.9
SU 62011	Raroia	♂	26.6	24.4	6.4	4.5	3.8	11.6	16.5	24.4	-	21.8
USNM 142182	Marshall Is.	♀	28.1	24.9	7.1	3.9	2.5	12.5	16.7	23.1	14.6	21.7
USNM 142160	Marshall Is.	♂	28.4	25.4	6.3	4.2	3.5	12.0	16.2	22.5	15.8	23.2
SU 62011	Raroia	♂	28.5	24.9	6.7	4.6	3.5	11.2	14.0	21.4	-	21.0
SU 62023	Raroia	♂	32.5	24.6	6.5	4.0	3.7	12.0	16.9	23.4	15.7	22.8
SU 62011	Raroia	♂	33.0	24.8	6.1	3.6	3.6	12.1	14.8	22.1	-	21.2
SU 62023	Raroia	♂	35.8	24.3	6.1	3.1	2.0	-	16.8	23.7	15.4	22.3
USNM 198654	Jarvis Is.	♀	35.8	23.2	6.1	3.4	3.1	10.0	13.4	22.9	15.1	21.5
USNM 198594	McKean Is.	♂	37.3	23.0	5.4	4.0	2.1	9.7	14.5	19.8	13.9	20.1
USNM 198654	Jarvis Is.	♂	40.4	23.7	5.9	4.2	2.5	10.4	16.1	19.5	13.1	21.8
SU 62023	Raroia	♂	40.5	23.5	5.9	4.2	3.5	10.6	15.0	21.0	13.3	21.0
USNM 198654	Jarvis Is.	♀	41.1	23.3	6.1	3.4	1.7	10.0	13.4	21.4	12.6	20.7
USNM 198654	Jarvis Is.	♂	45.8	23.1	5.5	4.6	2.4	9.6	16.4	21.0	12.7	23.1
USNM 198654	Jarvis Is.	♂	48.2	23.6	5.0	3.3	1.0	-	16.0	19.9	12.0	22.2

[1] Holotype of *Entomacrodus cymatobiotus*

intensified (or lack intensification). In terms of habitat occupied, *E. cymatobiotus* is most similar to *E. strasburgi*. Both these species occur in surge areas and on the ocean sides of reefs, whereas *E. chapmani* appears to be a tide pool form.

REMARKS.—*Entomacrodus cymatobiotus* has been collected with or from the same restricted locality as *E. striatus*, *E. rofeni*, *E. sealei*, *E. caudofasciatus*, and *E. t. thalassinus*. It differs: from *E. striatus*, in having usually fewer gill-rakers and dorsal rays, more predorsal commissural pores, and in lacking lateral branches on the main supraorbital cirrus; from *E. rofeni*, in having fewer vertebrae, soft dorsal and anal rays, and gill-rakers, and in having more predorsal commissural pores at any given size; from *E. sealei*, *E. caudofasciatus*, and *E. t. thalassinus*, in the disposition of its lip crenulae; from *E. sealei*, in having simple preopercular pores and fewer gill-rakers; and from *E. caudofasciatus*, in lacking a humeral blotch.

DISTRIBUTION (fig. 8).—*E. cymatobiotus* is restricted to the western and central Pacific islands.

MATERIAL.—Marshall Islands: Bikini Atoll, Eman Island: USNM 142183 (holotype of *Entomacrodus cymatobiotus*); Bikini Atoll, Namu Island: USNM 142160; Eniwetok Atoll, Mui Island: USNM 142181, 142182; Caroline Islands, Ifaluk Atoll: SU 62033; McKean Island: USNM 198594; Jarvis Island: USNM 198654; Phoenix Islands, Enderbury Island: USNM 178999; Malden Island: USNM 199456; Tuamotu Archipelago, Raroia: SU 62011, 62017, 62021, 62023.

Entomacrodus chapmani, new species

PLATES 16, 17*b*

DESCRIPTION.—(Figures in parentheses for holotype.) Segmented dorsal fin rays 14 or 15 (15); segmented anal fin rays 15–17 (16), usually 16; posteriormost anal pterygiophore supporting 1 or 2 (1) external elements (2 in 77 percent of specimens); total gill-rakers on first arch 13–18 (18); pseudobranchial filaments 5 or 6 (6); vertebrae 34; supraorbital cirri 4–8 (7), number not increasing much, if any, with increase in SL (table 43); main or longest supraorbital cirrus with all branches mesially (except holotype, which has one lateral branch); nape with 1 cirrus on each side; predorsal commissural pores 6–16 (7), number not increasing much, if any, with increase in SL (table 43); preopercular series of pores with all positions with simple pores (except one specimen with 1 pair of pores included in series); 1 pore before each anterior nostril; lateral line terminating on side in area below and between dorsal fin spine 11 and dorsal ray 4 (dorsal ray 1); ventral margin of upper lip completely crenulate; lip crenulae number 31–39 (37).

Proportional measurements: See tables 3, 4, and 44.

No males with fleshy rugose modifications of the skin of the anal spines and rays were seen, but two males, 53.5 and 63.8 mm SL, appeared to be developing such modifications on the anal spines, which probably indicates approaching maturity. The largest specimen examined was a male, 73.7 mm SL, the largest female 52.5 mm. The smallest specimen examined, 25.6 mm SL, was not an ophioblennius stage.

Color pattern of holotype (preserved).—The sides of the body exhibit five pairs of irregular dark bands: the first pair, almost fused, is under dorsal spines 8–10; the last pair is on the caudal peduncle. Anterior to these pairs are two much paler, irregular bands, the posteriormost split ventrally. Each member of each of the paired bands consists of about three vertically arranged blotches, the ventralmost blotch, the palest. The head is dusky with an irregular dark spot, deeper than wide, placed posterodorsally and bounded ventroposteriorly by a narrow pale margin, below which is a large dusky area, paler than the dark spot. The dorsal and ventral portions of the head are uniformly dusky. The upper lip is uniformly dusky except for a faint band at each corner.

The spinous dorsal fin bears irregular light dusky spots, most conspicuous over the spines. The interradial membrane is unmarked distally between the spines. The soft dorsal fin bears three, sometimes two, dusky spots over each ray; the spots arranged in diagonal series from one ray to the next. The anal fin is more or less uniformly dusky over its anterior two-thirds, grading into spots, mostly over the rays, posteriorly. The caudal fin bears about seven irregular vertical rows of spots which are mostly centered over the rays. The pectoral fin is light dusky over the rays; the interradial membrane is immaculate. The fleshy pectoral base is uniformly dusky. The pelvic fins are light dusky.

Other females are similar to the holotype but may be more intensely marked. The number of rows of caudal spots is variable.

Males differ from females in generally having the bands on the body much paler, the spot on the head (pls. 16*c*, 17*b*) much larger, the nar-

TABLE 43.--Frequency distribution of number of predorsal commissural pores and supraorbital cirri of specimens of *Entomacrodus chapmani* arranged by SL classes (in mm)

Classes	Predorsal pores											Supraorbital cirri							
	6	7	8	9	10	11	12	13	14	15	16	1	2	3	4	5	6	7	8
25-29.9	1	-	-	-	1	1	-	-	-	-	-	-	-	-	2	-	1	-	-
30	-	-	-	-	1	1	-	1	-	-	-	1	-	-	-	3	-	-	-
35	-	-	-	1	1	-	1	1	-	-	-	-	-	-	3	-	1	-	-
40	-	-	1	-	1	1	1	-	-	-	1	-	-	-	-	4	-	-	1
45	1	-	1	-	1	-	-	-	-	-	-	-	-	-	-	1	2	-	-
50-54.9	-	1	-	1	1	-	1	1	-	-	-	-	-	-	-	2	2	1	-
70-74.5	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-

row pale margin bounding the ventroposterior margin of the spot better delineated, the blotch following the pale margin much darker (sometines approaching the spot in intensity). Occasionally, there are faint indications of pale and light dusky stripes extending posteroventrally from the eye (adumbrating the condition in males of *E. cymatobiotus*) (pl. 17). The spinous and soft dorsal fins are more uniformly dusky, the spinous darker. The anal fin is also much darker then that of females and lacks the spotting posteriorly.

RELATIONSHIPS.—*Entomacrodus chapmani* is most closely related to *E. cymatobiotus* and *E. strasburgi* (for differentiation, see key couplets 24 and 25). Of the latter two species, *E. chapmani* appears to be closer to *E. cymatobiotus* (for discussion, see "Relationships" under *E. cymatobiotus*).

DISTRIBUTION (fig. 8).—*Entomacrodus chapmani* is known only from Easter Island, where it is also the only member of its genus known. *E. chapmani* is the same species as the misidentified *Entomacrodus striatus* reported by de Buen (1963, p. 59).

HOLOTYPE.—MCZ 29446, an adult female, 52.5 mm SL, with a label reading: "E. Pacific Ex. 1904–05. 'Albatross'. Easter Island, Dec. 20. Shore." This is presumably one of the two specimens mentioned by Kendall and Radcliffe (1912, p. 154) as MCZ 29436. I have been unable to locate the other specimen.

PARATYPES.—Easter Island, Hanga Roa: UBC BC65–410 (2 specimens), BC65–455 (3), BC65–458 (1); Hanga Pico: UBC BC65–428 (2), BC65–438 (1); Vinapu: UBC 65–449 (1); Anekena: UBC BC65–440 (1); Rano Raraku: UBC 65–430 (9), BC 65–429 (2); Cave Bay: MNHN 1942–76 (2); Easter Island (only): BMNH 1913.12.7.10 (1).

TABLE 44.--Proportional dimensions as percent SL of specimens of *Entomacrodus chapmani* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL
UBC BC 65-455	Easter Is.	♀	29.5	26.4	6.4	3.4	2.7	10.2	14.9	25.1	17.6	21.7
UBC BC 65-455	Easter Is.	♂	37.5	24.0	6.4	4.0	1.6	8.5	11.7	21.9	16.3	20.5
UBC BC 65-428	Easter Is.	♀	39.5	21.3	6.1	3.0	1.3	8.9	13.7	22.5	14.7	21.3
UBC BC 65-430	Easter Is.	♀	43.6	23.0	5.5	4.1	1.6	8.9	13.3	23.9	14.4	19.5
UBC BC 65-458	Easter Is.	♀	44.3	23.2	5.6	3.8	1.8	9.5	13.8	22.6	14.9	19.2
UBC BC 65-410	Easter Is.	♀	48.2	22.8	5.4	4.6	2.1	10.4	15.6	25.7	16.2	21.2
UBC BC 65-430	Easter Is.	♂	52.4	22.5	5.0	3.8	1.1	9.0	13.4	22.1	13.9	20.0
MCZ 29446[1]	Easter Is.	♀	52.5	22.9	5.5	3.0	1.9	9.1	13.9	24.8	15.4	21.3
UBC BC 65-449	Easter Is.	♂	53.5	23.4	5.2	5.0	2.4	9.5	15.1	23.6	14.6	21.5
UBC BC 65-410	Easter Is.	♂	63.8	22.7	4.9	5.0	1.3	9.4	15.0	23.7	14.4	21.5
BMNH 1913.12.7.10	Easter Is.	♂	73.7	22.8	4.6	4.7	2.1	8.7	12.2	19.0	12.9	21.0

[1] Holotype of *Entomacrodus chapmani*

ETYMOLOGY.—This species is named for Wilbert M. Chapman in recognition of his studies on blenniid fishes. Since the foregoing description, I have learned that Chapman, many years ago, independently concluded that this form represented a new taxon—making it doubly appropriate that the species be named for him.

Entomacrodus sealei Bryan and Herre

PLATE 18

Entomacrodus sealei Bryan and Herre, 1903, Occ. Pap. Bernice P. Bishop Mus., vol. 2, no. 1, pp. 138–139 [Marcus Island].

Entomacrodus incisolabiatus Schultz and Chapman, 1960, Bull. U.S. Nat. Mus., vol. 202, pt. 2, pp. 332–334 [ocean reef and surf, southeast end Enyu Island, Bikini Atoll].

DESCRIPTION.—Segmented dorsal fin rays 13–16 (15 in 80 percent of specimens); segmented anal fin rays 15–17 (16 in 85 percent of specimens); posteriormost anal pterygiophore supporting 1 or 2 external elements (2 in 93 percent of specimens); total gill-rakers on first arch 15–21 (16–19 in 92 percent of specimens); pseudobranchial filaments 4–7 (6 or 7 in 90 percent of specimens), number not increasing with increase in SL; vertebrae 33 or 34 (33 in 2 of 23 specimens); supraorbital cirri 1–7, number increasing with increase in SL (table 45); main or longest supraorbital cirrus with all branches mesially; nape with 1 cirrus on each side; predorsal commissural pores 3–34, number increasing with increase in SL (table 46); preopercular series of pores including 3–5 positions with pairs or multiples of pores (pore positions never all simple in specimens over 22 mm SL); 1 pore before each anterior nostril; lateral line pores terminating on side in area below and between dorsal fin spine 11 and dorsal ray 5; ventral margin of upper lip crenulate on lateral thirds, entire on middle third (one specimen, 22 mm SL, from Raroia had upper lip completely crenulate); lip crenulae usually numbering 7–10 on each side.

Proportional measurements: See tables 3, 4, and 47.

Males develop fleshy rugose modifications of the skin of the anal spines and the anterior first to third rays. If one considers males with these modifications to be mature, the smallest mature male examined was 39.0 mm SL. Mature and immature males may occur in the same collection and in these collections immature males may be as much as 7 mm longer than mature males.

The largest specimen examined was a male, 64.2 mm SL; the largest female was 54.1 mm SL; below the latter size males and females occur with relative equal frequency. Only two specimens, males, were larger than 59.9 mm SL. Males and females occurred in collections in about equal numbers. The smallest specimen examined was 18.0 mm, not an ophioblennius stage. It had two pairs of pores included in the preopercular series. Several nonophioblennius stage specimens as small as 15.7 mm SL were examined from lots containing specimens identifiable as *E. sealei*, but these specimens had all preopercular pores simple and no lip crenulae. It is possible that these specimens belong to another species (i.e., *E. thalassinus*) and the data from these specimens were not included in the description and tables in this paper. Positive identification awaits more information on developmental stages (small specimens of *E. thalassinus*, to less than 15.0 mm, could be identified when present in large series by following gradual morphological changes throughout the series, but isolated small specimens, such as mentioned above, could not be so identified with the material available).

Color pattern of preserved material.—Specimens from the same collection may have almost no distinct markings on the body sides, or they may have several dusky blotches, or pairs of blotches of variable intensity on the midline of the side. These blotches, grouped in six or seven areas on the sides, appear to correspond to the bands of other species of the *E. nigricans* group to which *E. sealei* belongs. The posterior two pairs of blotches, at the caudal peduncle and under the posterior soft dorsal rays, are often pale or absent. A conspicuous blotch may be present in the humeral region but usually is lacking. Infrequently there are faint marks at the base of the dorsal fin that are probably disconnected dorsal extensions from the body blotches. Extensions from these faint marks may enter the dorsal fin, where, on the soft dorsal, they may intensify as stripes and become dorsoposteriorly directed. The dorsal fin may be almost uniformly light dusky or have a pale or dark distal margin.

On the side of the head a number of irregular dusky marks are

TABLE 45.--Frequency distribution of number of supraorbital cirri of left eye of specimens of *Entomacrodus sealei* arranged by SL classes (in mm)

Classes	Number of cirri							
	1	2	3	4	5	6	7	Average
15-19.9	1	-	2	1	-	-	-	2.8
20	-	-	5	10	2	-	-	3.8
25	-	-	2	13	12	2	-	4.5
30	-	-	2	7	8	4	1	4.8
35	-	-	-	2	10	4	-	5.1
40	-	-	-	1	2	1	-	5.0
45	-	-	-	2	3	2	-	5.0
50	-	-	-	1	3	5	1	5.6
55	-	-	-	-	1	1	-	5.5
60	-	-	-	-	-	1	1	6.5

separated by pale areas; infrequently there is a darkly dusky area (spot) just behind the eye, which, when present, is the most conspicuous mark on the side of the head. The upper lip usually bears seven pale, slender stripes alternating with eight light to dark dusky bands, more than twice the width of the stripes. The dark band at each corner of the lip is the narrowest and may be only slightly wider than the adjacent stripe. The lip bands may be almost absent in females. Extensions of the lip bands and stripes may appear on the underside of the head as chevrons.

The anal fin is light to dark dusky with scattered pale spots. The spots may be absent in males. The anal spines of males are dark dusky, those of females, pale. The caudal fin bears about three to six irregular dusky bands alternating with pale areas, the number depending on the length of the specimen (larger specimens tend to have more bands).

Nomenclature.—*Entomacrodus sealei* was described from a single specimen. This specimen is now in very poor condition, the head almost detached, but it was possible to determine that the upper lip was crenulate on at least one side and entire in the middle; the opposite side was damaged. There were at least three pore pairs included in the preopercular series and there were indications of pale stripes and dusky bands on the upper lip. With this information it is possible to place *E. incisolabiatus* in the synonymy of *E. sealei*. The holotype of *E. incisolabiatus* has four pairs or multiples of pores included in the preopercular series and pale stripes and dusky bands on the upper lip. Schultz and Chapman (1960) apparently overlooked the description of *E. sealei* at the time of their description of *E. incisolabiatus*.

Relationships.—*Entomacrodus sealei* is a member of the *E. nigricans* species group. Of this group it is most closely related to *E. corneliae* from which it differs usually in having pale stripes and dark bands on the upper lip and in lacking dark vertical stripes on the head behind the eye (see "Relationships" under *E. corneliae*).

Entomacrodus sealei (and *E. corneliae*) is next most closely related to *E. chiostictus* (see "Relationships" under *E. chiostictus*). It differs from *E. chiostictus* in having three to five pairs or multiples of pores included in the preopercular series (only 2.8 percent of *E. chiostictus* specimens overlap *E. sealei* in this character) and in the nature of the lip stripes and bands (adumbrated by a few Clipperton Island specimens of *E. chiostictus*). Usually *E. chiostictus* specimens have more complete banding of the body than do specimens of *E. sealei*.

Remarks.—*E. sealei* is occasionally collected with *E. caudofasciatus*, from which it can be distinguished (and from all Atlantic Ocean species of the genus also) by having three or more pairs of pores

TABLE 46.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus sealei* arranged by SL classes (in mm)

Classes	Number of pores																
	3-4	5-6	7-8	9-10	11-12	13-14	15-16	17-18	19-20	21-22	23-24	25-26	27-28	29-30	31-32	33-34	Average
15-19.9	1	1	2	1	-	-	-	-	-	-	-	-	-	-	-	-	6.4
20	-	3	4	6	1	2	1	-	1	-	-	-	-	-	-	-	9.8
25	-	1	2	9	8	5	3	-	-	-	-	-	-	-	-	-	11.1
30	-	1	-	2	6	6	4	-	-	-	1	-	-	-	-	-	13.0
35	-	-	-	4	2	3	4	-	-	1	1	-	-	-	-	-	13.9
40	-	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	16.5
45	-	-	-	-	-	-	-	1	-	1	2	1	1	1	-	-	23.6
50	-	-	-	-	1	-	1	2	3	1	1	-	-	-	-	1	19.6
55	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	23.5
60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	32.5

included in the preopercular series and by the pale stripes and dark bands on the upper lip. It further differs from *E. caudofasciatus* in usually lacking a humeral blotch and by commonly having more than 13 predorsal commissural pores. (For further distinguishing characters, see "Relationships" under the Atlantic species of *Entomacrodus*.)

Entomacrodus sealei has also been collected with or from the same restricted geographic locality, as: *E. t. thalassinus*, from which it differs obviously in having crenulae on the upper lip and more gill-rakers, and paired pores included in the preopercular series;

TABLE 47.--Proportional dimensions as percent SL of specimens of *Entomacrodus sealei* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL
USNM 123934	Guam	♀	27.7	26.0	7.6	3.2	3.6	10.8	13.7	25.3	18.0	23.5
USNM 111883	Samoa	♂	31.2	26.3	7.4	5.1	3.8	11.5	14.1	26.6	17.6	24.3
SU 62077	Saipan	♀	32.4	24.7	7.1	3.7	3.1	9.3	15.1	24.7	-	22.2
SU 62052	Ifaluk	♂	32.8	24.4	6.7	5.8	3.7	10.4	11.6	23.2	-	23.8
SU 62052	Ifaluk	♂	32.8	24.4	7.3	4.6	3.4	10.4	12.8	23.2	-	22.0
SU 62012	Raroia	♀	36.0	25.0	8.1	3.1	3.9	11.1	14.4	24.4	-	22.5
USNM 198140	Phoenix	♂	36.1	23.8	6.4	4.2	4.2	-	14.7	24.9	16.6	23.5
USNM 198140	Phoenix	♀	36.1	24.4	6.9	3.9	3.0	9.1	13.8	25.2	16.3	23.6
USNM 142189	Bikini	♂	36.7	24.5	6.8	4.4	3.0	10.6	14.2	22.6	16.3	22.6
USNM 111882	Saipan	♀	37.0	24.3	7.0	4.3	3.0	8.9	10.8	22.7	14.9	21.1
SU 62077	Saipan	♂	37.1	24.2	6.7	5.7	3.2	10.5	13.7	22.1	-	22.1
SU 62012	Raroia	♀	41.5	24.3	7.2	3.9	3.6	10.8	14.5	23.9	-	21.9
BMHN 1943.8.23.3	Swains	♀	43.0	24.4	5.8	3.0	3.5	10.5	12.8	23.0	16.5	23.5
USNM 198140	Phoenix	♂	44.8	24.3	6.0	6.0	3.3	10.0	14.5	21.9	16.3	23.4
USNM 142188[1]	Bikini	♂	45.2	23.2	6.6	5.5	2.4	10.4	12.2	20.8	14.2	23.0
SU 62022	Raroia	♂	45.8	24.0	6.8	4.6	3.9	10.7	14.4	22.3	-	23.2
USNM 62012	Raroia	♀	46.4	24.8	6.7	4.1	3.7	10.8	16.8	24.1	-	23.1
USNM 147654	Swains	♂	46.7	23.1	6.0	4.9	3.2	10.7	-	-	14.3	23.6
USNM 111881	Guam	♂	50.0	24.2	6.0	5.2	3.0	10.8	14.2	20.0	14.0	21.2
SU 62012	Raroia	♂	51.0	23.5	6.5	4.7	3.1	10.0	14.1	22.5	-	21.8
USNM 198653	Jarvis	♀	51.7	23.9	5.9	4.1	3.1	10.2	13.5	22.3	14.3	23.5
SU 62019	Raroia	♀	53.4	23.4	6.6	3.6	3.6	10.9	14.2	22.8	15.4	22.3
SU 62012	Raroia	♀	54.1	23.7	5.9	4.1	3.7	11.1	15.2	23.7	-	22.6
USNM 198653	Jarvis	♂	59.2	22.8	5.4	4.7	2.4	10.5	14.0	18.7	13.7	20.8
SU 62019	Raroia	♂	63.4	23.8	5.7	4.6	3.2	11.4	15.0	19.7	14.2	21.9

[1] Holotype of *Entomacrodus incisolabiatus*

E. s. stellifer, from which it differs obviously in the disposition of its lip crenulae and in having more and shorter supraorbital cirri, fewer vertebrae, and paired pores included in the preopercular series; *E. decussatus*, from which it differs obviously in the disposition of its lip crenulae and in having a smaller eye at comparable SL's, usually fewer vertebrae, gill-rakers, and dorsal and anal segmented rays; *E. striatus*, from which it differs obviously in the disposition of its lip crenulae and in having paired pores included in the preopercular series and more predorsal commissural pores at comparable SL's; *E. cymatobiotus*, from which it differs obviously in the disposition of its lip crenulae and in having paired pores included in the preopercular series, usually more gill-rakers and pale stripes and dusky bands on the upper lip; *E. niuafoouensis*, from which it differs obviously in the disposition of its lip crenulae and in having only one pore before each anterior nostril, shorter supraorbital cirri, and fewer gill-rakers; *E. epalzeocheilus*, from which it differs obviously in the disposition of its lip crenulae and in having only one cirrus on each side of the nape and one pore before each anterior nostril; and *E. rofeni*, from which it differs in the disposition of its lip crenulae and in having paired pores included in the preopercular series, fewer segmented anal rays, vertebrae, and more predorsal commissural pores.

DISTRIBUTION (fig. 9).—*Entomacrodus sealei* is known only from the islands of the western and central Pacific Ocean. Collection data indicate that this species occurs on the outer (ocean) sides of reefs along open or surge channels.

MATERIAL.—Marcus Island: BPBM 2458 (holotype of *E. sealei*); Marianas, Guam: USNM 111881, 123934; Saipan: SU 62055, 62077, USNM 111882; Carolines, Ifaluk: SU 62039, 62052; Kapingamarangi: SU 62029; Marshalls, Bikini: USNM 142188 (holotype of *E. incisolabiatus*), 142189; Phoenix Group, Phoenix Island: USNM 198140; McKean: USNM 198593; Jarvis: USNM 198653; Swains: BMNH 1943.8.23.3, USNM 147654; Samoa, Tutuila: USNM 111883; Malden: USNM 199457; Tuamotus, Raroia: SU 62012, 62016, 62019, 62022.

Entomacrodus corneliae (Fowler)

PLATE 19

Giffordella corneliae Fowler, 1932a, Proc. U. S. Nat. Mus., vol. 80, no. 6, pp. 14–15 [near light, Nuku Hiva, Marquesas Islands].

DESCRIPTION.—Segmented dorsal fin rays 13–15 (13 only in holotype); segmented anal fin rays 16–17; posteriormost anal pterygiophore supporting 1 or 2 external elements (supporting 1 in 4 of 11 specimens); total gill-rakers on first arch 16 or 17; pseudobranchial filaments 5 or 6; vertebrae 34; supraorbital cirri 3–6 (too few specimens available to determine if cirri or predorsal commissural pores increase in number with increase in size); main or longest supraorbital cirrus with all branches mesially; nape with 1 cirrus on each side; predorsal commissural pores 8–19 in specimens 23–40 mm SL; preopercular series of pores with at least 5 pairs or multiples of pores included in the series; 1 pore before each anterior nostril; lateral line terminating on side of body in area below and between dorsal rays 2 and 4; ventral margin of upper lip crenulate on lateral thirds, entire on middle third; lip crenulae number 6–10 on each side.

Proportional measurements: Only one specimen, female, 35.3 mm SL, was in sufficiently good condition to allow measurement. Measurements as percent SL on this specimen: HL 23.8; OL 6.5; OCL 4.0; NCL 4.5; DS3 10.2; DR1 12.5; PECL 23.5; PELL 17.3; CL 21.5.

Of the nine subadult-adult specimens available, only one was a male, approximately 40 mm SL and immature.

Color pattern of preserved specimens.—In specimens with the most developed color pattern there are 6½ pairs of pale dusky, vertical bands on the body (half pair on side beneath anterior dorsal spines). The bands are darkest in their midportions. Ventrally the bands fail to reach the ventral body contour. Dorsally the bands extend onto the dorsal fin where they intensify considerably and take a dorsoposterior direction. On the midside between the band pairs, some specimens show indications of pearly white spots. The head, posterior to the eye, bears as its darkest markings two short, more or less vertical stripes separated by a broader pale area. Ventral to the stripes, some specimens bear a short pearly white horizontal stripe or band. The upper lip is variably dusky, sometimes bearing several irregular bands extending onto the snout. The underside of the head is uniformly dusky.

The anal fin (for dorsal fin, see above) is evenly dusky anteriorly, grading darker distally. Posteriorly, the fin is dusky with included pale spots. The pectoral fin is dusky, darkest on the ventralmost rays. The pelvic fins are dusky. The caudal fin bears three or four dark vertical stripes composed of series of dark spots overlying the rays.

Nomenclature.—Fowler (1932a) described *Giffordella corneliae* (new genus, new species, monotypic) from a larval (ophioblennius) specimen (and 10 larval paratypes) from the Marquesas Islands. The holotype (USNM 91821), approximately 17 mm SL, has 13 dorsal spines, 13 segmented dorsal rays (in four countable paratypes, 14, 15, 15, and 15 rays), 16 segmented anal rays (the last split to the base), 14 pectoral rays, I,4 pelvic rays, a notch between the spinous and soft dorsal fins, nasal, nuchal, and supraorbital cirri (one each on each side), a pair of pores included in the circumorbital series (left side only), and three predorsal commissural pores. This combination of characters leaves no doubt in my mind that the holotype is a species of *Entomacrodus* (*Giffordella* is therefore a junior generic synonym of

Entomacrodus). Lip crenulae, vomerine teeth, and posterior canines in the lower jaw are absent in the type material but are usually not developed in larval stages of *Entomacrodus*.

It is not possible to positively identify the types of *Giffordella corneliae* with the adults of any of the three species of *Entomacrodus* known from the Marquesas. Inasmuch as the three adult forms of *Entomacrodus* known from the Marquesas are all endemics (*E. macrospilus*, *E. randalli*, and the adults included here as *E. corneliae*), it seems that the types probably represent an endemic species also—one of the three forms known from the Marquesas.

E. macrospilus can be eliminated from consideration as the adult of *E. corneliae* because of the higher anal ray count and lack of nuchal cirri of *E. macrospilus*. It is more difficult to eliminate *E. randalli* as the possible adult, but since the dorsal ray count of *E. randalli* is slightly higher (15 or 16) than that of the *E. corneliae* types (13–15), I have elected to apply the latter name to the adults of the third species, which has similar dorsal ray counts (14 or 15) to those of the larvae.

Relationships.—*Entomacrodus corneliae* is a member of the *E. nigricans* species group. Of this group it is most closely related to *E. sealei*, from which it differs only in having two dark vertical stripes on the head behind the eye and in lacking pale stripes and dark bands on the upper lip. The fact that the other two species of *Entomacrodus* in the Marquesas are well differentiated from their nearest relatives and that *E. sealei* is widely distributed and relatively consistent in appearance enforces my decision not to consider *E. corneliae* and *E. sealei* as conspecific. The Marquesas are high islands and of probably more recent origin than the low Tuamotu islands, the nearest island group to the Marquesas (*E. sealei* occurs in the Tuamotus). It seems, therefore, that *E. corneliae* is a more recently evolved species than *E. sealei* and quite possibly a derivative of the widely occurring *E. sealei*.

Entomacrodus corneliae (and *E. sealei*) is next most closely related to *E. chiostictus* (see "Relationships" under *E. chiostictus*) and differs from that species in color pattern and in having all specimens with more pore pairs or groups of pores included in the preopercular series (only 2.8 percent of *E. chiostictus* specimens overlap *E. corneliae* and *E. sealei* in this character).

Remarks.—*Entomacrodus corneliae* (fig. 9) has been taken in the same collection as *E. randalli* and *E. macrospilus*. Adults of *E. corneliae* differ most obviously from the other two species in having two dark vertical stripes on the head posterior to the eye and in the disposition of the upper lip crenulae.

Material.—USNM 91821 (holotype of *Giffordella corneliae*), 91822, 199991.

Entomacrodus chiostictus (Jordan and Gilbert)

Plate 20

Salarias chiostictus Jordan and Gilbert, 1882, Proc. U.S. Nat. Mus., vol. 4, p. 363 [deep rock pool at Mazatlán, Mexico].

Entomacrodus cruentatus Garman, 1899, Mem. Mus. Comp. Zool., vol. 24, pp. 123–124 [off Cocos Islands].

Salarichthys vanderbilti Fowler, 1944, Acad. Nat. Sci. Philadelphia, monogr. 6, pp. 234–235 [Death River tide pools at foot of Mt. Sapo, Panama].

Description.—Segmented dorsal fin rays 14–16 (16 in less than 1 percent of specimens); segmented anal fin rays 15–17 (90 percent with 16), posteriormost anal pterygiophore supporting 1 or 2 external elements (96 percent supporting 2); total gill-rakers on first arch 14–20 (15–18 in 94 percent); pseudobranchial filaments 5–7 (84 percent with 6), number not increasing with increase in SL; vertebrae 33–35 (34 in 90 percent); supraorbital cirri 1–10, number increasing with increase in SL (table 48); main or longest supraorbital cirrus with all branches mesially (rarely with 1 lateral branch also); nape with 1 cirrus on each side (occasionally with 1, rarely 2, branches at tip of cirrus on one side); predorsal commissural pores 3–24 (rarely more than 17), number increasing with increase in SL (table 49); preopercular series of pores with all positions with simple pores in 40 percent of specimens, including 1–5 pairs of pores in series in 60 percent of specimens (usually only 1 or 2 pairs; 92 percent of specimens with 0–3 pairs of pores; fourth and fifth positions of series most frequently with paired pores):

number of pore pairs included in series	0	1	2	3	4	5
frequency of occurrence	204	165	97	29	12	2

1 pore before each anterior nostril; lateral line pores terminating on side in area below and between dorsal fin spine 12 and dorsal segmented ray 6 (usually anterior to dorsal ray 4); ventral margin of upper lip crenulate on lateral thirds, entire on middle third; lip crenulae usually numbering 7 to 10 on each side.

Proportional measurements: See tables 3, 4, and 50.

Remarks.—Males may develop fleshy rugose modifications of the skin of the anal spines and the anterior first to third anal rays, similar to those of *E. nigricans* (pl. 24*f*). If one considers males with these modifications to be mature, the smallest mature male examined was 30.6 mm SL. Mature and immature males may occur in the same collection and in these collections immature males may be as much as 15 mm longer than mature males.

The smallest nonophioblennius stage examined was 17.4 mm SL. Ophioblennius stages examined ranged from about 16 mm (holotype of *E. cruentatus*) to 22.5 mm. In the larvae there were one or two posterolaterally directed canines on each side of the lower jaw. Where two such canines on each side were present the posterior was about twice the size of the anterior. All the ophioblennius stages had small posterior canines in the lower jaw in relatively the same position as the adult canines.

The largest specimen examined was 68.3 mm SL, a male, the largest female was 55.4 mm, both specimens from Panama. If one excludes Panamanian specimens from consideration, the largest male examined was 60 mm SL and the largest female was 47 mm. Females slightly outnumbered males in collections at sizes below 41 mm SL; males greatly outnumbered females at sizes over 40 mm. In the Panamanian collection, females outnumbered males up to 49 mm SL; above 49 mm, males greatly outnumbered females. In most large collections the largest male usually was about 10 mm larger than the largest female.

Color pattern of preserved material.—In specimens with the most developed pattern there are 6½ pairs of dark bands, or where the members of these pairs are each fused, seven bands, on the sides. The bands are most intense in their midportions (frequently only the midportions are visible) abruptly decreasing in intensity dorsally and ventrally. The dorsal and ventral extensions of the bands may be displaced slightly in relation to the midportions. The posteriormost pair of bands, just anterior to the caudal base, and the anteriormost band (half pair), in the region below dorsal spines 2–4, are less intense than the others and may be absent. Upon entering the dorsal fin, the bands may increase in intensity but they never extend more than about midway onto the fin. Portions of the dorsal fin above and between the bands are diffusely dusky and paler than the banded portions. The area on the body above the lateral line, anterior to the anterior dorsal rays, frequently contains numerous small dark

TABLE 48.--Frequency distribution of number of supraorbital cirri of left eye of specimens of *Entomacrodus chiostictus* arranged by SL classes (in mm)

Classes	Number of cirri										Average
	1	2	3	4	5	6	7	8	9	10	
15-19.9	5	2	-	-	-	-	-	-	-	-	1.3
20	2	1	7	7	2	-	-	-	-	-	3.3
25	-	-	10	37	21	1	-	-	-	-	4.2
30	-	-	7	31	41	18	-	-	-	-	4.7
35	-	1	-	31	24	10	11	3	-	-	5.1
40	-	-	3	24	18	14	10	1	-	-	5.2
45	-	1	1	7	22	9	1	1	3	-	5.3
50	-	-	-	2	11	11	8	1	-	-	5.8
55	-	-	1	-	2	3	1	-	-	-	5.4
60	-	-	-	-	2	3	5	1	2	-	6.8
65	-	-	-	-	-	2	1	1	1	1	7.7

spots. The anal fin is variably dusky, always darker and more extensively pigmented in males than females from the same collection. There are indications of diffuse pale spots posteriorly on the anal fin in males, whereas in females the pale areas in this region may give the impression of banding. There is evidence of 3–5 irregular dusky bands on the caudal fin, darkest ventrally and sometimes restricted to the ventral portion of the fin. The pectoral fin is pale with a variable dusting of fine melanophores, concentrated ventrally and basally. There is frequently a dark vertical stripe on the pectoral base. The pelvic fins are pale.

The head is pale to dusky usually with a dark spot just posterior to the eye. The upper lip in most specimens from Panama and the Mexican mainland and adjacent islands, except Clarion Island, usually has or shows traces of 11–14 dark stripes alternating with paler interspaces. The stripes may be absent above the crenulated portions of the lip. There are about six stripes above the noncrenulated portion of the lip. The stripes are darkest ventrally on the lip and may grade into a pale stripe dorsally. Specimens from Clipperton and Socorro Islands may have the lip stripes, a complementary pattern (pale stripes and dusky interspaces or bands), or lack the stripes entirely. Specimens from Clarion Island either had only faint indications of the complementary stripe pattern or completely lacked stripes. The underside of the head frequently exhibits an extension of the upper lip pattern in the form of chevrons. Fowler (1944, as *Salarichthys vanderbilti*) described the color pattern of fresh alcoholic specimens. In contrast to the old preserved material I examined, he noted that numerous pearly white spots were scattered over the body.

GEOGRAPHIC VARIATION.—Aside from variation in color pattern (see above), there was little variation noted between collections of specimens from different localities. Series from Clipperton Island, Socorro Island, Acapulco, the Cape San Lucas area, and the Tres Marias

TABLE 49.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus chiostictus* arranged by SL classes (in mm)

Classes	Number of pores																						Average
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	17	19	20	21	22	23	24	
15-19.9	5	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.2
20	3	3	4	2	2	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.8
25	-	-	4	6	10	22	15	8	-	2	3	-	-	-	-	-	-	-	-	-	-	-	8.3
30	-	2	3	3	8	13	20	24	13	8	2	2	-	-	-	-	-	-	-	-	-	-	9.3
35	-	-	1	3	5	11	19	12	8	15	6	4	1	-	-	-	-	-	-	-	-	-	9.9
40	-	-	-	-	-	2	4	14	9	15	8	3	1	6	2	2	-	-	-	-	-	-	12.0
45	-	-	-	-	-	-	7	6	9	2	8	5	3	1	2	-	-	-	-	-	-	1	12.2
50	-	-	-	-	-	2	1	4	3	4	1	6	5	3	3	-	1	-	-	-	-	-	13.2
55	-	-	-	1	-	-	1	1	1	1	-	1	-	1	-	-	-	-	-	-	-	-	11.1
60	-	-	-	-	-	-	1	1	3	1	2	2	1	-	1	-	-	-	-	-	-	-	12.5
65	-	-	-	1	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	11.2

Islands had somewhat higher percentages of specimens with 14 dorsal soft rays than collections from other localities. Series from Acapulco and Clipperton Island had somewhat higher percentages of specimens with 15 anal soft rays than specimens from other localities. Since this variation is not great nor does it conform to a pattern, I have not reported these data uncombined. Specimens from the Gulf of California frequently had what appeared to be teratological development of the supraorbital cirri (short and club shaped, rather than long,

TABLE 50.--Proportional dimensions as percent SL of specimens of *Entomacrodus chiostictus*
(for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL
CNHM 63903	Acapulco	♀	24.4	25.8	7.0	4.1	3.3	11.1	15.2	25.8	18.5	25.4
CNHM 63903	Acapulco	♂	27.0	23.7	7.4	5.9	2.6	10.7	12.2	24.4	17.8	25.5
CNHM 63903	Acapulco	♀	27.5	24.4	6.9	3.6	3.3	10.6	12.7	24.0	17.4	23.3
SU 18973	Baja Calif.	♂	29.7	23.2	6.1	5.0	<1.7	10.1	-	22.6	15.2	24.2
USNM 181273	Clipperton	♀	29.8	25.2	6.7	4.0	2.7	10.7	12.1	24.8	15.4	22.8
USNM 181273	Clipperton	♂	30.5	24.9	7.2	5.6	2.6	11.1	13.4	23.9	15.7	22.9
ANSP 90026	Clipperton	♀	30.6	24.5	7.2	4.2	3.3	10.1	13.4	24.2	16.0	22.9
ANSP 90806	Baja Calif.	♀	31.8	22.6	7.5	4.1	2.8	10.4	11.3	22.6	14.5	23.9
SU 18973	Baja Calif.	♀	32.1	24.9	7.2	5.0	3.1	9.3	11.2	23.7	17.1	24.3
USNM 181273	Clipperton	♂	33.0	24.8	7.3	4.2	2.7	10.3	13.6	22.4	16.4	23.0
CNHM 63903	Acapulco	♀	35.4	25.4	7.3	4.5	2.3	9.9	14.1	25.4	16.7	25.4
CNHM 63903	Acapulco	♀	37.5	24.3	6.9	4.0	2.7	8.8	12.0	24.3	17.1	23.2
USNM 181273	Clipperton	♂	37.5	25.2	6.9	6.9	2.7	10.4	-	23.2	15.2	23.2
ANSP 90806	Baja Calif.	♂	38.2	24.9	6.8	5.2	2.6	10.5	12.3	23.6	16.5	23.6
ANSP 90026	Clipperton	♂	39.4	23.6	6.3	5.1	3.0	9.4	14.2	21.6	15.2	21.6
UCLA W59-248	Baja Calif.	♀	39.5	23.0	6.1	3.8	3.0	8.9	12.7	22.8	14.4	20.8
SU 18973	Baja Calif.	♀	40.2	23.1	6.2	4.0	2.5	9.2	11.9	19.9	15.4	22.4
ANSP 90026	Clipperton	♂	40.5	22.7	6.4	5.4	3.0	9.9	13.3	21.0	14.6	21.5
ANSP 90026	Clipperton	♂	41.0	23.4	5.1	5.6	2.9	10.0	13.7	21.5	14.6	22.9
ANSP 90026	Clipperton	♀	41.5	23.6	6.5	5.3	2.4	8.9	13.5	23.8	16.1	19.8
USNM 177784	Clipperton	♂	42.2	23.7	7.1	5.9	3.6	9.5	13.7	21.3	15.2	23.7
USNM 28117[1]	Mazatlan	♀	43.2	24.1	6.7	4.4	2.8	10.2	12.5	22.9	15.5	22.7
USNM 177784	Clipperton	♂	43.8	25.1	6.4	5.7	2.7	10.5	14.4	21.9	13.7	23.8
CNHM 63903	Acapulco	♂	44.0	23.0	5.9	5.0	2.3	10.2	13.2	22.0	14.8	22.7
ANSP 90026	Clipperton	♂	45.4	23.1	6.6	5.5	3.2	9.0	11.9	21.6	13.6	21.6
USNM 181273	Clipperton	♂	46.8	23.5	5.8	5.6	3.2	9.6	13.0	23.7	14.3	22.9
ANSP 90026	Clipperton	♂	47.6	22.7	5.5	5.9	2.5	9.4	14.7	21.4	14.5	22.7
CNHM 63903	Acapulco	♂	48.0	24.0	5.6	5.0	2.3	9.4	14.2	22.7	14.6	24.0
SU 18973	Baja Calif.	♂	49.9	24.0	5.8	6.0	2.6	8.0	13.0	21.6	14.8	22.4
CNHM 63903	Acapulco	♂	50.0	24.0	5.8	5.6	2.4	9.6	13.4	21.8	15.4	23.2
CNHM 63903	Acapulco	♂	52.7	23.0	5.5	4.2	1.9	9.5	14.8	22.4	14.2	23.0
USNM 177784	Clipperton	♂	54.6	23.1	6.0	5.5	3.1	9.7	14.6	20.9	13.0	23.3
UCLA W59-248	Baja Calif.	♂	59.2	23.0	5.2	6.8	2.7	8.6	13.5	21.1	13.5	22.5
UCLA W59-248	Baja Calif.	♂	60.1	22.8	5.2	5.0	2.7	9.8	13.3	21.3	13.0	22.0
ANSP (Argosy 13)	Panama	♂	64.3	23.2	5.1	5.9	3.1	10.3	15.4	21.2	13.8	21.3
ANSP (Argosy 13)	Panama	♂	65.6	23.0	4.9	5.6	3.4	9.4	13.6	20.3	13.7	20.6
ANSP (Argosy 13)	Panama	♂	66.8	21.9	5.2	4.6	3.0	9.6	12.9	19.8	12.7	20.8
ANCP (Argosy 13)	Panama	♂	68.3	22.0	4.7	4.5	2.6	9.2	12.6	19.3	13.0	20.0

[1] Lectotype of *Salarias chiostictus*

slender, and tapering). Much of the overlap in relative cirri lengths of *E. chiostictus* with *E. nigricans*, for example, as indicated in table 4, is the result of measurements based on Gulf of California specimens.

NOMENCLATURE.—*Entomacrodus cruentatus* Garman is an ophioblennius larval stage approximately 16 mm SL. The specimen is now in poor condition but still exhibits some of the posterolaterally directed canines in the lower jaw. The dorsal fin formula is XIII,15, the pectoral rays number 14. The only salarine blenniid in the eastern Pacific with this combination of counts is *E. chiostictus*. Garman did not compare his species with any other. *Salarichthys vanderbilti* Fowler is the normal adult of *E. chiostictus*. Fowler compared his species only with the Altantic *E. textilis*. The published description gives the type-locality of *S. vanderbilti* as Death River tide pools at the foot of Mt. Sapo, Panama. The label in the bottle with the holotype states only "Tidepools off Playa Muerto, Panama." Both the published description and the label give the date of collection as Apr. 16, 1941.

The syntypic material of *Salarias chiostictus* consists of two specimens, both females, USNM 28117. I here designate one of these specimens lectotype. The lectotype retains the orginial catalog number. The paralectotype is recataloged USNM 200284. The lectotype, 43.2 mm SL, has D. XIII,15, A. II,16S, and two pairs of pores included in the preopercular series. The paralectotype, 46.2 mm SL, has D. XIII,14, A. II,16N, and all preopercular pores simple.

RELATIONSHIPS.—*E. chiostictus* is a member of the *E. nigricans* species group. *E. chiostictus* differs from all the Atlantic species of the genus (and species group) in having a longer supraorbital cirrus and more lip stripes, as well as by having a much higher percentage of specimens with pore pairs included in the preopercular series. It differs from most populations of *E. caudofasciatus* in lacking a humeral blotch, usually having more lip stripes, and a much higher percentage of specimens with paired pores in the preopercular series. It differs from most specimens of *E. sealei* in having a different type color pattern on the upper lip and in usually not having as many as three pore pairs included in the preopercular series. It differs from *E. corneliae* in lacking a pair of dark vertical stripes on the head behind the eye and in rarely having as many as four or five pore pairs included in the preopercular series.

The members of the *E. nigricans* group are closely interrelated and some investigators might consider them merely populations of one species; however, this interpretation is in part excluded by the fact that two western Pacific forms (*E. sealei* and *E. caudofasciatus*) occur together and are always readily distinguishable (the third western Pacific form, *E. corneliae*, is endemic to the Marquesas, where no other member of the *nigricans* group occurs).

Some of the specimens of *E. chiostictus* from Clipperton and Clarion Islands appear to be intermediate between *E. sealei* and *E. caudofasciatus* and can be expected to key to either of these two western Pacific species, especially to the Rarotonga, Tahiti, Makatea, and Raroia populations of *E. caudofasciatus* (these populations represent the easternmost occurrences of *E. caudofasciatus;* the easternmost occurrence of *E. sealei* is Raroia). *E. chiostictus,* in common with *E. sealei* and *E. caudofasciatus,* has a proportionately longer supraorbital cirrus than is found in the Atlantic members of the *nigricans* species group. This fact and the increased occurrence of paired pores in the preopercular series of pores of *E. chiostictus* over their occurrence in the Atlantic species (and *E. caudofasciatus*) appears to relate *E. chiostictus* most closely with *E. sealei.* It would seem, therefore, that at some time individuals of the form ancestral to *E. sealei* and *E. chiostictus* reached eastern Pacific shores and diverged. Differentiation appears to be more advanced in the mainland populations than in the Clarion Island and Clipperton Island populations.

Support for an Indo-West Pacific origin of the species ancestral to *E. chiostictus* is the appearance in the eastern Pacific (but not the western or eastern Atlantic) of a blenniid genus, *Runula,* which has the Indo-West Pacific as its center of abundance. Other blennioids, certain Tripterygiidae (R. H. Rosenblatt, pers. comm.), subfamily Clininae, of the Clinidae (M. L. Penrith, in litt.), found in the eastern Pacific also have their closest relatives in the western Pacific and no closely related representatives in the Atlantic. Briggs (1961) has postulated a western Pacific origin of all the shore fishes not worldwide in distribution and found common to both the eastern and western Pacific ocean. He bases this on the direction of flow of ocean currents, the fact that most of the genera in common have far more species in the western Pacific than in the eastern Pacific, the fact that most of the forms occur primarily or only on the offshore islands in the eastern Pacific, and the fact that no species of a typically tropical New World genus has colonized the western Pacific. The evidence, though circumstantial, thus also favors an Indo-West Pacific origin of the form ancestral to *Entomacrodus chiostictus.*

I believe that *Entomacrodus* reached the eastern Pacific by island hopping and by movement of populations along rocky coasts. The most probable route would be along the chain of islands extending out to Easter Island and Sala-y-Gomez, thence along formerly existing islands of the Sala-y-Gomez and Nasca Ridges to Peru, and up the coast to Central America and Mexico. The movement would have taken place during a period of warmer climatic conditions than exist today. Subsequent climatic cooling would have eliminated the genus from South America. Menard (1964) reported that reef debris of from late Tertiary to Recent age has been dredged from the Nasca Ridge and that there were some Tertiary islands on the Nasca Ridge which no longer exist today. While there is no data available on the adjacent Sala-y-Gomez Ridge for the same period, the bathymetric similarity of the two ridges would tend to confirm similar geologic histories.

In this scheme the populations of *Entomacrodus* at Clipperton and Clarion Islands would be derivative of the mainland populations. The resemblance of the Clipperton Island and Clarion Island individuals to specimens of *E. sealei* or *E. caudofasciatus* would then be a secondary, parallel development. Some support for the derivation of the Clipperton Island (farthest offshore tropical eastern Pacific island) population of *Entomacrodus* from the eastern Pacific mainland form is to be found in the primarily New World salarine genus *Ophioblennius* Gill (eastern Pacific, western and eastern Atlantic in distribution—Springer, 1962). In the eastern Pacific, *O. s. steindachneri* Jordan and Evermann is distributed widely from Mexico to Peru, while the population at Clipperton, *O. s. clippertonensis* Springer, is endemic. In view of the predominant offshore flow of the currents from the mainland and the very large size attained by the larvae of *Ophioblennius* (up to 66 mm SL), specimens of which have been taken offshore over deep water (Springer, 1962), I believe it quite possible for *Ophioblennius* (and *Entomacrodus*) to have made the 600-mile journey from the Mexican mainland to Clipperton. The North Equatorial Current, which flows at the constant rate of 0.3 knot per hour (Wyrtki, 1965) would be the vehicle of transport and the time involved only 83 days. The main objection to this hypothetical origin of the Clipperton population is the question of how the population is able to maintain its distinctiveness in the face of a probable continuing inflow of larvae from the mainland. A conjecture proposed by Gosline (1957) to explain endemism of Hawaiian fishes may answer this objection. Gosline believes that once a population of a species colonizes a new area and becomes adapted to that area (evolved), it either competitively excludes subsequent colonization by the less adapted parental form or genetically swamps the subsequent arrivals. This conjecture requires a low intensity of continuing immigration of the parental form.

The alternative to the previous method of introducing *Entomacrodus* to the eastern Pacific is to bring the colonizers across open ocean. If the introduction was effected over the shortest route from the central Pacific, it is still necessary to explain the mechanism of transport. Such transport could be effected by the Equatorial Countercurrent, which occasionally skirts Clipperton Island (for discussion, see Sachet, 1962, p. 25; for diagrams of the current, see Wyrtki, 1965). Clipperton Island, closest tropical eastern Pacific island to the tropical central Pacific atolls, is 2300 miles from the nearest such atoll, the Tuamotus; however, the Tuamotus lie in the path of the South Equatorial Current and would not be expected to contribute faunal elements to the eastern Pacific. The Line Islands, over 4000 nautical miles from Clipperton, are the nearest central Pacific atolls to Clipperton lying in the path of the Equatorial Countercurrent. Movement of this current is about 0.75 knot per hour (Wyrtki, 1965). At this speed it would require well over 200 days for an individual larva to travel from the Line Islands to Clipperton. It seems unlikely that *Entomacrodus* larvae would be the forms transported, as it appears from the small size at transformation (less than 25 mm SL) that *Entomacrodus* species have only a brief larval life.

It is also difficult to postulate adult transport (for instance by flotsam). The problem here is that adults are bottom dwellers found only in rocky or coral reef areas; no adults have been recorded from the open ocean out of sight of land or from near floating objects.

Assuming that *Entomacrodus* did reach the eastern Pacific from the western Pacific, it seems probable that the genus moved from the eastern Pacific to the western Atlantic during times when there was a Central American passage between the eastern Pacific and the western Atlantic. When the isolating Central American land bridge appeared, the populations on either side diverged. (It seems probable, however, that the eastern Pacific population did not diverge from the central Pacific population until well after the isolation of the Pacific from the Atlantic, and therefore the Atlantic populations are more divergent from the ancestral form than are the eastern Pacific populations.) Subsequently, the western Atlantic form populated other areas of the Atlantic, and these populations in turn diverged. The progressively lower percentage of specimens with paired pores occurring in the preopercular series of pores as one examines populations from the central Pacific (*E. sealei* and *E. corneliae*), eastern Pacific (*E. chiostictus*), western Atlantic (*E. nigricans*, *E. vomerinus*), and eastern Atlantic (*E. cadenati*, *E. textilis*), would support this reasoning. In this scheme *E. caudofasciatus*, with predominantly simple pores, presents the only problem. Its distribution, eastern Indian Ocean to the Tuamotus, and the fact that there are several differentiated populations as opposed to the undifferentiated populations of *E. sealei*, seems to indicate a species of limited mobility which originated in the Indo-West Pacific area and has remained there. Confusing specimens of *E. chiostictus* would then represent convergent rather than direct relationship with *E. caudofasciatus* (and *E. sealei*).

Distribution (fig. 9).—*Entomacrodus chiostictus* is restricted to the eastern Pacific ocean. It has been collected as far north as the northern end of Isla Angel de la Guarda in the Gulf of California but is apparently uncommon north of Isla Cerralvo. It is not reported from the west coast of Baja California or the mainland coast of Mexico north of Mazatlán. It is known to reach as far south as Punta Galero, Oaxaca, on the Mexican coast but is not reported from the rockless area between this locality and Playa Muerto, Panama (see Springer, 1959, for this "Pacific Central American Faunal Gap"). The southernmost specimens come from Piñas Bay, Panama. *E. chiostictus* is recorded from the following major offshore islands: Trés Marias, Revillagigedos, Clipperton, Cocos.

Material studied.—Mexico: Gulf of California, Isla Angel de la Guarda: UCLA W59–183; Baja California, Cape San Lucas and vicinity: ANSP 90806, SU 18973, 18974, UCLA W52–263, W59–248, W61–35; Sinaloa, Mazatlán: USNM 28117 (lectotype of *S. chiostictus*), 120934, 200284; Islas Trés Marias: SIO 62–16, UBC 59–202, 61–142; Islas Revillagigedos, Socorro: SIO 57–134, SU 5885, UCLA W53–350 (now CAS), USNM 67572, 126986; Roca Partida: SIO 60–385; Clarion: BMNH 1898.19.29.64–65, CNHM 1786, LACM 1132, SU 2673, UBC 58–383, 59–254, USNM 54501; Colima, Ensenada Carrizal: UCLA W56–231; Nayarit, Chacala: UCLA W58–2, W58–5; San Blas: UCLA W58–30; Sayula: UMMZ 172089; Guerrero, Isla Grande: UBC 54–50, 61–130; Acapulco: CNHM 63903; Oaxaca, Punta Galero: SU 37572; Clipperton Island: ANSP 90026, SU 51230, USNM 177784, 181273; Islas Cocos: MCZ 28695 (holotype of *E. cruentatus*), UCLA W58–378; Panama, Playa Muerto: ANSP 70070 (holotype of *S. vanderbilti*), 70071, 70072, 70073; Piñas Bay: ANSP (Argosy station 13).

***Entomacrodus vomerinus* (Valenciennes)**

Plate 21

Salarias vomerinus Valenciennes, 1836, *in* Cuvier and Valenciennes, Hist. Nat. Poissons, vol. 11, p. 349 [near Bahia, Brazil].

Description.—Segmented dorsal fin rays 15–17 (16 in 80 percent of specimens); segmented anal fin rays 15–18 (17 in 76 percent of specimens 15 in only 1 of 126 specimens); posteriormost anal pterygiophore supporting 1 or 2 external elements (2 in 88 percent of specimens); total gill-rakers on first arch 16–24 (19–24 in 74 percent of specimens); pseudobranchial filaments 5–8 (6 in 75 percent of specimens), number not increasing with increase in SL; vertebrae 34–36 (35 or 36 in 85 percent of specimens); supraorbital cirri 4–15, number increasing with increase in SL (table 51), main, or longest supraorbital cirrus with most branches mesially, frequently with 1 or 2 branches laterally; nape with 1 cirrus on each side; predorsal commissural pores 3–16 (usually less than 11), number tending to increase with increase in SL (table 52); preopercular series of pores with all positions simple in 97 percent of specimens (only 3 specimens with 1 pair, and 1 with 2 pairs of pores included in series); 1 pore before each anterior nostril; lateral line pores terminating on side in area below and between dorsal fin spine 11 and ray 3 (usually between spine 12 and ray 1); ventral margin of upper lip crenulate on lateral thirds, entire on middle third; lip crenulae numbering 6–13 on each side (usually 7–10).

Proportional measurements: See tables 3, 4, and 53.

Only two males, 72.7 and 85.3 mm SL, were seen with fleshy rugose modifications of the skin of the anal spines and rays (first four rays). If one considers males with these modifications mature, then mature males occurred in the same collection with immature males as large as 100.5 mm SL.

Below 85 mm SL, males and females occur in collections with relatively equal frequency at various sizes; however, the largest female examined, 83.7 mm, was somewhat smaller than the largest male, 100.5 mm. Males larger than 84 mm are relatively common, indicating that males generally attain a larger size than females.

Color pattern of preserved material.—None of the material available to me was less than 50 years old and much of the color pattern in this material has been lost. The specimen illustrated in plate 21 shows a color pattern more clearly than any of the other available specimens but seems to be somewhat atypical in the evenness of shade of the body bands. In other specimens with preserved patterns, there appear to be indications of 6½ to 7 pairs of bands on the body. There are no indications of fusions between the midportions of the members of a pair, except possibly the anteriormost, shortest pair in the region above the pectoral axil. In many specimens the bands appear to have

TABLE 51.--Frequency distribution of number of supraorbital cirri of left eye of specimens of *Entomacrodus vomerinus* arranged by SL classes (in mm)

Classes	Number of cirri												Average
	4	5	6	7	8	9	10	11	12	13	14	15	
35-39.9	1	-	1	1	-	-	-	-	-	-	-	-	5.4
40	1	2	3	2	-	-	-	-	-	-	-	-	5.8
45	-	2	2	1	-	-	-	-	-	-	-	-	5.8
50	-	1	3	1	2	-	-	-	-	-	-	-	6.6
55	-	1	2	1	-	-	-	-	-	-	-	-	6.0
60	-	-	2	-	2	2	-	-	-	-	-	-	7.7
65	-	1	1	1	1	-	-	-	-	-	-	-	6.5
70	-	2	2	1	-	5	1	2	1	-	-	-	7.6
75	-	-	1	-	1	-	1	-	1	-	-	-	9.0
80-89.9	-	1	2	-	4	-	2	2	1	-	-	2	8.9
90	-	1	-	-	-	-	-	-	-	-	-	-	-
100	-	-	-	-	1	-	-	-	-	-	-	-	-

been composed of darker midportions and paler dorsal and ventral portions. Dorsally the bands enter the dorsal fin for a variable distance, taking on a posterodorsal direction, but failing to extend to the distal fin margin. There is no evidence of a humeral blotch, but the bands are most intense in the area where such a blotch might occur. Posteriorly on the side, the bands may be very faint to absent. Ventrally the bands become faint and may have reached the anal fin base but do not appear to have entered that fin. I find no evidence of the tiny dark spots that occur on the sides below the spinous dorsal fin in all the other Atlantic species.

The head is variably dark with two or one (when presumably the two are fused) dark stripes passing from the upper lip to the eye and then continuing dorsoposteriorly for a very short distance from the dorsal margin of the eye. Just posterior to the eye there is a pale area extending from the corner of the lip to the top of the head. The pale area may have a dark margin posteriorly, darkest at mideye level, giving the appearance of a spot. In small specimens, 7–9 dark, uninterrupted stripes may be seen on the upper lip. In large specimens the lip has become almost uniformly dark, but in some of these specimens indications of the stripes persist. Dark chevrons appear on the underside of the head in many specimens, but these are frequently diffuse or obscured.

Aside from the extensions of the body bands entering the dorsal fin, the soft dorsal fin shows some pale diffuse striping. Other than these marks the dorsal fin is more or less uniformly dusky. The anal fin membranes are uniformly dusky, except possibly for a basal pale area or some diffuse pale spots in the posterior distal region on the fin of some specimens. The caudal fin bears about 5–8 dark bands, depending on size; small specimens with fewer stripes than large specimens. The pectoral fin is variably dusky with possible indications basally of intensification of the melanophores. The pectoral base may have a pale area just proximal to the pectoral rays, followed by a diffuse dark cresentic mark. The pelvic fins are dusky.

I noted no evidence of sexual dichromatism, but better preserved material may alter this impression.

Remarks.—There is a tendency for males to have more segmented dorsal fin rays than females. Of 51 males examined, 3 had 15 rays, 41 had 16 rays, and 8 had 17 rays. Of 74 females examined, 13 had 15 rays, 60 had 16 rays, and 1 had 17 rays. No sexual dimorphism was noted for other meristic characters.

Relationships.—*Entomacrodus vomerinus* is a member of the *E. nigricans* species group. Of this group, the Atlantic species appear to be most closely interrelated (see "Relationships" under *E. nigricans*).

Entomacrodus vomerinus differs from all the other members of its group in usually having a higher number of soft dorsal and anal rays and more vertebrae. It differs: from *E. textilis* and *E. caudofasciatus*, in lacking a humeral blotch, and from the latter of these two in usually having a higher number of gill-rakers; from *E. cadenati*, in not having the lip stripes broken into spots and in lacking the peculiar well-developed markings on the head of that species; from *E. chiostictus*, *E. sealei*, and *E. corneliae*, in rarely having any of the pores of the preopercular series paired; from *E. chiostictus* and *E. sealei*, in having proportionately shorter supraorbital and nuchal cirri; from *E. chiostictus* also, in having fewer lip stripes, and from *E. sealei*, in having the pale areas between the lip stripes broader than the stripes.

The syntypic material of *S. vomerinus* in the Paris museum comprises eight specimens, all previously catalogued as MNHN 3082. I here designate one of these eight specimens lectotype. The lectotype retains the original catalog number. The paralectotypes are now MNHN B2526. The lectotype is a male, approximately 69 mm SL, with the following characters: dorsal, XIII,17; anal, II,18S; predorsal commissural pores 4; vomerine teeth 6; pseudobranchial filaments 6.

Distribution (fig. 9).—*Entomacrodus vomerinus* is known from the coast of Brazil from Natal to Bahia, and from the island of Fernando de Noronja. One specimen, MCZ 4637, collected by Agassiz and Bourget on the Thayer Expedition, is labeled as having come from Para. The best known "Para," of which there are many, is another name for Belem in the north of Brazil on the Para River. Although the Thayer Expedition visited Belem, it is doubtful that they obtained an *Entomacrodus* there as none of the species of this genus have been

TABLE 52.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus vomerinus* arranged by SL classes (in mm)

Classes	Number of pores 3	4	5	6	7	8	9	10	11	12	13	14	15	16	Average
35-39.9	1	-	2	2	-	-	-	-	-	-	-	-	-	-	5.0
40	2	1	2	2	-	-	-	-	-	-	-	-	-	-	4.6
45	-	2	3	1	2	-	-	-	-	-	-	-	-	-	5.4
50	2	1	1	3	-	-	1	-	-	-	-	-	-	-	5.2
55	-	1	1	3	-	1	-	1	-	-	-	-	-	-	6.4
60	1	2	1	3	1	1	-	1	-	-	-	-	-	1	6.8
65	-	2	2	8	3	-	3	-	-	-	-	-	-	-	6.3
70	-	2	3	8	3	6	1	3	-	-	-	-	-	-	6.9
75	-	2	1	2	4	2	1	1	-	1	-	-	-	-	7.1
80-89.9	1	1	-	4	6	3	-	2	1	-	-	-	-	-	7.1
90	-	1	-	-	-	-	1	-	-	-	-	-	-	-	6.5
100	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-

recorded from freshwater. The Thayer Expedition visited other points on the Brazilian coast within the verifiable range of *E. vomerinus*, points which various atlases and gazetteers show have also been known as "Para." It seems more likely that the MCZ specimen came from one of these localities.

MATERIAL.—Brazil, Natal: (all originally SU 22443), AMNH 3842, CNHM 59056, IFAN (no number), SU 22443, USNM 112264; Pernambuco: BMNH 1887.12.3.11, MCZ 12535, CNHM 7225; Bahia: MNHN 3082 (lectotype of *Salarias vomerinus*), B2526 (paralectotypes), USNM 43283; Fernando de Noronja: BMNH 1888.19.72–81; "Para": MCZ 4637 (see "Distribution").

TABLE 53.--Proportional dimensions as percent SL of specimens of *Entomacrodus vomerinus* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL
SU 22443	Brazil	♂	37.0	23.8	7.6	4.1	<1.3	10.0	12.2	23.0	16.5	23.8
SU 22443	Brazil	♂	37.4	25.4	6.7	5.4	2.1	10.7	13.4	24.1	15.8	23.5
SU 22443	Brazil	♀	40.0	24.5	7.0	4.2	1.8	9.2	13.0	25.0	16.8	24.2
SU 22443	Brazil	♀	42.8	24.1	6.3	3.7	1.2	9.3	12.6	25.5	15.6	22.9
SU 22443	Brazil	♂	44.5	23.6	5.8	3.4	1.1	9.0	13.5	22.5	15.7	23.6
SU 22443	Brazil	♀	46.2	24.2	6.5	4.3	1.7	10.0	13.4	24.9	16.9	23.2
SU 22443	Brazil	♀	48.4	23.4	6.2	3.3	2.1	10.3	13.0	23.8	14.3	23.8
SU 22443	Brazil	♂	52.5	24.2	6.1	3.8	1.3	9.5	12.4	24.6	14.3	22.9
SU 22443	Brazil	♀	59.0	23.7	5.6	3.7	1.7	11.0	13.9	24.9	16.4	24.9
SU 22443	Brazil	♀	61.5	22.6	5.2	3.9	2.0	9.8	12.3	23.7	15.2	22.0
USNM 112264	Brazil	♀	68.9	22.6	5.1	4.2	2.2	8.9	12.9	24.5	14.1	23.2
SU 22443	Brazil	♀	70.4	22.2	5.7	5.7	2.1	10.1	13.6	25.3	13.9	23.4
USNM 112264	Brazil	♀	72.2	22.2	5.3	4.3	1.8	10.8	14.8	24.9	14.4	22.4
SU 22443	Brazil	♀	73.7	22.7	5.0	3.4	1.4	9.5	14.0	23.5	14.9	22.7
USNM 112264	Brazil	♀	74.5	22.8	5.2	4.0	1.7	9.9	12.3	21.1	13.5	21.1
SU 22443	Brazil	♀	76.4	24.2	5.1	3.9	1.2	10.2	14.1	22.4	13.3	23.5
SU 22443	Brazil	♂	80.4	22.1	4.7	4.2	1.5	9.6	14.2	23.6	12.7	22.0
USNM 112264	Brazil	♂	80.7	21.8	5.0	4.0	1.2	9.9	11.3	21.7	14.1	23.2
SU 22443	Brazil	♂	81.0	23.1	4.6	3.7	1.2	-	14.1	22.2	13.0	22.3
SU 22443	Brazil	♂	82.8	23.0	4.8	4.6	1.3	12.6	13.5	23.2	13.3	23.1
USNM 112264	Brazil	♀	83.7	22.9	4.8	3.7	1.7	9.8	14.7	23.2	13.6	23.3
SU 22443	Brazil	♂	84.4	23.0	5.3	3.9	1.5	9.5	13.6	23.5	13.0	21.9
SU 22443	Brazil	♂	85.5	24.3	5.4	4.8	2.2	11.6	11.8	21.9	12.2	22.8
USNM 112264	Brazil	♂	87.5	22.9	4.6	4.3	1.4	11.4	15.4	22.5	12.3	23.2
USNM 112264	Brazil	♂	90.5	22.4	4.4	4.4	1.1	10.7	13.8	21.3	11.7	-
USNM 112264	Brazil	♂	100.5	23.0	4.5	2.9	2.0	9.1	13.6	21.4	12.7	21.6

Entomacrodus textilis (Quoy and Gaimard)

Plate 22

Salarias textilis Quoy and Gaimard, 1836, *in* Cuvier and Valenciennes, Hist. Nat. des Poissons, vol. 11, p. 307 [Ascension].

Description.—Segmented dorsal fin rays 14 or 15 (15 in 84 percent of specimens); segmented anal fin rays 15 or 16 (16 in 89 percent of specimens); posteriormost anal pterygiophore supporting 1 or 2 external elements (supporting 2 in 92 percent of specimens); total gill-rakers on first arch 15–23 (16–20 in 94 percent of specimens); pseudobranchial filaments 4–7 (6 in 76 percent of specimens) number not increasing with increase in SL; vertebrae 34 (10 specimens); supraorbital cirri 1–8, number increasing with increase in SL (table 54), main, or longest, supraorbital cirrus with most branches mesially, sometimes with 1 or 2 branches laterally; nape with 1 cirrus on each side; predorsal commissural pores 3–12 (usually less than 9), number increasing with increase in SL (table 55); preopercular series of pores with all positions with simple pores (only 1 specimen with 1 pair of pores included in preopercular series); 1 pore before each anterior nostril; lateral line pores terminating on side in area below and between dorsal fin rays 4 and 7; ventral margin of upper lip crenulate on lateral thirds, entire on middle third; lip crenulae usually numbering 7–11 on each side.

Proportional measurements: See tables 3, 4, and 56.

No males with the skin of the anal spines and rays modified into fleshy rugose pads were seen. It is presumed that all males available were immature. The largest of these was 60.5 mm SL. The largest female examined was 54.8 mm SL. The smallest specimen examined was 18.5 mm. No ophioblennius stages were seen.

Color pattern of preserved material.—The most striking and characteristic marking of this species is a dark subquadrate blotch in the humeral region between the pectoral axil and the lateral line. This mark was present in all specimens examined.

In specimens with the most developed color pattern there are seven pairs of bands on the sides of the body (fusions between the mid-portion of the members of a pair as in *E. chiostictus* were not noted). Each member of the posterior six pairs of bands may be broken vertically into three subquadrate sections, the middle section of which is usually most intense (whether or not the band is broken into sections), and the ventral section usually least intense. The posteriormost two pairs of bands are usually paler than the others and may be only diffusely represented or absent. The anterior pair of bands consists of an anterior, slender, dark to faint member and the posterior much darker and larger subquadrate humeral blotch previously mentioned. The dorsal portions of the body bands extend onto the dorsal fin for a variable distance taking a dorsoposterior direction on the fin.

The ventral portions of the body bands do not extend onto the anal fin. The areas between the pairs of bands and between the members of each pair are usually narrower than the width of a single member of each band pair. The anterodorsal portion of the sides in the region below the spinous dorsal (usually anterior to dorsal spine seven) frequently bears a variable number of small dark spots. The head is variably marked with distinct spots and diffuse splotches, but a simple accentuated spot just posterior to the posterior margin of the orbit is usually not present. The upper lip is usually marked with seven to nine dark stripes, narrower than the paler interspaces. Some of the lip stripes extend onto the ventral side of the head as chevrons.

TABLE 54.--Frequency distribution of number of supraorbital cirri of left eye of specimens of *Entomacrodus textilis* arranged by SL classes (in mm)

Classes	Number of cirri 1	2	3	4	5	6	7	8	Average
15-19.9	1	-	2	-	-	-	-	-	2.3
20	-	-	3	-	-	-	-	-	3.0
25	-	-	4	4	-	-	-	-	3.5
30	-	-	3	1	2	1	-	-	4.1
35	-	-	-	4	3	1	2	-	5.1
40	-	-	1	2	5	6	-	-	5.1
45	-	-	-	2	3	2	2	2	5.9
50	-	-	-	1	3	1	-	-	5.0
55	-	-	-	1	-	-	1	-	5.5
60	-	-	-	-	-	-	1	-	-

TABLE 55.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus textilis* arranged by SL classes (in mm)

Classes	Number of pores 3	4	5	6	7	8	9	10	11	12	Average
15-19.9	3	-	-	-	-	-	-	-	-	-	3.0
20	4	-	1	-	-	-	-	-	-	-	3.4
25	2	4	1	-	1	-	-	-	-	-	4.2
30	1	2	1	2	-	-	-	-	-	-	4.7
35	3	-	3	3	-	2	-	-	-	-	5.3
40	1	3	-	7	3	-	-	-	-	-	5.6
45	-	1	-	5	2	2	-	-	-	1	6.9
50	-	1	1	2	-	-	-	-	-	-	5.2
55	-	-	-	-	-	1	-	-	-	-	8.0
60	-	-	-	-	-	-	-	-	1	-	-

The spinous dorsal fin is variably dusky, frequently with a narrow pale distal margin. The soft dorsal is usually dusky between and also distal to the body band extensions on the fin. In males the anal fin is uniformly dusky with a narrow proximal pale stripe. In females the anal fin is variably dusky anteriorly but posteriorly with pale areas forming diffuse spots distally on the fin. The caudal fin bears three to five (usually four) dusky, sometimes irregular, bands, palest posteriorly and dorsally. The pectoral fin is dusky with a darker, sometimes well-defined area basally on the ventral rays. There is a pale band anterior to this last area on the fleshy pectoral base, followed by a dark crescentic mark and sometimes additional dark marks, also on the base. The pelvic fin is variably pale to dusky.

Lectotype designation.—The syntypic material upon which Valenciennes based his description of *Salarias textilis* is contained in three lots, MNHN A2025 (1 specimen), A2026 (3 specimens), and B2524. I here designate A2025, a 60.5 mm SL male, as lectotype.

TABLE 56.--Proportional dimensions as percent SL of specimens of *Entomacrodus textilis*
(for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL	HBL
BMNH 1935.5.2.25-30	Ascencion	♂	27.0	25.2	7.4	3.7	3.3	11.1	14.8	25.8	16.7	24.8	4.8
BMNH 1946.5.23.10-12	St. Helena	♂	27.1	24.7	7.4	3.7	1.8	10.7	13.6	24.0	17.0	23.6	3.3
BMNH 1960.3.1.45-60	St. Helena	♀	28.1	25.3	7.1	3.6	2.8	10.0	13.5	24.9	18.9	23.1	2.1
BMNH 1960.3.1.45-60	St. Helena	♀	32.2	24.8	6.2	2.2	1.9	9.3	12.4	24.2	16.8	23.3	4.7
BMNH 1960.3.1.45-60	St. Helena	♀	33.0	26.0	6.7	3.3	2.4	10.0	13.6	24.5	16.7	23.0	3.3
BMNH 1960.3.1.45-60	St. Helena	♀	36.9	24.4	6.8	3.3	2.4	10.0	14.1	24.9	16.8	23.0	4.1
MNHN A2025	Ascencion	♀	37.4	24.6	6.7	4.5	2.4	10.2	13.6	24.6	16.0	24.1	5.3
BMNH 1960.3.1.45-60	St. Helena	♂	39.2	24.0	6.4	4.1	2.6	10.2	12.5	23.0	16.8	24.2	4.1
BMNH 1960.3.1.45-60	St. Helena	♂	40.8	24.8	6.1	4.7	2.5	9.8	12.5	23.5	17.2	22.8	3.9
BMNH 1960.3.1.45-60	St. Helena	♂	43.0	23.2	6.0	4.2	2.1	8.6	13.5	23.5	17.2	22.1	4.2
BMNH 1960.3.1.45-60	St. Helena	♀	43.0	24.2	6.0	4.0	1.2	8.8	12.1	24.9	16.7	24.0	4.7
BMNH 1960.3.1.45-60	St. Helena	♂	43.1	24.4	5.6	4.2	2.6	9.3	12.5	24.4	16.2	23.2	2.8
MNHN A2025	Ascencion	♀	45.1	24.4	6.0	3.3	2.4	8.6	15.1	23.0	15.5	22.2	4.9
BMNH 1960.3.1.45-60	St. Helena	♂	46.4	24.2	6.7	3.9	2.6	9.5	13.6	21.8	15.7	21.9	4.5
MNHN A2025	Ascencion	♂	47.5	24.2	5.9	3.8	2.1	8.9	14.3	23.0	13.7	21.5	3.4
BMNH 1935.5.2.25-30	Ascencion	♀	49.9	24.1	6.0	3.2	2.6	8.4	16.0	23.6	15.4	25.1	5.4
BMNH 1960.3.1.45-60	St. Helena	♀	50.7	23.7	6.1	3.5	2.0	9.5	13.8	25.0	16.4	24.5	3.4
BMNH 1960.3.1.45-60	St. Helena	♀	52.0	24.0	5.8	2.9	1.9	9.6	13.4	21.5	16.1	22.1	4.8
BMNH 1960.3.1.45-60	St. Helena	♀	54.8	23.0	5.8	3.3	3.3	9.5	13.0	23.5	15.7	21.9	5.5
MNHN A2026	Ascencion	♂	57.1	24.4	5.3	3.0	2.3	8.8	13.0	23.5	14.5	23.6	5.1
MNHN A2025[1]	Ascencion	♂	60.5	23.8	5.0	3.0	2.5	8.4	13.9	21.6	13.9	21.5	4.5

[1] Lectotype of *Salarias textilis*

Relationships.—*Entomacrodus textilis* is a member of the *E. nigricans* species group. Of this group the Atlantic species appear to be most closely interrelated (see "Relationships" under *E. nigricans*). *Entomacrodus textilis* differs from its geographically closest relative, *E. cadenati*, in having the stripes on the upper lip solid and in having a well-developed subquadrate humeral blotch. *Entomacrodus cadenati* frequently has as the most prominent markings on each side of the body two rectangular humeral blotches (comprising the anterior pair of body bands). The anterior of these blotches is much more prominent than marks in a comparable position on *E. textilis*. The posterior of these two blotches in *E. cadenati* is never as prominent (or large) or uniformly dark as that in *E. textilis*. The peculiar dark markings behind the eye in *E. cadenati* are not found in *E. textilis*. *E. textilis* differs: from *E. vomerinus*, in having typically lower dorsal, anal, vertebral, and gill-raker counts, and in having a humeral blotch; from *E. nigricans*, in having a humeral blotch, in not having a prominent spot just posterior to the eye, and in having the pores of the lateral line terminating farther posteriorly; from *E. chiostictus* and *E. sealei*, in having a humeral blotch, a proportionately shorter supraorbital cirrus, and in almost never having any paired pores included in the preopercular series; from *E. chiostictus*, in having fewer lip stripes; and from *E. sealei*, in having a shorter nuchal cirrus and third dorsal spine (in specimens over 39 mm SL), fewer predorsal commissural pores at any particular size, and in having the dark upper lip stripes narrower than the pale interspaces; and from *E. corneliae*, in having a humeral blotch and lip stripes and in lacking two dark stripes on the head behind the eye and pairs or multiples of pores in the preopercular series. It can be differentiated from *E. caudofasciatus* by the characters given in key couplet 10.

Distribution (fig. 9).—*E. textilis* is endemic to Ascension and St. Helena Islands. These two islands have a high proportion of endemics among their fish fauna (24.3 percent—Cadenat and Marchal, 1963).

Material.—Ascension Island: BMNH 1881.11.10.3, 1908.7.24.23–4, 1935.5.2.25–30, MNHN A2025 (lectotype of *S. textilis*), A2026, B2524; St. Helena Island: BMNH 1946.5.23.10–12, 1960.3.1.45–60, 1964.2.3.1–7, 1964.2.3.8–28, USNM 42318.

Entomacrodus cadenati Springer

Plate 23

Entomacrodus cadenati Springer, 1966, Atlantide Rep., no. 9, pp. 59–61, pl. 6 [Gorée-Senegal].

Description.—Segmented dorsal fin rays 14–16 (15 in 77 percent of specimens); segmented anal fin rays 15–17 (16 in 63 percent of specimens); posteriormost anal pterygiophore supporting 1 or 2 external elements (supporting 2 in 75 percent of specimens); total gill-rakers on first arch 17–22 (17–20 in 90 percent of specimens); pseudobranchial filaments 5–7 (6 in 78 percent of specimens), not increasing in number with increase in SL; vertebrae 34; supraorbital cirri 1–15, number increasing with increase in SL (table 57), main or longest supraorbital cirrus with most branches mesially, commonly with several lateral branches; nape with 1 cirrus on each side; predorsal commissural pores 3–16 (rarely more than 11), number increasing with increase in SL (table 58); preopercular series of pores with all positions with simple pores; 1 pore before each anterior nostril; lateral line pores terminating on side in area below and between dorsal fin spines 13 and dorsal fin ray 10 (usually between dorsal rays 3–6); ventral margin of upper lip crenulate on lateral one-third, entire on middle third; lip crenulae usually numbering 7–11 on a side.

Proportional measurements: See tables 3, 4, and 59.

No males with the skin of the anal spines and rays modified into fleshy rugose pads were seen. A few males showed incipient development of these modifications. It is presumed that all males available were immature. The largest male examined was 68.8 mm SL and the largest female 66.9 mm SL. Males and females occurred with about relative equal frequency in all size classes. The smallest specimen seen was 17.5 mm SL. No ophioblennius stages were seen.

COLOR PATTERN OF PRESERVED SPECIMENS.—In specimens with what appears to be the most developed pattern there are 6½ to 7 pairs of irregular dark bands on the sides of the body (except for the anterior and posteriormost pairs, there were no fusions between the midportions of the members of a pair). The anteriormost pair of bands, over the pectoral base and axil, is the shortest and frequently the darkest of the bands. Occasionally the anteriormost band pair

TABLE 57.—Frequency distribution of number of supraorbital cirri of left eye of specimens of *Entomacrodus cadenati* arranged by SL classes (in mm)

Classes	Number of cirri															Average
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
15-19.9	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0
20	-	1	2	1	1	-	-	-	-	-	-	-	-	-	-	3.4
25	-	-	-	2	1	2	-	-	-	-	-	-	-	-	-	5.0
30	-	-	1	5	3	-	1	1	-	-	-	1	-	-	-	5.4
35	-	-	-	1	-	1	5	1	1	-	-	-	-	-	-	6.9
40	-	-	-	-	1	2	2	-	-	-	-	-	-	-	-	6.2
45	-	-	-	-	1	2	1	2	1	2	-	-	-	-	-	7.7
50	-	-	-	-	1	1	4	3	2	1	-	-	-	-	-	7.6
55	-	-	-	-	-	-	2	4	4	1	1	-	1	-	2	9.7
60	-	-	-	-	-	-	3	-	1	2	2	1	-	-	1	9.9
65-69.9	-	-	-	-	-	-	-	2	-	-	1	-	1	1	1	11.5
75-79.9	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-

forms a small double blotch or, when fused, a single blotch, which is the most obvious mark on the body. The composition of the body bands is variable; sometimes each member of a pair is in three vertically arranged portions, either connected with or detached from each other. The middle of these three portions is usually the darkest, and the ventral portion the palest (the ventral portion fails to reach the anal fin base). The dorsal portions of the bands reach to and enter the dorsal fin taking a posterodorsal direction, sometimes reaching the distal dusky margin of the fin. The area between the bands on the body may be pale or dusky, usually with some short, slender, dark markings, which may extend dorsally to the dorsal fin base but usually do not extend ventrally much lower than the middle of the side. The dorsal portions of the body below the dorsal fin, as far posteriorly as the anterior four soft rays, usually is marked with a number of tiny dark spots. These spots usually appear along the margins of the bands. The head is strikingly marked with a J- or U-shaped dark area behind the eye (see pl. 23*a*, *d*) which is separated by a pale area from the eye. The area between the arms of the J or U may be pale or dusky, and the entire mark extends dorsoposteriorly from behind the eye across the top of the head, where it may join with the same mark from the other side. A dark, sometimes interrupted stripe begins at the margin of the upper lip, extends to the ventroposterior margin of the orbit, where the stripe is interrupted by the eye, and begins again at the dorsoposterior margin of the eye, where it may join across the top of the head with a similar stripe from the other side. There are irregular dusky areas and numerous tiny dark spots on the sides of the head. The upper lip has numerous tiny dark spots (comprised of groups of melanophores) that are frequently

TABLE 58.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus cadenati* arranged by SL classes (in mm)

Classes	Number of pores														
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Average
15-19.9	2	-	-	-	-	-	-	-	-	-	-	-	-	-	3.0
20	4	1	-	-	-	-	-	-	-	-	-	-	-	-	3.2
25	1	-	1	1	2	-	-	-	-	-	-	-	-	-	5.6
30	3	-	2	3	1	3	-	-	-	-	-	-	-	-	5.7
35	1	-	-	2	4	1	-	-	-	-	-	-	-	-	6.4
40	-	-	-	2	2	1	-	1	-	-	-	-	-	-	7.3
45	-	-	3	-	1	1	2	-	-	-	-	-	-	-	6.8
50	-	-	1	4	2	2	1	2	-	-	-	-	-	-	7.3
55	-	1	-	1	4	2	1	2	3	1	-	-	-	-	8.5
60	-	-	-	1	2	2	1	2	-	-	-	-	-	2	9.7
65-69.9	-	-	1	1	1	1	1	-	-	1	-	-	-	-	7.8
75-79.9	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-

aligned in 7–10 more or less vertical rows corresponding to the lip stripes of *E. nigricans* and *E. textilis*. The underside of the head may bear several dark or dusky chevrons.

The anal fin membrane is uniformly dusky anteriorly, but the duskiness becomes separated posteriorly into two portions by a pale diffuse stripe. The anal rays are dark distally but become paler proximally, except for a slight, diffusely pale-dusky sub-basal stripe. The caudal fin bears three to six irregular dark bands, depending on the length of the specimen (the longer the specimen, the more the bands). The pectoral is dusky, though much paler dorsally; there may be on the fleshy pectoral base one or a few dark blotches separated by a pale cresentic mark. A dusky area, also on the fleshy pectoral base, is proximal to the pale area. The pelvic fins vary from pale to dusky.

In general, males are more uniformly colored than females, but there are exceptions.

Relationships.—*Entomacrodus cadenati* is a member of the *E. nigricans* species group. Of this group the Atlantic species appear

TABLE 59.--Proportional dimensions as percent SL of specimens of *Entomacrodus cadenati* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL
MNHN 1965-706	Senegal	♂	28.4	25.0	7.0	2.5	2.8	9.9	12.7	26.8	15.8	23.2
MNHN 1965-706	Senegal	♂	30.4	23.7	7.3	3.0	2.0	9.6	13.5	25.6	17.1	24.7
USNM 199481	Senegal	♂	34.2	24.0	6.4	2.9	2.0	9.4	13.2	22.5	17.0	24.6
MNHN 1965-706	Senegal	♂	34.7	25.1	6.9	3.5	1.4	10.1	12.1	23.6	16.1	23.0
MNHN 1965-706	Senegal	♀	37.2	23.4	6.7	3.0	2.2	9.1	12.6	24.2	15.3	24.2
MNHN 1965-706	Senegal	♀	38.2	24.1	5.7	2.6	1.6	9.7	11.0	24.6	15.7	22.8
MNHN 1965-706	Senegal	♂	39.0	23.8	6.2	2.6	1.8	10.2	12.8	24.4	15.1	24.1
USNM 199481	Senegal	♂	41.5	23.4	5.5	2.6	1.4	9.6	12.0	23.8	16.1	21.7
MNHN 1965-706	Senegal	♀	45.1	24.4	6.8	3.1	2.2	10.0	14.0	26.2	14.9	26.0
MNHN 1965-706	Senegal	♀	49.5	24.4	5.5	3.0	2.6	10.1	13.3	23.8	15.8	22.8
USNM 199481	Senegal	♀	50.0	23.8	6.0	3.0	1.4	9.8	12.0	25.2	15.0	23.0
USNM 199481	Senegal	♀	52.8	22.9	5.5	3.0	1.5	9.5	12.7	23.7	14.2	21.4
MNHN 1965-706	Senegal	♀	56.7	25.0	6.0	3.4	1.6	10.0	12.9	24.8	14.3	22.8
USNM 199481	Senegal	♀	58.0	23.4	5.2	2.2	1.9	9.3	12.8	24.4	14.5	22.1
USNM 199481	Senegal	♂	61.8	21.7	5.3	2.6	1.6	9.4	12.6	24.7	14.9	22.7
MNHN 1965-705	Senegal[1]	♂	64.0	23.8	5.5	3.1	1.9	9.5	13.4	23.2	14.4	23.0
MNHN 1965-706	Senegal	♀	64.4	23.9	5.9	2.3	1.6	10.4	14.1	25.6	14.4	22.6
USNM 199481	Senegal	♂	68.8	23.0	5.1	2.9	1.7	9.9	14.5	24.2	12.8	23.4

[1] Holotype of *Entomacrodus cadenati*

to be most closely interrelated (see "Relationships" under *E. nigricans* and *E. chiostictus*).

Entomacrodus cadenati differs: from all its closest relatives, in having numerous dark spots on the upper lip (arranged in more or less vertical rows) and in the peculiar well-developed dark marks behind its eye; from its geographically closest relative, *E. textilis*, in not having a relatively large, well-developed subquadrate blotch in the humeral region; from *E. vomerinus*, in having fewer segmented dorsal and anal fin rays and vertebrae; from *E. chiostictus*, *E. caudofasciatus*, and *E. seali*, in its usually shorter supraorbital and nuchal cirri; and from the latter species and *E. corneliae* (and frequently *E. chiostictus*), in having no paired pores in the preopercular series. *E. cadenati* has fewer predorsal commissural pores at any particular size than does *E. sealei*, and more gill-rakers than *E. caudofasciatus*.

Remarks.—There is a tendency for males to have a higher average number of segmented dorsal fin rays than females. Of 30 males examined, 2 had 14 rays, 26 had 15 rays, and 2 had 16 rays. Of 47 females examined, 14 had 14 rays and 33 had 15 rays. There was no evidence of sexual dimorphism in other meristic characters.

Distribution (fig. 9).—*Entomacrodus cadenati* is known only from the eastern Atlantic Ocean from the Cape Verde Islands to the Ile de Roumé, French Guinea. According to J. Cadenat (in litt.), the species is characteristic of the wave-battered rocky shores of Goreé, Senegal.

Material.—Cape Verde Islands, Ile de Sao Thiago: USNM 199623; Ile de Sal: IFAN (no number); Senegal, Goreé: MNHN 1965–705 (holotype of *E. cadenati*), 1965–706, USNM 199481; French Guinea, Ile de Roumé: IRSN 401; Liberia, Robertsport: RMNH 5323; Ghana, Takoradi: CU 44175 44176; French Congo, Bata: MNHN 92–24.

Entomacrodus nigricans Gill

Plate 24

Entomacrodus nigricans Gill, 1859, Proc. Acad. Nat. Sci. Philadelphia, vol. 11, p. 168 [near Bridgetown, Barbados].

Salarias margaritaceus Poey, 1860, Memorias sobre la historia natural de la Isla de Cuba, vol. 2, pp. 289–290 [Cuba].

Entomacrodus decoratus Poey, 1868, Reperterio fisico-natural de la Isla de Cuba, vol. 2, p. 398 [Cuba].

Description.—Segmented dorsal fin rays 13–16 (14 or 15 in all but 2 specimens); segmented anal fin rays 14–17 (89 percent with 16); posteriormost anal pterygiophore supporting 1 or 2 external elements (supporting 2 in 90 percent of specimens); total gill-rakers on first arch 14–20 (15–18 in 86 percent of specimens); pseudobranchial filaments 5–7 (6 in 80 percent of specimens, number not increasing with increase in SL); vertebrae 33–35 (34 in 95 percent of specimens); supraorbital cirri 1–11, number increasing with increase in SL (table

60); main or longest supraorbital cirrus with most branches mesially, not uncommonly with a short lateral branch; nape with 1 cirrus on each side; predorsal commissural pores 2–23 (rarely more than 17), number increasing with increase in SL (table 61); preopercular series of pores with all positions with simple pores (93 percent of specimens, including 1 or 2 pairs of pores in series in 6 and 1 percent of specimens respectively; fourth pore of series most frequent paired pore); 1 pore before each anterior nostril; lateral line pores terminating on side in area below and between dorsal fin spine 10 and dorsal soft ray 2 (usually between spine 11 and ray 1); ventral margin of upper lip crenulate on lateral thirds, entire on middle third; lip crenulae usually numbering 6–11 on each side.

Proportional measurements: See tables 3, 4, and 62.

Males develop fleshy, rugose modifications of the skin of the anal spines and the anterior first to fourth anal rays (pl. 24*f*). If one considers males with these modifications to be mature, the smallest mature male examined was 34 mm SL. Mature and immature males may occur in the same collection and in these collections immature males may be as much as 22 mm SL longer than mature males.

Largest specimen examined, 62.6 mm SL, a size achieved by both males and females. There does not appear to be any difference in proportional numbers of males and females in any given size class, although in total numbers males outnumber females. The smallest nonophioblennius stage and the largest ophioblennius stage examined were both 15.5 mm SL and occurred in the same collection, indicating that transformation occurs at about this size.

The ophioblennius larval stage of *E. nigricans* is characterized by the presence of a pair of posterolaterally directed canines anteriorly on each side of the lower jaw. The more median and anterior canine on each side is about one-third the size of the more posterior canine.

TABLE 60.--Frequency distribution of number of supraorbital cirri of left eye of specimens of *Entomacrodus nigricans* arranged by SL classes (in mm)

Classes	Number of cirri 1	2	3	4	5	6	7	8	9	10	11	Average
15-19.9	20	4	4	1	-	-	-	-	-	-	-	1.5
20	1	6	16	7	-	1	-	-	-	-	-	3.1
25	-	-	5	29	13	1	-	-	-	-	-	4.2
30	-	-	11	21	22	7	2	-	-	-	-	4.5
35	-	-	7	18	30	14	3	1	-	-	-	4.9
40	-	1	1	14	23	18	5	3	2	-	-	5.4
45	-	-	-	6	15	17	1	1	-	1	-	5.5
50	-	-	1	3	7	7	6	2	-	1	1	6.1
55	-	-	-	1	3	2	-	1	-	-	-	5.6
60	-	-	-	-	-	-	1	-	2	-	1	9.0

The smaller canines are either lost first during transformation or fail to develop in some specimens, as several specimens had only the larger canines. The posterolaterally directed canines occur internal to the salarine type dentition. In some specimens the posterior recurved canine of the adult (not included in the canines just discussed) is just noticeable; vomerine teeth have not been noted in the ophioblennius stage. The ophioblennius stage specimens are either uniformly pale or have some indications of paired vertical stripes on the sides of the body.

Color pattern of preserved specimens.—In specimens with the most developed color pattern there are 6 to 6½ pairs of dark bands on the sides of the body (fusion between the midportion of the members of a pair, as in *E. chiostictus,* were not noted). The posteriormost two pairs of body bands are usually less intense than the others and may be absent. The anteriormost half-pair band is frequently broken into irregular markings or may be absent altogether. The interspaces between the bands may be marked with pale or pearly white spots. The anterodorsal portion of the sides, in the region below the spinous dorsal, frequently bears a variable number of small dark spots.

The head is pale to deep dusky with a dark spot just posterior to the eye. The upper lip of most specimens bears 7–10 dark, narrow stripes alternating with broader, paler bands. The basic number of stripes is seven, but three of these stripes may divide, usually dorsally only, and be interpreted as two stripes each. The stripes may be fewer in number in small or occasional specimens. The underside of the head usually exhibits a pattern of dark chevrons, which are extensions from some of the lip stripes.

Portions of the dorsal fin above and between the body bands are marked with a variable number of diffuse dusky spots. These spots sometimes coalesce, especially on the posterior soft dorsal fin, and the markings thus formed alternate with pale spots. The anal fin is variably dusky, always darker and more extensively pigmented in

TABLE 61.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus nigricans* arranged by SL classes (in mm)

Classes	Number of pores																						
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Average
15-19.9	1	16	2	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.4
20	-	4	3	5	2	7	3	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-	6.1
25	-	1	-	7	9	5	7	6	11	4	2	1	1	-	1	-	-	-	-	-	-	-	8.3
30	-	-	-	2	4	7	9	13	10	5	3	4	1	-	-	1	-	-	-	-	-	-	9.2
35	-	-	-	1	4	6	10	14	12	5	13	5	3	3	1	-	-	-	-	-	-	-	10.1
40	-	-	-	-	-	1	4	12	18	10	11	6	4	2	2	-	1	-	1	-	-	-	11.2
45	-	-	-	-	2	4	3	7	5	5	7	4	1	2	1	1	1	1	-	-	-	-	11.0
50	-	-	-	-	-	-	3	2	4	3	1	5	5	1	-	-	-	-	1	-	1	1	12.7
55	-	-	-	-	-	-	-	-	1	3	1	1	-	-	1	-	-	-	-	-	-	-	12.0
60	-	-	-	-	-	-	-	-	1	1	-	-	-	1	-	1	-	-	-	-	-	-	13.2

TABLE 62.--Proportional dimensions as percent SL of specimens of *Entomacrodus nigricans* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL
USNM 197324	Serrana Bank	♀	25.1	24.3	8.0	2.4	1.6	10.0	13.5	23.9	15.5	22.7
USNM 195755	Venezuela	♀	27.5	24.7	7.3	2.5	2.2	10.9	12.4	25.1	14.2	23.3
UF 8866	Bahamas	♂	31.1	25.4	6.8	2.9	2.6	10.6	13.5	24.1	17.7	24.1
LACM 5017	Pedro Cay	♀	31.5	24.4	7.0	2.2	2.2	9.8	13.0	23.8	17.5	21.6
UF 9606	Bahamas	♂	32.1	24.0	6.9	2.5	2.2	10.0	14.6	23.4	16.8	23.4
USNM 192201	Cuba	♂	33.2	23.5	6.3	3.0	1.5	9.9	13.3	23.2	15.0	22.6
USNM 197324	Serrana Bank	♂	34.0	24.4	6.5	2.6	1.8	10.3	13.2	21.5	15.3	22.3
USNM 192201	Cuba	♀	35.0	22.3	6.3	2.9	1.7	10.0	13.1	22.8	16.3	22.9
USNM 195754	Venezuela	♂	35.6	22.8	7.0	2.8	2.8	11.2	14.0	23.0	16.9	24.4
USNM 195755	Venezuela	♀	37.1	23.2	6.7	2.7	1.6	10.8	13.5	24.2	17.5	22.9
USNM 197668	Bermuda	♂	37.8	24.1	6.6	2.6	1.8	10.6	13.0	24.3	_	23.3
UF 9606	Bahamas	♂	39.6	23.5	6.3	3.3	2.5	9.1	13.9	22.5	14.9	23.7
LACM 5017	Pedro Cay	♀	39.8	23.6	6.5	2.8	2.0	11.0	13.6	23.6	16.3	22.1
UF 8866	Bahamas	♂	41.8	22.7	6.5	3.3	1.4	9.3	14.8	23.2	15.8	23.4
USNM 192201	Cuba	♀	42.0	22.1	6.2	2.4	1.2	10.2	13.1	23.8	15.2	23.3
USNM 197324	Serrana Bank	♂	43.3	23.3	6.5	3.7	1.8	11.1	15.0	21.7	15.0	25.0
UF 9606	Bahamas	♀	43.8	24.2	6.4	2.3	2.0	10.7	14.4	22.8	15.3	23.3
USNM 192201	Cuba	♀	44.0	25.0	6.6	2.7	1.8	10.2	13.4	23.9	15.9	22.3
USNM 178738	Bermuda	♀	44.8	22.8	6.0	2.5	1.6	10.0	13.6	25.7	16.5	24.3
USNM 195752	Venezuela	♂	45.0	22.2	5.8	3.1	1.3	9.5	13.8	21.1	14.0	22.2
USNM 192201	Cuba	♀	45.4	23.1	5.9	2.2	1.5	10.4	13.2	22.9	16.5	23.1
USNM 195755	Venezuela	♂	46.2	23.2	6.1	2.8	1.9	9.5	13.8	23.8	15.1	21.9
LACM 5013	Jamaica	♀	46.7	23.4	5.8	2.6	2.4	9.8	14.1	22.7	14.4	22.3
USNM 197324	Serrana Bank	♂	48.5	22.9	5.8	3.3	1.4	9.7	13.8	21.6	15.0	22.7
USNM 192201	Cuba	♀	48.6	23.9	5.8	2.1	1.6	10.9	13.4	21.8	14.4	23.0
USNM 178738	Bermuda	♀	49.2	23.0	5.7	2.8	2.1	9.1	14.2	24.4	16.2	23.2
ANSP 81749	Bahamas	♂	50.0	22.6	5.8	2.4	2.0	9.8	14.0	21.2	13.0	22.0
USNM 178738	Bermuda	♂	50.2	23.1	6.0	2.8	1.6	10.0	14.9	25.1	15.9	23.3
USNM 178738	Bermuda	♂	51.8	22.2	5.8	2.2	1.5	7.7	13.9	21.6	14.5	22.8
LACM 5021	Morant Cay	♀	53.0	23.0	5.7	2.6	1.9	10.6	12.8	23.2	14.3	23.2
USNM 197324	Serrana Bank	♂	56.1	22.8	5.3	3.2	1.4	9.6	14.3	20.9	14.3	22.6
USNM 195753	Venezuela	♀	58.3	22.6	5.5	2.1	1.4	9.8	13.7	23.3	13.7	22.6
USNM 178738	Bermuda	♂	59.8	22.1	5.3	3.2	2.2	9.4	13.0	23.4	14.7	21.7
USNM 197324	Serrana Bank	♀	61.9	24.2	5.5	2.4	1.9	8.7	13.1	22.6	15.5	21.8
USNM 178738	Bermuda	♂	62.6	22.0	5.1	3.2	1.6	9.6	13.3	24.0	14.4	22.7

males than females from the same collection. A few diffuse pale spots occur posteriorly on the anal fin. There are three to six, usually five, irregular dusky bands on the caudal, darkest ventrally and palest dorsoposteriorly. The pectoral fin is pale to dusky, darker basally where a dark crescentic stripe or some diffuse spots may occur. A dusky stripe is usually present on the pectoral base. The pelvic fins are pale.

Life coloration.—(Described from an immature male of adult size from Dominica, B.W.I.) The nasal and orbital cirri were light coral pink; the lip stripes light olive brown; a dark brown spot with a bright white posterior margin was present below the eye; the white margin was followed posteriorly by a pale area. There were dark brown spots posterior to the eye and on the anterodorsal area of the body of the same color as the spot behind the eye. The paired body bands were chocolate brown, much paler on the ventral portion of the body. Bright white spots were present in pale interspaces between the bands on the body. The interspaces were pale olive yellow dorsally and extended onto the ventral portion of the dorsal fin. This same olive-yellow color occurred distally on the soft dorsal. Chocolate-brown marks were present on the caudal fin, pectoral base, and dorsal fin. The anal rays graded distally from olive yellow to dusky; the pectorals were dusky and the pelvics, pale.

Geographic variation.—There appears to be little variation between collections from diverse localities, except possibly those from Bermuda as compared with collections from other localities. Specimens from the Caribbean, Florida, and the Bahamas show essentially a one-to-one ratio of specimens with 14 and 15 dorsal rays. Of the 53 Bermuda specimens counted, 12 had 14 rays, 40 had 15 rays, and 1 had 16 rays (the only specimen with this count, of over 500 examined of the species).

Nomenclature.—*Salarias margaritaceus* Poey was described without comparison. The holotype is a normal adult of *E. nigricans*. In the jar containing the holotype (MCZ 12513) are three specimens. The largest of these, 57 mm total length, is more than 10 mm larger than the next size (the largest is a female, the two smaller, males). Poey gave the total length of the holotype as 60 mm; the largest specimen in the bottle must therefore be considered the holotype with the difference in size noted accounted for by shrinkage.

I have been unable to locate type material of *Entomacrodus decoratus* Poey (nor did Longley, *in* Longley and Hildebrand, 1941). The description clearly indicates a salarine blenniid. The only other salarine in the Caribbean area, besides *E. nigricans*, is *Ophioblennius atlanticus macclurei* (Silvester). The dorsal fin formula given by Poey, XII,19, could apply only to *O. a. macclurei;* the anal and pectoral fin formulae, 15 and 14 respectively, could apply only to *E. nigricans.* The color description is applicable to *E. nigricans* and positively excludes *O. a. macclurei.* I therefore place *E. decoratus* in synonymy with *E. nigricans* and ascribe Poey's dorsal fin formula to an error.

RELATIONSHIPS.—*Entomacrodus nigricans* is most closely related to the Atlantic Ocean species *E. cadenati, E. textilis,* and *E. vomerinus* and the Pacific Ocean species *E. caudofasciatus* (also Indian Ocean), *E. sealei, E. corneliae,* and *E. chiostictus* (the *E. nigricans* species group) (see "Relationships" under *E. chiostictus*). All these species have the crenulations of the upper lip predominantly restricted to the lips' lateral thirds. Of this group the Atlantic species appear to be most closely interrelated. I base this conclusion on certain similarities of color pattern (the basic lip pattern of 7–10 dark stripes), relative lengths of the supraorbital cirri, and the usual presence of only simple pores in the preopercular series. *Entomacrodus nigricans* differs from *E. cadenati* in having the lip stripes as solid lines, whereas *E. cadenati* has the stripes as a series of more or less vertically arranged spots. The peculiar U-shaped black marking behind the eye in *E. cadenati* also distinguishes that species from *E. nigricans,* where the marking is not present. The lateral line pores of *E. cadenati* and *E. textilis* usually terminate farther posteriorly than those of *E. nigricans. E. nigricans* is further distinguished from *E. textilis* in that *E. nigricans* lacks the black humeral blotch of the latter. It differs from *E. vomerinus* in having typically fewer dorsal and anal fin rays, fewer gill-rakers, and vertebrae, and, at any given size, usually more predorsal commissural pores. None of the specimens of *E. vomerinus* examined had any dark spots on the sides in the region below the spinous dorsal as found in *E. nigricans.* The lip stripes in *E. vomerinus* are usually not so obvious as those in *nigricans.*

Many recent writers have considered all four Atlantic species of *Entomacrodus* that I recognize as conspecific, under the specific name *textilis* (combined with *Alticus, Rupiscartes, Salarichthys,* or *Entomacrodus*). Although the differences between the species as conceived here are not great, my reasons for recognizing them as distinct are as follows: On the basis of color pattern and/or meristic characters, four distinct, homogeneous groupings (populations) of specimens are discernible; each of these four groupings is restricted to a particular geographic range well separated from that of any of the others; the ranges, except for the Ascension-St. Helena area, are extensive, covering several thousand miles of latitude and/or longitude, which indicates long term stability of the populations. The sum of these reasons implies isolation and fixation of subsequent divergences of each population. It is assumed that the immense distances separating the populations combined with a probable short pelagic larval stage are the bases for continued separation. The present distribution of the four species would favor a continental drift theory, wherein an initially homogeneous single population was gradually broken up as shorelines separated.

Distribution (fig. 9).—*Entomacrodus nigricans* is restricted to the rocky shores of the tropical-subtropical western Atlantic north of the equator. It is found only at depths of a few centimeters to a meter and, as noted by Breder (1948, as *Salarichthys textilis*), is a common tide pool form. Specimens that I collected on the bottom in deeper water (to 5 meters) were actually residents on rocks near the surface of the water. The specimens had become incapacitated by rotenone and had fallen to the bottom. I mention this because I have seen collection data for *Entomacrodus* reporting occurrences as deep as 7 meters; I doubt that any species of the genus occurs naturally at depths of much more than 1 or 2 meters.

Material.—Bermuda: USNM 21936, 21944, 23802, 178367, 178738, 178834, 178967, 178968, 178969, 178970, 197668; south Florida: UMML 3011, 5704, 6647, 9872, 9939, USNM 116832; Bahamas: ANSP 81739, 81742, 81749, 81752, UF 8866, 8867, 8868, 8869, 8870, 8871, 9606; Cuba: MCZ 12513 (holotype of *Salarias margaritaceus*), USNM 37534, 192201; Haiti: CNHM 72334, 72335; Dominican Republic: BMNH 1938.6.20.9; Puerto Rico: UMML 1776, UPR 130, 381, 724, 842, USNM 117410; Virgin Islands: UMML 2471, 3735, 5457, 6223; St. Martins: UMML 6480; St. Eustatius: RMNH 18748; Antigua: USNM 178978; Dominica: USNM 198279, 198280; Union Island: USNM 178424; Barbados: BMNH 1922.3.26.14, SU 32036, 32037, 37304, USNM 34625 (holotype of *E. nigricans*), 86745, 86746, 86749; Los Roques (Venezuela): USNM 195752, 195753, 195754, 195755; Venezuela: USNM 259156 F-1; Bonaire: RMNH 23579; Aruba: RMNH 23540, 23586; Curacao: RMNH 9820; Panama (Atlantic): MCZ 41492; Costa Rica: CNHM 72359, LACM 2557; British Honduras: UMML 9981; Yucatan: UCC (no number), UMML 9213, 9363; Cayman Islands: BMNH 1939.5.12.175; Jamaica: CNHM 72326, 72327, LACM 5013, 5017, 5021; Serrana Bank: USNM 197324.

***Entomacrodus caudofasciatus* (Regan)**

Plates 25, 26, 27

Salarias caudofasciatus Regan, 1909, Proc. Zool. Soc. London, p. 405 [Christmas Island, Indian Ocean].

Salarias rarotongensis Whitley, 1965, Australian Zool., vol. 13, no. 2, p. 118 [Rarotonga, Cook Islands].

Description.—Segmented dorsal fin rays 14–16 (table 63); segmented anal fin rays 15–17 (table 63); posteriormost anal pterygiophore supporting 1 or 2 external elements (supporting 2 in 67–100 percent of specimens depending on population); total gill-rakers on first arch 13–18 (table 63); pseudobranchial filaments 5–8 (usually 6 or 7, number not increasing with increase in SL); vertebrae 33–35 (34 in 93 percent of specimens); supraorbital cirri 1–8, increasing in number with increase in SL (table 64); main or longest supraorbital cirrus with all branches mesially (2 specimens only had 1 branch laterally); nape with 1 cirrus on each side (2 on one side in 1 specimen); predorsal commissural pores 4–25 (number increasing with increase in SL, table 65); preopercular series of pores with all positions with simple pores (4 specimens, of 145 examined, each with 1 pair of pores included in series); lateral line pores terminating on side in area below and between dorsal fin spine 8 and dorsal soft ray 5; ventral margin of upper lip mainly crenulate on lateral thirds, entire to very weakly crenulate on middle third; main (lateral) crenulae usually numbering 7–11 on each side.

Proportional measurements: See tables 3, 4, and 66, and "Discussion."

Males develop fleshy rugose modifications of the skin of the anal spines and anterior first to third anal rays. If one considers males with these modifications to be mature, the smallest mature male examined was 29.6 mm SL (Swains Island). Mature and immature males may occur in the same collection and in these collections immature males may be as much as 14 mm longer than mature males.

Largest specimen examined, a male, 54.8 mm SL (Tongatapu); largest female was approximately 47.8 mm SL (Tongatapu). Males and females occurred with about equal frequency in collections except for the Swains Island collection, in which males greatly outnumbered females. The smallest specimen examined, 17.7 mm, was not an ophioblennius larva. It had a humeral blotch and vomerine teeth but no canine teeth.

TABLE 63.--Frequency distribution of number of segmented dorsal and anal rays and gill-rakers of specimens of *Entomacrodus caudofasciatus* arranged geographically

Locales	Dorsal rays			Anal rays			Gill-rakers					
	14	15	16	15	16	17	13	14	15	16	17	18
Indian Ocean	-	3	-	-	3	-	-	-	-	1	1	-
Poulo Cécir de Mer (S. China Sea)	-	4	-	-	4	-	-	-	-	2	2	-
Philippines	6	7	-	-	8	4	3	4	1	1	-	-
Palaus	-	1	-	1	-	-	-	-	-	1	-	-
Waigeo	-	1	-	-	-	1	-	-	1	-	-	-
New Britain	-	6	-	-	1	5	1	2	2	1	-	-
New Georgia	-	2	-	-	-	2	-	1	-	1	-	-
McKean	-	6	-	-	5	1	1	1	2	1	-	1
Swains	3	28	-	1	30	-	-	4	7	9	3	-
Tutuila	-	1	-	-	-	1	-	-	-	-	-	-
Tau	-	2	1	-	2	1	-	-	3	-	-	-
Tongatapu	-	39	10	-	31	15	2	3	13	14	8	2
Rarotonga	2	6	-	-	7	1	-	1	1	1	-	-
Tahiti	-	1	-	-	-	1	-	1	-	-	-	-
Makatea	-	15	1	-	14	2	-	5	4	6	-	-
Raroia	1	-	-	-	1	-	-	-	1	-	-	-

Color pattern of preserved material.—There are several different types of color pattern found in this species. By and large, these types are associated with geographic destribution, with no two types occurring in the same area. All specimens except those from Rarotonga, Tahiti, Makatea, and Raroia, are characterized by having a dark humeral blotch on the body. The nature of this blotch is more or less characteristic within a given geographic area.

A tentative grouping of specimens on the the basis of similarity of color pattern is as follows:

1. Indian Ocean: A relatively large, dark humeral blotch is present. The bands on the body are relatively well developed. In the holotype of *E. caudofasciatus*, there appear to be pearly white spots in irregular longitudinal rows. There is no dark spotting on the body. There may be present indistinct or irregular dark or dusky stripes or bands on the upper lip.

2. Philippine Islands and the Palaus (pl. 26): A relatively small humeral blotch is present and there is usually present a much smaller and paler secondary humeral mark separated by an immaculate area immediately anterior to the main (largest) humeral blotch. The bands on the body are relatively well developed. There are no white spots on the body (although these might have been present in fresh material), and dark spots, if present, are paler than the humeral blotch and not easily distinguished. Such spots are restricted to the anterior area of the sides. There are no stripes or bands on the upper lip.

3. Waigeo, New Britain, New Georgia (pl. 27): A relatively small dark humeral blotch is present and there may be a secondary mark similar to that described for the Philippine Islands and Palaus specimens. Indications of banding may be present on the body appearing usually as paired blotches along the midlength of the sides. There are no white spots on the body, but there are numerous small dark spots, several of which are equally as dark as the main humeral blotch. There are no stripes or bands on the upper lip.

TABLE 64.--Frequency distribution of number of supraorbital cirri of left eye of specimens of *Entomacrodus caudofasciatus* (all populations combined) arranged by SL classes (in mm)

Classes	Number of cirri								Average
	1	2	3	4	5	6	7	8	
15-19.9	2	3	3	2	-	-	-	-	2.5
20	-	-	2	5	1	-	-	-	3.9
25	-	-	3	8	13	2	-	-	4.5
30	-	-	2	14	11	9	-	-	4.8
35	-	-	-	5	9	8	-	-	5.1
40	-	-	-	3	7	10	1	-	5.4
45	-	-	-	-	2	5	2	1	6.2
50	-	-	-	-	-	2	1	-	6.3

4. Poulo Cécir de Mer, McKean, Swains, Tutuila, Tau, and Tongotapu Islands (pl. 25): A relatively large dark humeral blotch is present; there is no secondary humeral mark. There may be little or no color pattern on the body other than the humeral blotch or there may be faint indications of the body bands, or indications of the body bands and irregular longitudinal rows of pale dusky spots, or only dusky spots. There are occasionally present indistinct or irregular dark or dusky stripes and bands on the upper lip.

5. Tahiti, Makatea, Raroia, and Rarotonga: No humeral dark blotch is present; the only markings in the humeral region are small scattered dusky spots. There are weak to strong indications of the paired body bands but no distinct pale or dark spots. There may be seven dark stripes on the upper lip.

The body bands in the various populations are usually represented only by diffuse pairs of blotches along the midline of the body and the dark humeral blotch (and the secondary humeral mark), which represents the anteriormost pair of bands. The pair of bands frequently found on the caudal peduncle of other members of the *Entomacrodus nigricans* species group is frequently absent.

The head is variably and irregularly marked, usually pale in females, darker in males. Only a few specimens exhibited any indication of a dark spot just posterior to the eye. The underside of the head may be uniformly dusky (usually so in females), may bear broad dusky chevrons separated by pale stripes (some males) or, in some New Britain specimens, may bear faint indications of dark chevrons.

The color pattern types of the fins can be best determined from the plates (25, 26, 27), although the dorsal fins of specimens from Poulo Cécir de Mer appear to be almost uniformly dusky rather than variably dusky as appears in the illustrated specimens. The stripes on the caudal fin increase in number with increase in SL. The anal fin of females is always paler (spines frequently without melanophores) than in males from the same collection. In only one specimen (USNM 200100) was there a dark crescentic mark on the fleshy

TABLE 65.--Frequency distribution of number of predorsal commissural pores of specimens of *Entomacrodus caudofasciatus* (all populations combined) arranged by SL classes (in mm)

Classes	Number of pores																				
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	25	Average
15-19.9	3	-	4	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.7
20	-	1	1	2	3	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	6.8
25	-	1	1	3	2	3	3	4	4	1	3	1	-	-	-	-	-	-	-	-	9.3
30	-	-	3	1	2	3	5	6	4	3	3	2	2	-	-	-	-	-	-	-	10.0
35	-	-	-	1	2	3	2	4	1	2	2	1	1	-	1	1	2	-	-	-	11.1
40	-	-	-	-	-	1	1	3	2	1	1	4	2	1	1	1	1	2	-	-	13.8
45	-	-	-	-	1	1	-	-	-	1	1	1	-	-	2	-	-	-	2	1	15.5
50	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	1	-	-	-	14.3

pectoral base although faint indications of such a mark may occur on the pectoral rays of some specimens.

GEOGRAPHIC VARIATION.—Aside from the differences in color pattern discussed above, there appears to be some slight meristic (number of dorsal and anal rays, table 63) and proportional (dorsal spine three, dorsal ray one, and horizontal humeral blotch lengths, table 66) differences which are associated with some of the various color pattern types. Also, specimens from the Philippines, Palaus,

TABLE 66.--Proportional dimensions as percent SL of specimens of *Entomacrodus caudofasciatus* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL	HBL
BMNH 1949.11.29.633	Cocos-Keeling Is.	♂	33.0	25.4	7.0	4.5	1.8	11.5	14.8	23.3	16.7	21.7	4.8
BMNH 1949.11.29.634	Cocos-Keeling Is.	♂	38.5	24.2	6.5	4.2	2.3	10.4	14.3	21.3	14.3	22.3	3.9
BMNH 1909.3.4.68[1]	Christmas Is.	♂	43.3	23.3	5.8	5.5	1.6	10.2	13.9	18.9	13.9	22.6	4.6
SU 62000	Viet Nam	♀	33.8	24.2	6.8	3.6	3.0	10.9	13.9	23.4	16.3	23.4	4.1
SU 62000	Viet Nam	♂	40.0	24.0	6.5	6.0	2.2	11.2	15.0	23.8	15.0	22.5	5.0
SU 62000	Viet Nam	♂	45.4	23.6	6.2	6.6	2.9	10.4	14.1	22.2	16.5	22.2	3.3
SU 62000	Viet Nam	♂	51.0	23.9	6.1	7.4	2.0	10.8	15.1	22.0	14.5	23.1	3.7
UW 11373	Philippines	♂	33.1	24.2	6.0	4.5	2.7	9.7	11.2	21.2	14.5	21.7	3.3
SU 32303	Philippines	♀	33.2	23.5	6.6	3.6	1.8	9.0	12.0	23.2	-	24.1	2.4
SU 32303	Philippines	♂	35.0	24.3	6.3	5.1	2.3	10.9	13.7	20.3	-	22.0	2.9
UW 10320	Philippines	♀	36.8	22.8	6.7	3.3	2.7	9.5	10.9	21.7	14.9	23.4	3.5
UW 10320	Philippines	♂	39.9	23.1	6.5	5.0	2.3	10.8	12.5	22.0	14.8	22.6	4.0
USNM 144704	Solomon Is.	♂	27.0	22.6	8.8	3.7	1.9	9.3	13.0	23.3	16.3	24.1	3.0
USNM 195779	Solomon Is.	♂	28.4	24.6	7.7	5.3	2.8	8.8	11.6	21.5	13.7	22.9	3.5
SU 62070	New Britain	♂	33.5	23.6	6.2	5.6	2.1	8.4	11.9	20.6	13.1	21.5	2.7
SU 62070	New Britain	♀	34.4	23.2	7.0	3.5	2.9	8.7	12.5	22.1	14.2	22.7	3.5
SU 62070	New Britain	♂	43.0	21.4	6.3	4.6	-	9.3	13.0	20.5	12.8	20.9	2.8
USNM 198592	McKean Is.	♀	29.8	24.2	7.4	4.0	2.7	10.1	11.7	-	15.4	21.1	3.3
USNM 198592	McKean Is.	♂	41.7	22.8	6.0	6.0	2.2	10.6	13.2	21.1	12.7	22.1	4.6
USNM 198592	McKean Is.	♂	48.1	23.1	6.0	5.2	1.2	7.8	12.7	20.6	11.2	22.2	5.0
USNM 150586	Swains Is.	♂	31.5	24.8	6.8	6.2	2.5	11.1	14.6	21.3	15.9	22.8	4.6
USNM 150586	Swains Is.	♂	32.2	24.8	7.8	6.5	3.1	11.2	14.0	21.7	16.5	23.7	5.6
USNM 150586	Swains Is.	♀	33.5	25.1	7.5	3.6	4.2	10.4	14.3	-	17.0	23.0	6.0
USNM 150586	Swains Is.	♂	34.2	24.0	7.6	6.1	2.6	9.6	13.4	-	14.9	21.3	5.0
USNM 150586	Swains Is.	♂	35.2	24.4	7.4	6.5	3.4	11.1	14.5	22.2	15.3	22.2	5.1
USNM 150586	Swains Is.	♂	38.8	23.2	6.3	8.0	2.6	11.3	13.7	21.9	16.0	22.4	5.0
USNM 150586	Swains Is.	♂	38.9	24.7	6.3	8.0	3.0	11.8	14.1	21.8	15.4	21.8	5.5
USNM 150586	Swains Is.	♂	40.3	25.3	6.7	5.2	3.5	9.9	13.1	-	13.6	19.8	5.0
USNM 150586	Swains Is.	♂	41.6	22.8	6.2	6.7	2.4	10.8	13.9	19.5	13.7	20.9	5.3
UH 03085	Tongatapu	♂	53.7	22.9	6.0	6.3	2.6	10.2	14.4	20.3	11.6	22.0	3.4
USNM 199496	Rarotonga	♂	30.4	23.4	7.2	4.9	2.6	9.5	13.8	23.0	16.1	21.7	-
SU 62013	Raroia	♂	37.9	24.3	7.1	5.5	2.9	10.5	13.5	21.4	14.2	20.6	-

[1] Holotype of *Salarias caudofasciatus*

New Georgia, New Britain, and Waigeo may have the midportion of the ventral margin of the upper lip very weakly crenulate. A great deal more material from many localities will be necessary to determine if any of the populations merit naming. The two most obviously distinct groups are the Tahiti-Makatea-Raroia-Rarotonga group, which lacks a humeral blotch, and the New Georgia-New Britain-Waigeo group, which shows the dark-spotted color pattern associated with a high anal ray count, shorter dorsal spine three, shorter dorsal ray one, shorter horizontal humeral blotch length, and, in some specimens, a weakly crenulated midportion of the upper lip ventral margin.

It can be assumed from the population variations noted that there is relatively little dispersal and interbreeding among the various island populations. There is no information available to explain the initial and subsequent factors that distributed this species and then isolated the various populations. Why the South China Sea specimens are similar to the populations much farther to the east in the Pacific, in spite of the presence of the intervening and different Philippine-Palaus populations, requires attention. One would expect the South China Sea populations to have diverged—perhaps most of all—in view of the fact that two (*E. thalassinus* and *E. stellifer*) of the other four species of *Entomcarodus* present in that area are represented by endemic subspecies. Perhaps the South China Sea population of *E. caudofasciatus* has in fact diverged, but along parallel rather than derivative lines, from that population which gave rise to the Pacific populations to which it bears resemblance. One cannot exclude the possibility, however, that the South China Sea and Pacific populations represent a relict distribution or a once more widely distributed form.

Discussion.—The spotted appearance of the body and nature of the upper lip crenulations of the specimens from Waigeo and New Georgia caused Chapman (1951, p. 285) to mistakenly identify these specimens as *E. striatus*. The pattern of spots on the body of *E. striatus* is of an entirely different nature (pls. 7*c*, *d*, 12) than that of these specimens (plate 27, of a New Britain specimen, exhibits the same type spotting as does the New Georgia and Waigeo specimens). When a humeral blotch does occur in specimens of *E. striatus*, it is never so distinct or relatively so large as that of specimens of *E. caudofasciatus*. Specimens of *E. striatus* have a distinct dark spot behind the eye, a mark not found in *E. caudofasciatus* specimens. The gill-raker count of 14–16 in the Waigeo-New Georgia specimens is at the extreme low end of the range for *E. striatus*. In 84 specimens of *E. striatus*, 25.0 to 34.9 mm SL, the predorsal commissural pores ranged from 2 to 6 (only 6 specimens with 5 pores and 1 with 6) while the 3 Waigeo-New Georgia specimens, 27.0 to 29.0 mm SL, had 4, 7, and 9 predorsal commissural pores, generally higher than would be expected for *E. striatus*. All these characters exclude the possibility that the Waigeo-New Georgia specimens belong in *E. striatus*.

Further discussion of the specimens from Tahiti, Raroia, Makatea, and Rarotonga is given in "Relationships" under *E. chiostictus*.

NOMENCLATURE.—*Salarias rarotongensis* was described without comparison. I have examined the holotype and find it a typical specimen of the Tahiti-Makatea-Raroia-Rarotonga populations of *E. caudofasciatus*. Should that group warrant a name, *S. rarotongensis* is the only name available.

RELATIONSHIPS.—*Entomacrodus caudofasciatus* is a member of the *E. nigricans* species group. Of this group *E. caudofasciatus* appears to be most closely related to the Pacific species in generally having a relatively long supraorbital cirrus (distinguishes *E. caudofasciatus* from most Atlantic specimens of *Entomacrodus*) (see also "Relationships" under *E. chiostictus*). *E. caudofasciatus* is distinguished from *E. orneliae* and *E. sealei* and from most specimens of *E. chiostictus* in having only simple pores in the preopercular series (only four specimens of *E. caudofasciatus*, each with one pair of pores in the series, were encountered). The presence of a dark humeral blotch in most populations of *E. caudofasciatus* distinguishes that species from *E. chiostictus* and the Atlantic species, except *E. textilis* (differentiated from the latter species in key couplet 10).

REMARKS.—*E. caudofasciatus* has been collected with or from the same restricted geographic areas as *E. thalassinus*, both subspecies, from which it differs obviously in having crenulae on the ventral margin of the upper lip and, usually, a humeral blotch; *E. decussatus*, from which it differs obviously in the disposition of the upper lip crenulae and in having usually fewer dorsal and anal rays, gill-rakers, pseudobranchial filaments, and in having a humeral blotch; *E. striatus* (for differences, see "Discussion" above); *E. cymatobiotus*, from which it usually differs obviously in the disposition of the upper lip crenulae, in modal number of dorsal and anal rays, and in having a humeral blotch; *E. rofeni*, from which it differs obviously in the disposition of the upper lip crenulae and in having a humeral blotch and usually fewer vertebrae and dorsal and anal rays, and more predorsal commissural pores; and *E. epalzeocheilus*, from which it differs obviously in the disposition of the upper lip crenulae and in having fewer nuchal cirri, pores before the anterior nostril, gill-rakers, pseudobranchial filaments, and in having simple preopercular pores.

DISTRIBUTION (fig. 9).—*Entomacrodus caudofasciatus* is known from the islands of the mideastern Indian Ocean, the South China Sea, Zulu Sea, and the tropical western Pacific from the Palaus to Raroia.

MATERIAL.—INDIAN OCEAN: Christmas Island: BMNH 1909.3.4.68 (holotype of *Salarias caudofasciatus*); Cocos-Keeling Island: BMNH 1949.11.29.633–634.

SOUTH CHINA SEA: Poulo Cécir de Mer: SU 62000; Zulu Sea, Philippines, Nusugbu: SU 32303; Duamaguete: SU 14730, UW 10320, 11373.

PACIFIC OCEAN: Palau Islands, 8 miles north of Koror: SU 62050; Waigeo: SU 28082; New Britain: SU 62070, USNM 200100, 200101; New Georgia: USNM 144704, 195779; McKean Island: USNM 198592; Swains Island: USNM 150586; Tutuila: USNM 179899; Tau Island: USNM 115476; Tongatapu: UH 03085; Rarotonga: AM IA5358 (holotype of *Salarias rarotongensis*), USNM 199496; Tahiti: ANSP 89164; Raroia: SU 62013; Makatea: USNM 200281.

Entomacrodus thalassinus (Jordan and Seale)

(For synonymy, see subspecies)

DESCRIPTION.—Segmented dorsal fin rays 13–15 (table 67); segmented anal fin rays (15–17); posteriormost anal pterygiophore supporting 1 or 2 external elements (2 in 86 percent of specimens of *E. t. thalassinus* and 54 percent of *E. t. longicirrus*); total gill-rakers on first arch 9–18 (11–13 in 84 percent of specimens; only one specimen with 18)[1] pseudobranchial filaments 3–6 (5 in 89 percent of specimens), not increasing in number with increase in SL; vertebrae 33–35 (34 in 90.5 percent of specimens); supraorbital cirri 1–8, number increasing with increase in SL (table 68); supraorbital cirri subequal and arising from a common base, or main or longest cirrus with short branches mesially, rarely 1 or 2 branches laterally; nape with 1 cirrus on each side (frequently missing from one or both sides). Occasionally the cirri appear to be aborted in development; in the figure of the holotype of *E. t. longicirrus* (pl. 29), the left nuchal cirrus is actually missing; the right has been illustrated in its place; predorsal commissural pores 3–17, number increasing with increase in SL (table 69); preopercular series of pores with all positions with simple pores; 1 pore before each anterior nostril; lateral line pores terminating on side in area below and between dorsal fin spines 8 and 13; ventral margin of upper lip entire (no crenulations).

Proportional measurements: See tables 3, 4, and 70, and fig. 11.

Males develop fleshy rugose modifications of the skin of the anal spines and the first to third anal rays (see Schultz and Chapman, 1960, pl. 115E). If one considers males with these modifications to be mature, the smallest mature male examined was 24.3 mm SL. Mature and immature males may occur in the same collection and in these collections immature males may be as much as 7.9 mm longer than mature males.

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[1] Gill-rakers in this species are sometimes difficult to count because they may merge dorsally in a continuous line (arch) with rakers associated with the pseudobranchial filaments. Under these circumstances the dorsalmost gill-raker of the first arch is usually abruptly larger than the adjacent raker of the pseudobranchiae.

The largest specimen of *E. t. thalassinus* examined was a male, 39.7 mm SL; the largest female was 34.4 mm. Males were relatively common over 35.0 mm, but females occurred rarely at sizes larger than 28.0 mm. In general, males were more numerous than females in collections. The smallest nonophioblennius stage was 13.4 mm SL and the largest ophioblennius larva was 13.7 mm. The larvae had five anterior canines, two directed posterolaterally on each side of the lower jaw and one directed posteriorly at the symphysis of that jaw. There were no posterior canines in specimens below 14.1 mm, but vomerine teeth were visible in nonlarvae 13.4 mm. Head cirri were well developed in a larva 13.7 mm.

There was no apparent sexual dimorphism of meristic characters among specimens of *E. t. thalassinus*.

The largest specimen of *E. t. longicirrus* examined was a male, 49.7 mm; the largest female was 39.0 mm. Males are common at lengths over 40.0 mm; below this size the sexes occur with relatively equal frequency. In general, males were much more numerous than females in collections. The smallest specimen examined, 18.5 mm, was not an ophioblennius larva.

Males tend to have a higher average number of segmented dorsal rays than females. Of 44 males examined, 4 had 13 rays, 38 had 14 rays, and 2 had 15 rays. Of 40 females examined, 15 had 13 rays, 23

TABLE 67.--Frequency distribution of number of segmented dorsal and anal fin rays and vertebrae of specimens of subspecies of *Entomacrodus thalassinus* arranged geographically

Subspecies	Dorsal rays			Anal rays			Vertebrae		
	13	14	15	15	16	17	33	34	35
longicirrus	-	-	-	-	-	-	6	20	2
Thailand	19	48	4	21	45	5	-	-	-
Viet Nam	1	11	-	3	9	-	-	-	-
Hong Kong	-	3	-	-	3	-	-	-	-
thalassinus	-	-	-	-	-	-	-	41	4
Seychelles Is.	9	61	5	19	49	1	-	-	-
Riu Kiu Is.	-	1	-	-	1	-	-	-	-
Marianas Is.	1	5	5	-	6	5	-	-	-
Ifaluk	1	15	2	2	14	1	-	-	-
Kapingamarangi	1	1	-	-	2	-	-	-	-
Marshall Is.	4	14	1	4	15	-	-	-	-
Phoenix Is.	7	49	1	5	51	1	-	-	-
Jarvis	-	9	-	-	9	-	-	-	-
Malden	5	40	4	7	39	3	-	-	-
Samoa	1	13	2	1	13	1	-	-	-
Raroia	6	37	-	7	35	1	-	-	-

had 14 rays, and 2 had 15 rays. I noted no other sexual dimorphism of meristic characters.

Color pattern of preserved specimens.—*E. t. thalassinus:* The body is uniformly pale, or pale with a single concentrated spot of melanophores midlaterally, or pale with scattered sprinklings of melanophores, some of which may be concentrated into a few midlateral blotches (see: Jordan and Seale, 1906, fig. 106; Schultz and Chapman, 1960, pl. 115D). In freshly preserved specimens there is evidence of a number of vertical orange bands on the body (pl. 28: pattern indicated on body). These bands fade completely in alcohol. Specimens of less than 16 mm SL from Raroia exhibited four types of body coloration: (1) completely pale; (2) a loose concentration of melanophores at the caudal base; (3) a loose concentration of melanophores midlaterally; and (4) a loose concentration of melanophores midlaterally and at the caudal base. The head is pale with a dark spot behind the eye, sprinklings of melanophores on the upper lip and snout, and a concentration of melanophores on the ventral surface, which in mature males forms a noticeable blotch (see Schultz and Chapman, 1960, pl. 115E). The fins are essentially as described for *E. t. longicirrus* (see below), but the dark spots and stripes are smaller (on the caudal fin they may be completely absent).

E. t. longicirrus: Specimens exhibit more markings on the body, in general, than do specimens of the other subspecies. The body

TABLE 68.--Frequency distribution of number of supraorbital cirri of left eye of specimens of subspecies of *Entomacrodus thalassinus* arranged by SL classes (in mm)

Subspecies	Classes	Number of cirri								Average
		1	2	3	4	5	6	7	8	
thalassinus	10-14.9	1	-	-	-	-	-	-	-	1.0
thalassinus	15	3	24	13	2	-	-	-	-	2.3
longicirrus		-	1	-	1	-	-	-	-	3.0
thalassinus	20	-	12	31	23	3	-	-	-	3.2
longicirrus		-	-	1	1	1	-	-	-	4.0
thalassinus	25	1	8	50	31	5	3	-	-	3.2
longicirrus		-	-	9	6	10	1	-	-	4.1
thalassinus	30	1	2	17	16	6	2	-	-	3.7
longicirrus		-	-	-	11	9	1	1	-	4.6
thalassinus	35	-	-	3	7	-	2	-	-	4.1
longicirrus		1	-	3	5	3	3	2	1	4.7
longicirrus	40	-	1	2	2	3	1	1	-	4.4
longicirrus	45	-	-	1	-	2	-	-	-	4.3

markings are irregular and highly variable but there are usually present indications of three or four pairs of dark vertical bands in the region below the dorsal fin and between the posterior dorsal spines and the last dorsal ray. The bands may be absent or represented only as pairs of midlateral dark spots; the members of one or more pairs may be fused. Females frequently have more distinct banding than males. In females the bands may be complete and almost uniformly dark, or darker in their midportions, and extend from the dorsal to the ventral body contour. The sides and venter are everywhere marked with splashes of melanophores giving the specimens a smudged appearance. Specimens of less than 25 mm SL exhibit few or no markings on the body. The head always bears a dark spot just behind the eye; in females a secondary, usually paler, spot follows the first and is sometimes linked ventrally to it, giving the appearance of a U. The head is variably splashed with melanophores; the upper lip is irregularly marked but may show adumbrations of about eight dusky bands and eight pale stripes. The underside of the head is splotched and dusky, frequently with a large noticeable concentrated area of melanophores.

The spinous dorsal bears various dark and pale spots, which may be regularly or irregularly distributed. There is a pale distal band along the length of the spinous dorsal. The fin is darker in males than in females from the same collection. The soft dorsal bears one to four dusky spots over each ray with scattered, paler, dusky markings on the fin membrane basally. Distally the soft dorsal has a broad, pale to

TABLE 69.--Frequency distribution of number of predorsal commissural pores of specimens of subspecies of *Entomacrodus thalassinus* arranged by SL classes (in mm)

Subspecies	Classes	Number of pores															
		3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Avg.
thalassinus	10-14.9	2	1	1	2	1	-	1	-	-	-	-	-	-	-	-	5.3
thalassinus	15	-	-	4	5	6	12	11	6	3	1	-	1	-	-	-	8.3
longicirrus		-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	8.0
thalassinus	20	-	-	-	2	5	12	16	12	10	5	2	-	1	1	-	9.6
longicirrus		-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	9.0
thalassinus	25	-	-	3	5	10	17	18	16	11	7	6	-	-	-	2	9.4
longicirrus		-	-	1	-	1	2	9	6	2	4	-	1	1	-	-	9.9
thalassinus	30	1	-	-	4	7	8	6	6	6	2	3	1	-	-	-	9.0
longicirrus		-	-	-	1	1	2	7	3	2	1	2	-	1	1	-	10.1
thalassinus	35	-	-	-	1	1	3	2	2	2	1	-	-	1	-	-	9.5
longicirrus		-	-	-	-	-	2	4	2	3	1	1	2	1	1	1	11.4
longicirrus	40	-	-	-	-	-	4	2	-	1	1	-	1	-	1	-	10.3
longicirrus	45	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-	11.3

dusky margin. The anal fin is variably dusky, frequently with dusky spots posteriorly (especially obvious in females). The tips of the anal rays are frequently much paler than the distal portions of the interradial membrane. The pectoral fin and its fleshy base are splashed with melanophores; there are no dark crescentic marks on either.

TABLE 70.--Proportional dimensions as percent SL of specimens of subspecies of *Entomacrodus thalassinus* (for meaning of abbreviations see methods section)

Catalog no.	Locale	Sex	SL	HL	OL	OCL	NCL	DS3	DR1	PECL	PELL	CL
longicirrus												
SU 63345	Thailand	♂	29.8	22.4	6.7	6.7	<1.7	11.4	13.4	22.1	15.1	21.8
SU 63345	Thailand	♀	31.6	24.0	6.6	6.0	1.6	10.1	12.3	23.4	16.4	20.6
SU 63345	Thailand	♀	34.5	23.7	6.4	4.9	1.4	9.6	13.0	21.2	13.9	20.6
SU 63345	Thailand	♂	35.4	22.9	6.8	8.5	<1.1	11.0	14.4	22.0	15.0	21.8
SU 63345	Thailand	♂	35.7	23.2	6.4	7.3	-	9.5	12.6	19.6	13.2	20.7
SU 63345	Thailand	♀	37.5	22.4	6.7	4.5	1.3	9.6	12.2	21.3	14.1	19.7
USNM 199480	Thailand	♀	38.0	23.7	6.1	4.2	1.8	9.7	13.2	21.6	-	19.5
SU 62089[1]	Thailand	♂	40.7	23.3	5.4	7.6	<1.2	10.3	12.8	20.9	13.3	21.1
SU 63345	Thailand	♂	43.6	21.8	5.7	6.6	1.1	9.2	12.6	19.5	13.1	20.2
SU 63345	Thailand	♂	49.7	22.2	5.4	6.2	<1.0	9.5	10.0	20.1	13.7	21.6
thalassinus												
USNM 115478	Tutuila	♂	20.0	26.0	8.0	3.0	2.0	12.0	13.0	-	-	23.0
USNM 115478	Tutuila	♀	21.2	26.4	7.5	4.7	1.9	11.3	13.2	23.6	17.0	20.8
SU 8693	Samoa	♀	22.5	24.9	8.0	3.1	-	11.1	13.3	22.2	-	21.3
SU 62032	Ifaluk	♂	24.4	23.8	7.4	3.3	<2.0	11.5	12.3	21.7	-	21.3
USNM 51790[2]	Samoa	♀	25.7	24.1	7.4	2.7	<1.9	10.5	12.1	19.4	-	19.4
USNM 115478[3]	Tutuila	♀♂	26.3	25.1	7.2	3.8	2.3	11.4	12.9	21.3	17.1	19.8
USNM 115478	Tutuila	♂	26.8	26.1	7.5	4.1	1.1	10.8	14.2	-	16.0	22.0
USNM 115478	Tutuila	♂	27.7	25.2	7.2	4.0	2.9	10.5	15.2	21.6	15.5	19.9
SU 62081	Saipan	♂	27.8	21.9	6.8	3.6	<1.8	10.1	12.6	18.0	-	20.1
SU 62076	Saipan	♂	32.2	22.0	5.6	3.7	<1.6	9.3	9.9	18.6	-	19.2
USNM 124193	Guam	♂	32.9	22.2	6.2	3.0	<1.5	10.0	11.2	16.7	12.2	18.5
SU 62076	Saipan	♂	33.1	24.2	6.3	3.0	-	11.5	12.7	18.4	-	20.8
SU 51795[4]	Samoa	♂	33.4	22.8	6.0	3.0	1.5	9.9	12.0	17.4	12.0	18.3
USNM 198591	McKean	♂	36.2	21.6	5.0	2.5	<1.0	9.4	13.0	20.2	12.4	20.2
USNM 124193	Guam	♂	37.5	21.8	5.3	-	-	-	12.2	-	-	18.9
USNM 198652	Jarvis	♂	39.7	21.4	5.3	2.5	-	8.6	12.1	19.6	12.1	21.4

[1] Holotype of *Entomacrodus thalassinus longicirrus*
[2] Holotype of *Alticus musilae*
[3] Hermaphrodite
[4] Holotype of *Alticus thalassinus*

The pelvic fin is uniformly pale dusky. The caudal fin bears up to nine dark stripes composed of regularly arranged spots appearing over the caudal rays; the number of stripes increases with size.

RELATIONSHIPS.—*Entomacrodus thalassinus* is most closely related to *E. macrospilus.* (For differentiation, see "Relationships" under *E. macrospilus.*)

REMARKS.—*Entomacrodus thalassinus* has been collected with or from the same restricted geographic locality as *E. stellifer* (both subspecies), *E. decussatus*, *E. vermiculatus*, *E. niuafoouensis*, *E. epalzeocheilus*, *E. cymatobiotus*, *E. striatus*, *E. rofeni*, *E. sealei*, and *E. caudofasciatus.*

For geographic distribution, discussion, and material, see subspecies accounts.

***Entomacrodus thalassinus thalassinus* (Jordan and Seale)**

PLATE 28

(For differentiation, see *E. t. longicirrus*)

Alticus thalassinus Jordan and Seale, 1906, U. S. Bur. Fish. Bull. 25 (1905), p. 425 [Apia, Samoa].

Alticus musilae Jordan and Seale, 1906, U. S. Bur. Fish. Bull. 25 (1905), pp. 425–426 [Apia, Samoa].

Salarias lacunicola Fowler, 1948, Proc. Acad. Nat. Sci. Philadelphia, vol. 98, p. 178 [Agu-Shima, Ryukyu Islands].

NOMENCLATURE.—*Alticus thalassinus* and *Alticus musilae* were described in the same paper and were not differentiated from each other. The former is based on a male and the latter, a female of the same species. *Salarias lacunicola* was described without comparison with other species. The noncrenulated ventral margin of the upper lip, presence of vomerine teeth, color pattern, short supraorbital cirrus and low gill-raker and fin ray counts are sufficient to synonymize these three nominal forms. Of the two described together, *A. thalassinus* appeared first in the paper and is the name in most common usage. Since the original description, *A. musilae* has been considered a synonym of one species or another of *Entomacrodus.* Schultz (1943) first placed *A. musilae* in synonymy with *A. thalassinus.* Schultz and Chapman (1960, p. 343) synonymized *S. lacunicola* with *E. niuafoouensis* but gave no reasons for their action. *Entomacrodus niuafoouensis* differs in many ways from *E. t. thalassinus*, but it is sufficient to mention here that *E. niuafoouensis* has a crenulated ventral margin of the upper lip, pairs or multiples of pores included in the preopercular series of pores, and more than one pore before each anterior nostril.

DISTRIBUTION (fig. 10).—*Entomacrodus t. thalassinus* is an island form known from the Seychelles, Indian Ocean, and in the Pacific Ocean from the Ryukyus to Raroia. Collection data indicate that this subspecies occurs on the outer (ocean) sides of reefs along surge or open channels.

MATERIAL.—INDIAN OCEAN: Seychelle Islands: ANSP 102184, 102185.

PACIFIC OCEAN: Ryukyu Islands: ANSP 72049 (holotype of *S. lacunicola*); Marianas Islands, Guam: USNM 124193; Saipan: USNM 149914, SU 62076, 62081; Caroline Islands, Ifaluk: SU 62026, 62032, 62034, 62036, 62045, 62046; Marshall Islands, Bikini: USNM 142184, 142185, 142190; Eniwetok: USNM 142186, 142187; Kapingamarangi: SU 62028, 62040; Phoenix Islands, Howland: USNM 179904; Enderbury: USNM 115480, 197908; Hull: USNM 115477, 116173; McKean: USNM 198591; Jarvis Island: USNM 198652; Malden Island: USNM 199458; Samoan Islands, Tutuila: USNM 115478; Samoa: SU 8693, USNM 51795 (holotype of *A. thalassinus*), USNM 51790 (includes holotype of *A. musilae*); Swains Island: USNM 115479; Tuamotus, Raroia: SU 62010, 62015, 62018, 62020, 62024, 62025.

Entomacrodus thalassinus longicirrus, new subspecies

PLATE 29

DISCUSSION.—*E. t. longicirrus* differs from *E. t. thalassinus* primarily in having a much longer supraorbital cirrus (fig. 11). There are minor differences in color pattern, which are manifested in *E. t. longicirrus* having more melanic pigment. The new subspecies appears to attain a larger size than the nominal subspecies.

DISTRIBUTION (fig. 10).—*E. t. longicirrus* is an island form restricted to the South China Sea and its extension, the Gulf of Thailand. This area is more or less enclosed by a chain of closely approximated islands extending from Taiwan to Sumatra (see "Distribution" under the nominal subspecies). A South China Sea endemic subspecies is also indicated for *E. stellifer*.

HOLOTYPE.—SU 62089, a mature male, 40.7 mm SL, shore reef region on east side at Goh Kram Island, east side Gulf of Thailand, 12°41′33″N, 100°48′28″E, Oct. 25, 1957, collected by R. R. Rofen.

PARATYPES.—SU 63345, 45 specimens, and USNM 199480, 10 specimens, all with same data as holotype. SU 62001, 10 specimens, South China Sea, Ilot du Sud, 10°29′15″N, 108°57′30″E; SU 62092, 4 specimens, Gulf of Thailand, Go Samet Island, 12°31′15″N, 101°26′45″E; SU 62009, 1 specimen, Gulf of Thailand, rocky shore reef in Ao Mae Hat Bay, Goh Tao Island; SU 62048, 12 specimens, Viet Nam, neighborhood of Nahtrang, Binchang Bay, 12°21′40″N, 109°15′38″E; USNM 197978, 3 specimens, Hong Kong, Shelter Island.

ETYMOLOGY.—From Latin, "longi" (long) + "cirrus" (a curl) refers to the distinguishing characteristic of a long supraorbital cirrus.

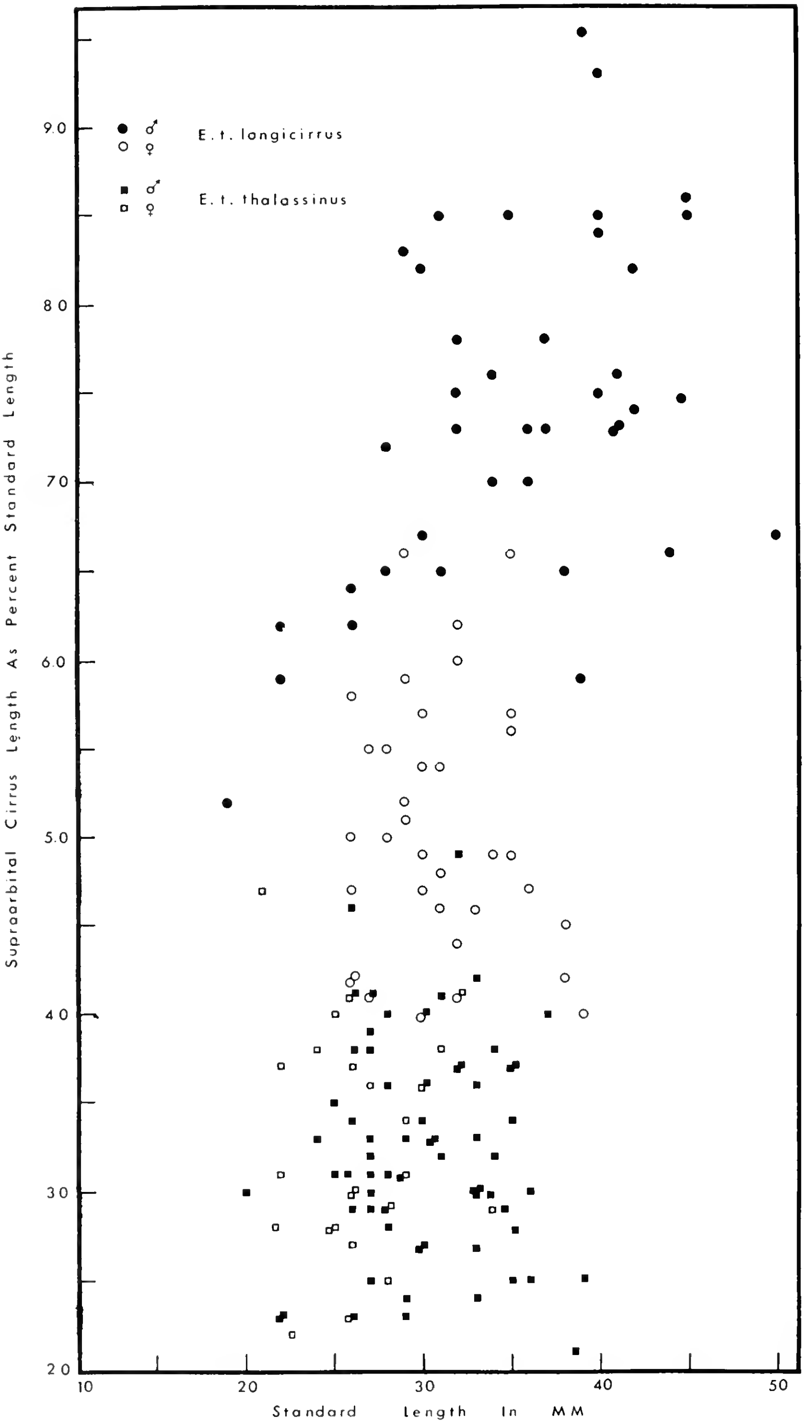

FIGURE 11.—Graphical comparison of supraorbital cirri lengths in subspecies of *Entomacrodus thalassinus*.

Entomacrodus macrospilus, new species

PLATE 30

DESCRIPTION.—(Character for holotype in parentheses.) Segmented dorsal fin rays 15 or 16 (16); segmented anal rays 17 or 18 (18); posteriormost anal pterygiophore supporting 1 or 2 external elements (2); total gill-rakers on first arch 13 or 14; pseudobranchial filaments 5; vertebrae 35 or 36 (35); 1 supraorbital cirrus on each eye; nape without cirri; predorsal commissural pores 9–18 (13) (too few specimens available to determine if pore number increases with increase in size); preopercular series of pores with all positions with simple pores; 1 pore before each anterior nostril; lateral line pores terminating on side in area below and between dorsal spines 10 and 11 (10); ventral margin of upper lip entire (without crenulations).

Proportional measurements (as percent SL, except as noted; only the holotype was in sufficiently good condition to afford measurement; for abbreviations, see "Methods"): SL 18.7, HL 24.6, OL 8.0, OCL 5.3, DS3 10.2, DR1 10.7, PECL 21.4, PELL 14.4, CL 18.2.

No mature males were recognizable. The largest specimen was a male, approximately 21.9 mm SL; the smallest, a male, approximately 14.0 mm SL, was not an ophioblennius stage.

COLOR PATTERN.—The color pattern is best discerned from plate 30, the holotype. The paratypes are essentially similar except that the smallest specimen lacked the large dark spot on the head.

RELATIONSHIPS.—*Entomacrodus macrospilus* is a member of the *E. thalassinus* species group. It differs from *E. thalassinus*, the only other member, in having higher average dorsal ray, anal ray, and vertebral counts; in having a single cirrus above each eye (apparently constant with size), and in having on the head a large dark spot that does not encroach on the circumorbital pores.

The Marquesas Islands, only locality from where *E. macrospilus* is known (fig. 10), are probably of more recent origin than the low Tuamotus, nearest island group to the Marquesas. As *E. thalassinus* is widely distributed in the central Pacific and occurs in the Tuamotus, it seems possible that *E. macrospilus* is a derivative of *E. thalassinus*.

REMARKS.—*Entomacrodus macrospilus* has been collected with *E. corneliae* and *E. randalli*, both endemic to the Marquesas. *E. macrospilus* differs most prominently from both these species in having only simple pores in the preopercular series, no crenulae on the upper lip, no nuchal cirri, and probably more predorsal commissural pores at comparable sizes.

HOLOTYPE.—USNM 200279, an immature male, 18.7 mm SL, from east side of Anaho Bay, near cliffs at shore, coll. J. E. Randall, July 17, 1957.

PARATYPES.—USNM 200280, five specimens about 14.0 to about 21.9 mm SL, collected with holotype.

ETYMOLOGY.—The specific name, *macrospilus*, means "large spot," and refers to the head spot characteristic of this species.

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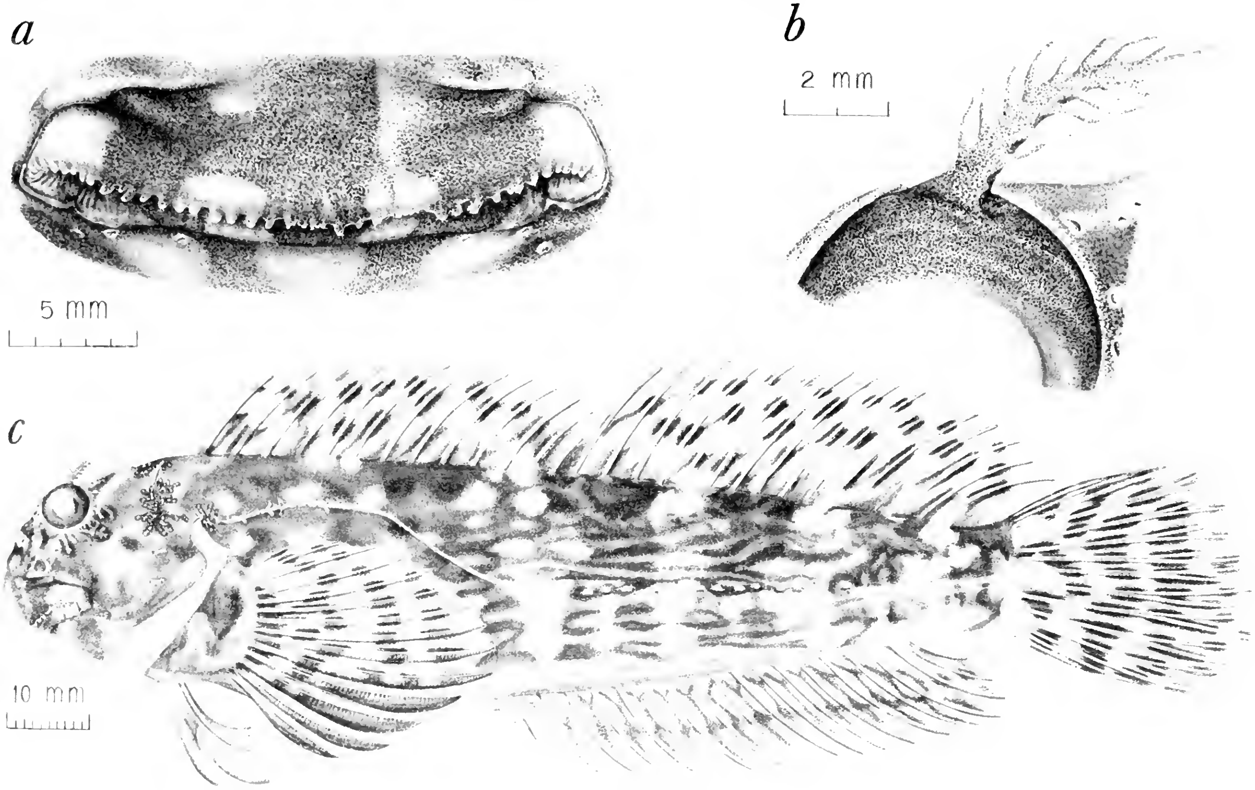
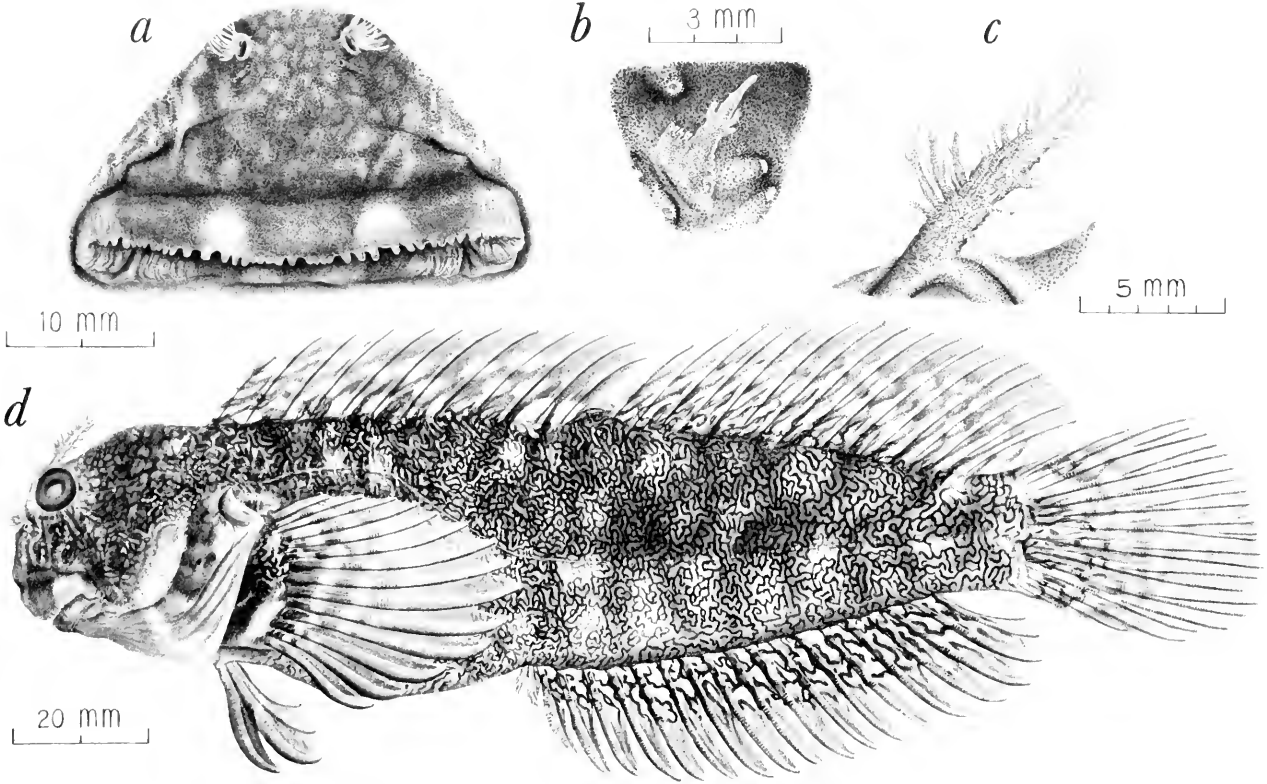
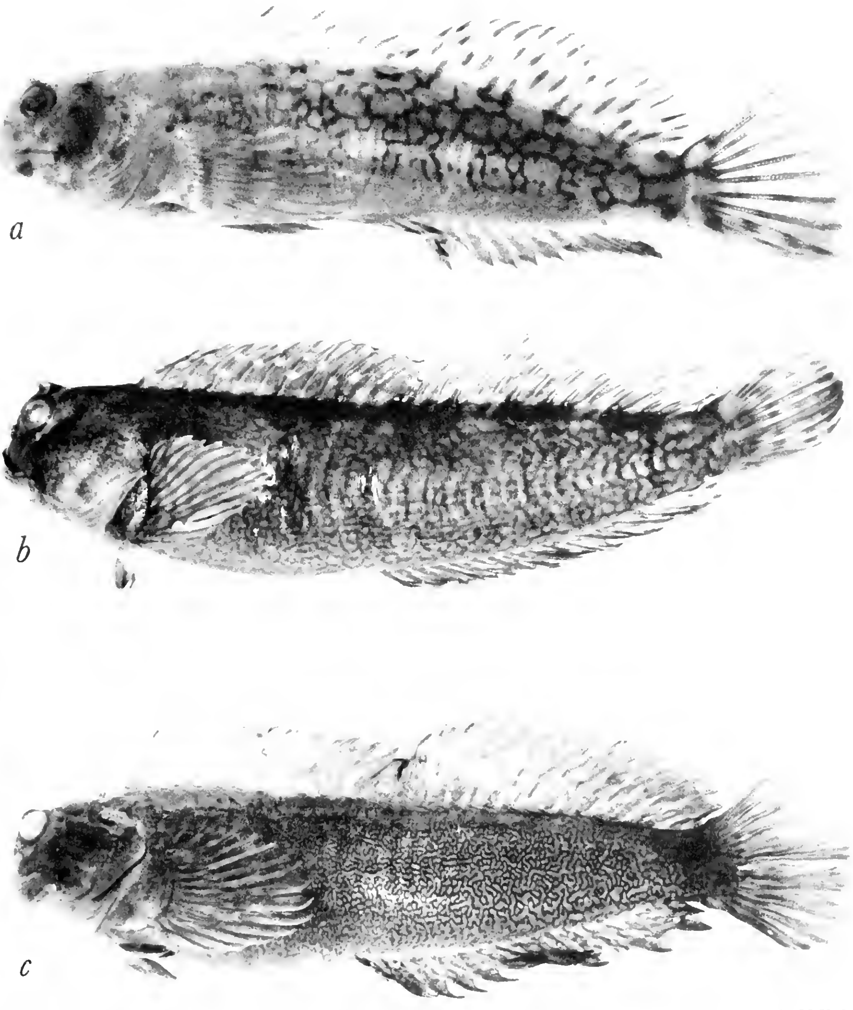
PLATES



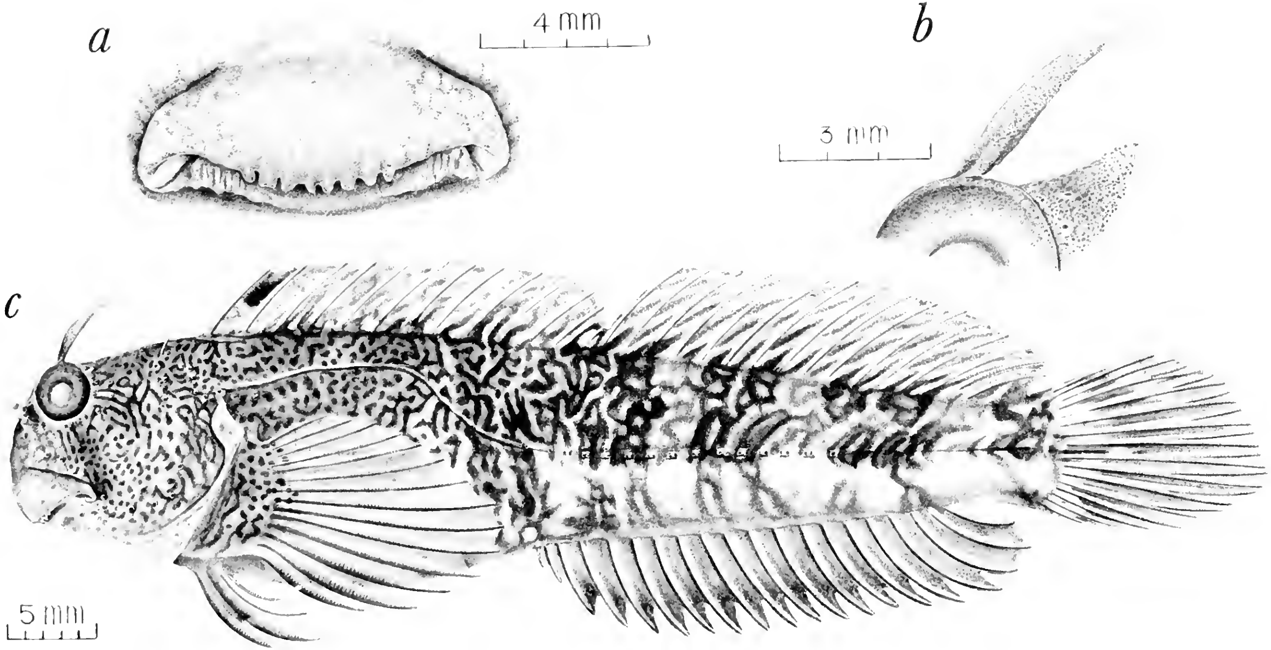
Entomacrodus decussatus, SU 62005, female, 125 mm SL, Gulf of Thailand: *a*, upper lip; *b*, left supraorbital cirri; *c*, lateral view.



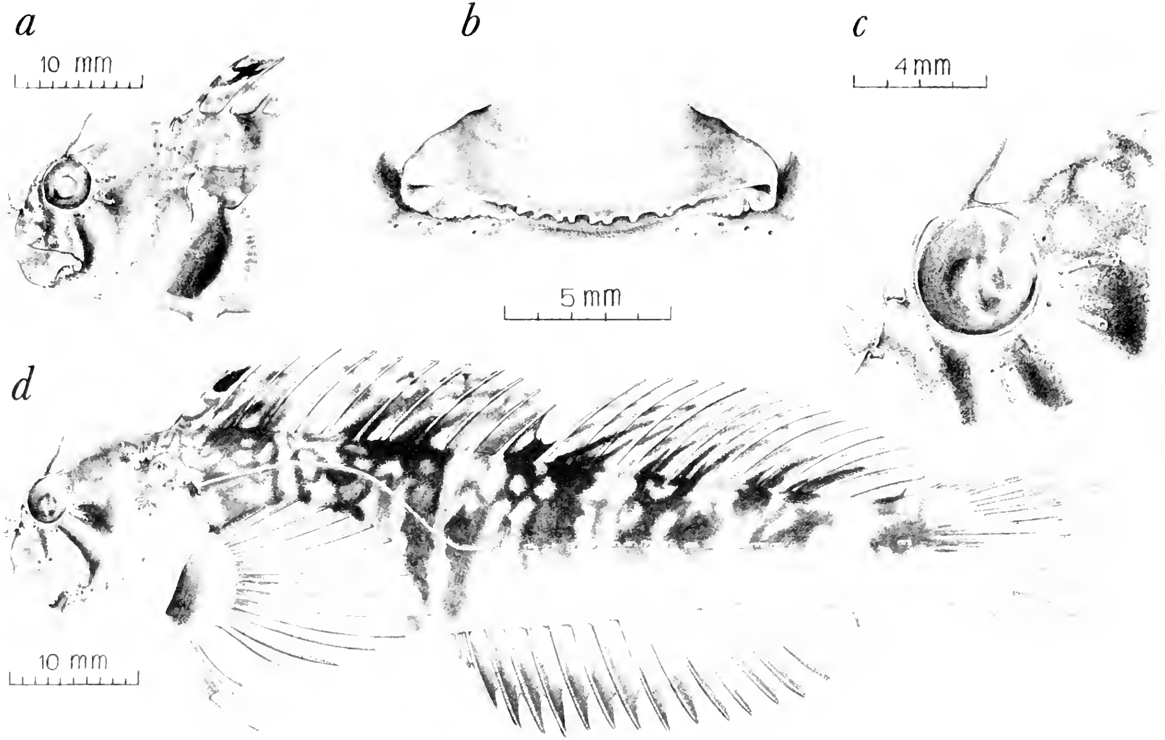
Entomacrodus vermiculatus, ANSP 102198, male, 149 mm SL, Seychelles: *a*, upper lip; *b*, left nuchal cirri; *c*, left supraorbital cirri; *d*, lateral view.



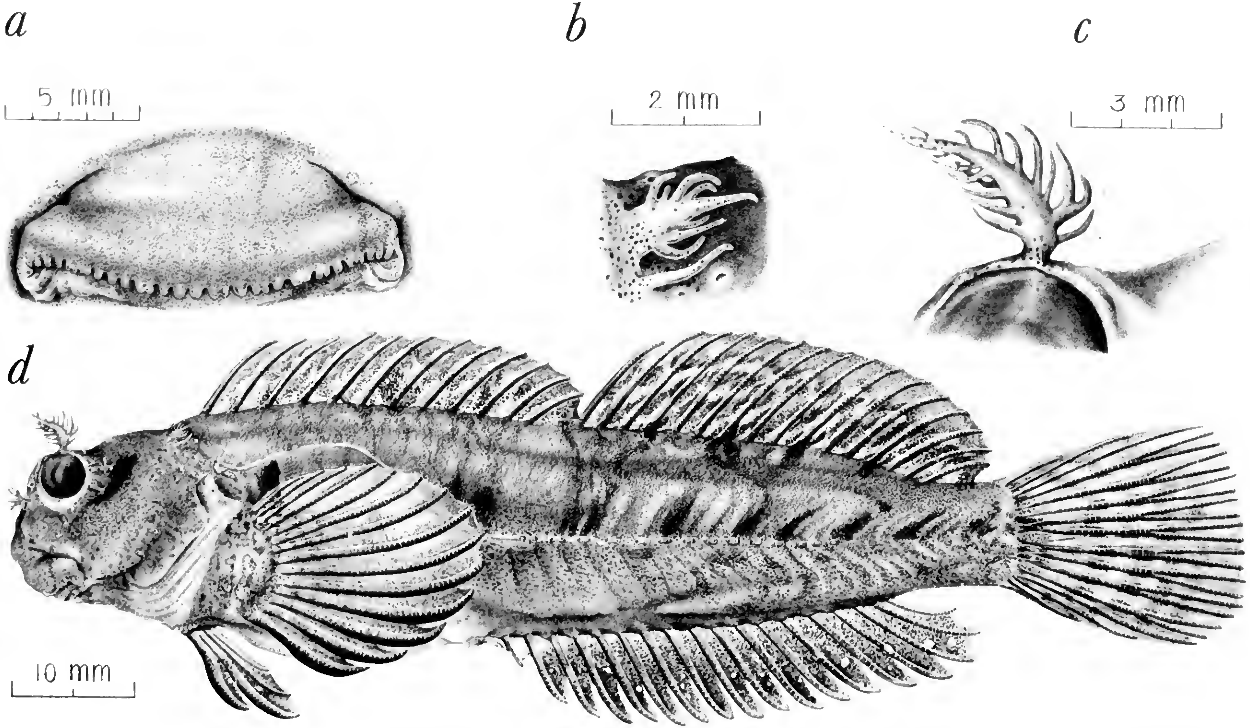
Entomacrodus vermiculatus: a, RU (no number), male, 64.2 mm SL, Seychelles; *b*, USNM 197636, female, 89.0 mm SL, Seychelles; *c*, RU (no number), male, 115 mm SL, Mozambique.



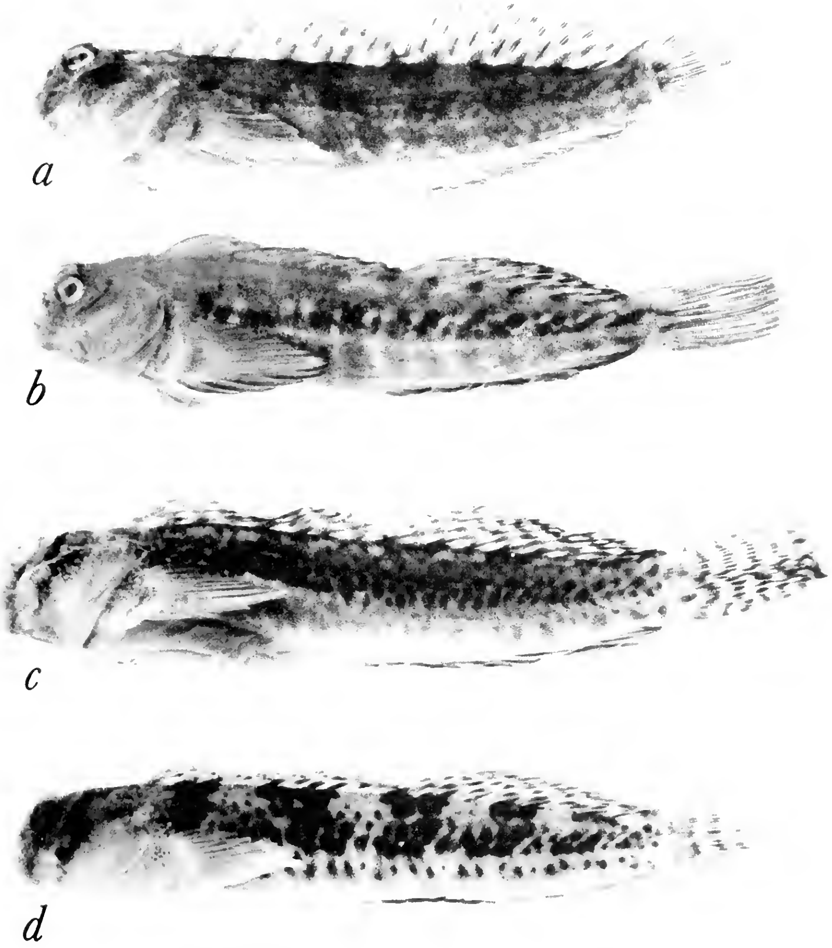
Entomacrodus stellifer stellifer, USNM 132795, male, 60.8 mm SL, Okinawa: *a*, upper lip; *b*, left supraorbital cirrus; *c*, lateral view.



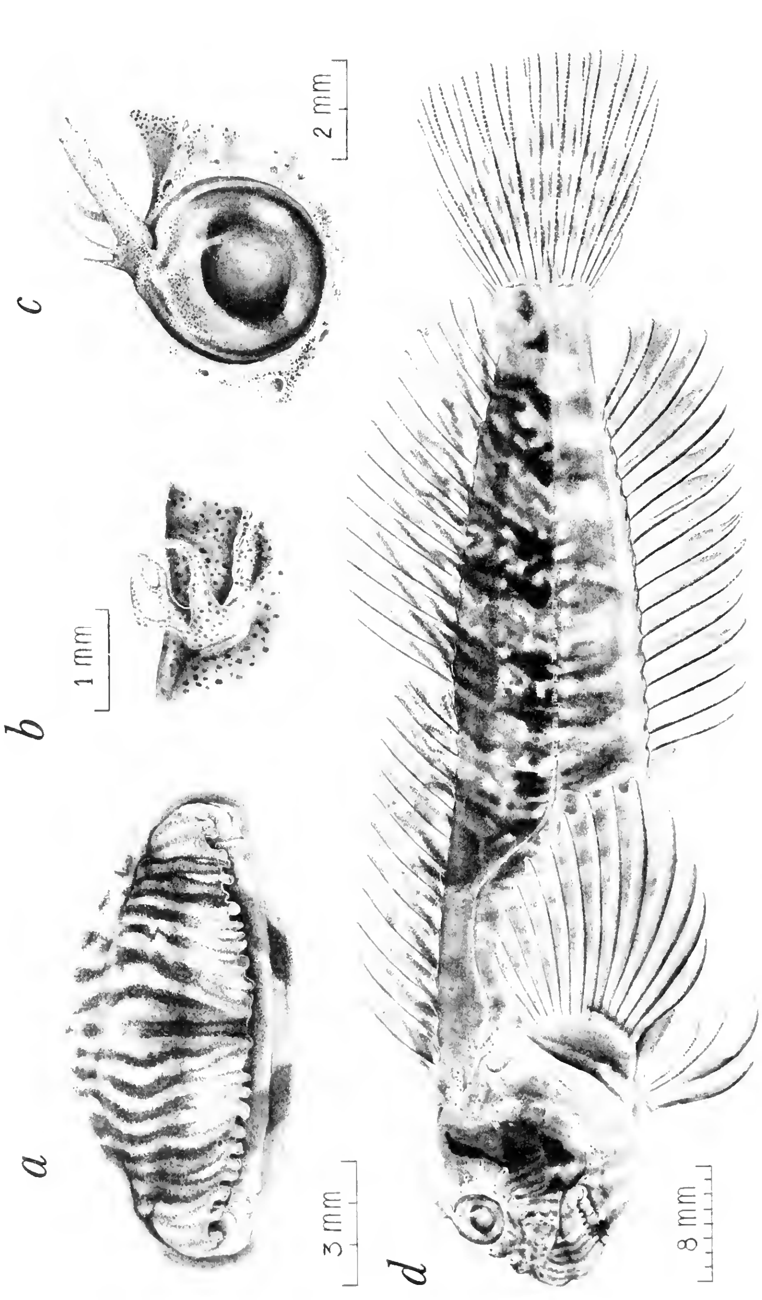
Entomacrodus stellifer lighti, SU 62071, Hong Kong: *a*, female, 73.0 mm SL, head; *b*, male, 73.8 mm SL, upper lip; *c*, male, 73.8 mm SL, left supraorbital cirrus; *d*, male, 73.8 mm SL, lateral view.



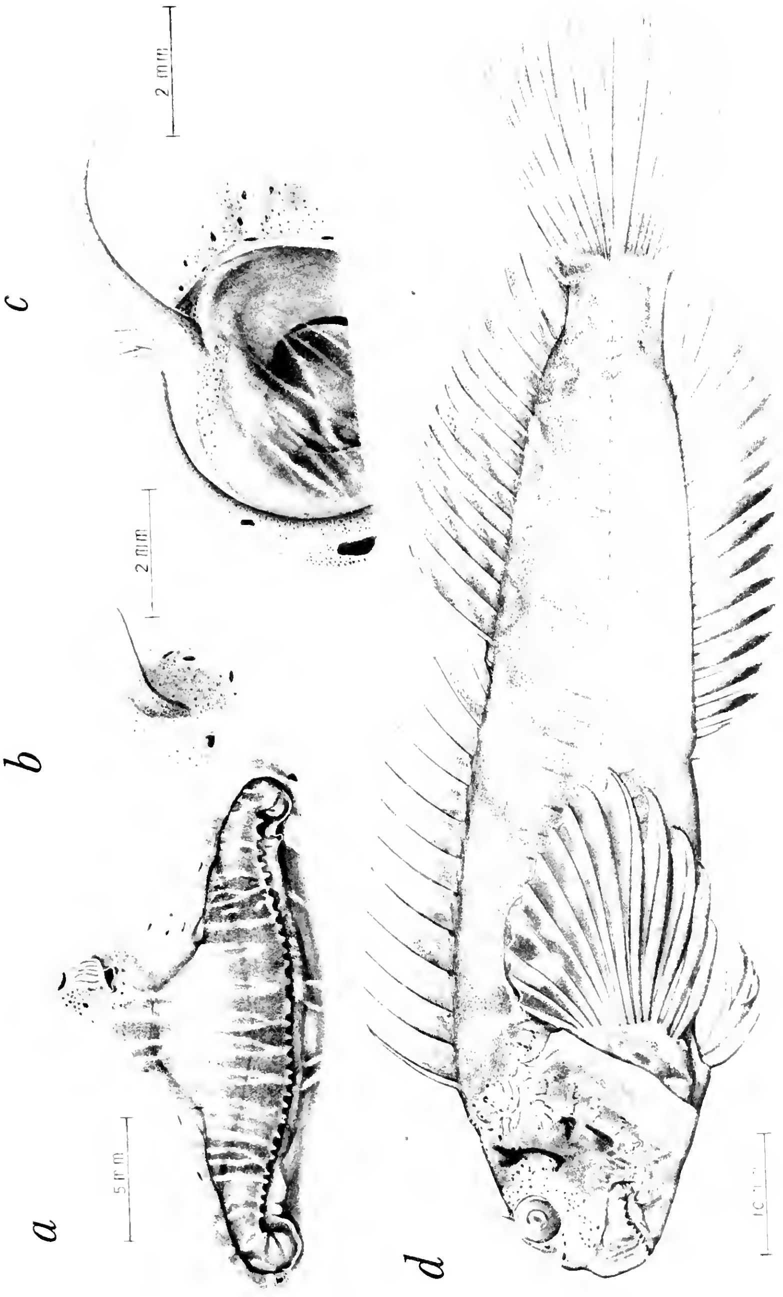
Entomacrodus marmoratus, UH 933, female, 82.0 mm SL, Midway: *a*, upper lip; *b*, left nuchal cirri; *c*, left supraorbital cirri; *d*, lateral view.



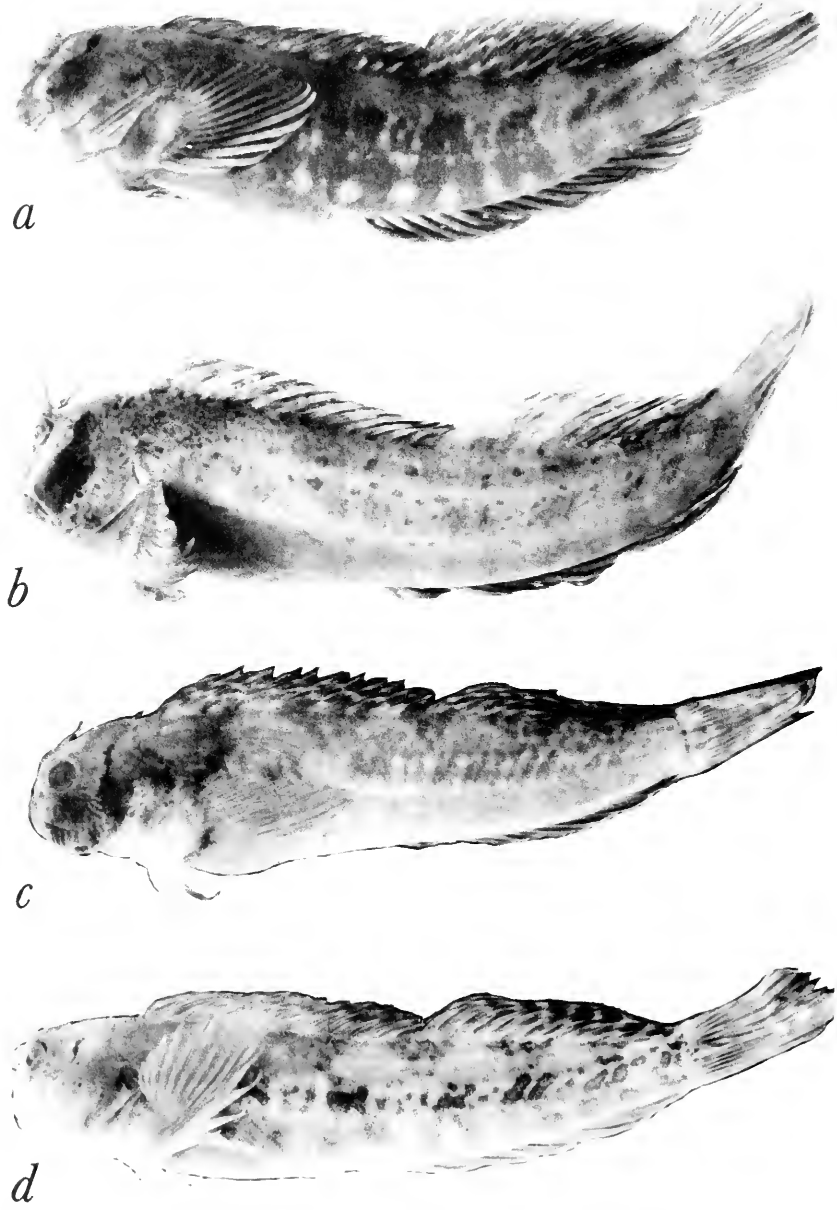
Entomacrodus marmoratus, USNM 197201, females, Oahu: *a*, 55.9 mm SL; *b*, 67.7 mm SL; *Entomacrodus striatus*, males: *c*, UH 03081, 54.7 mm SL, Tahiti; *d*, SU 62002, 54.0 mm SL. South China Sea.



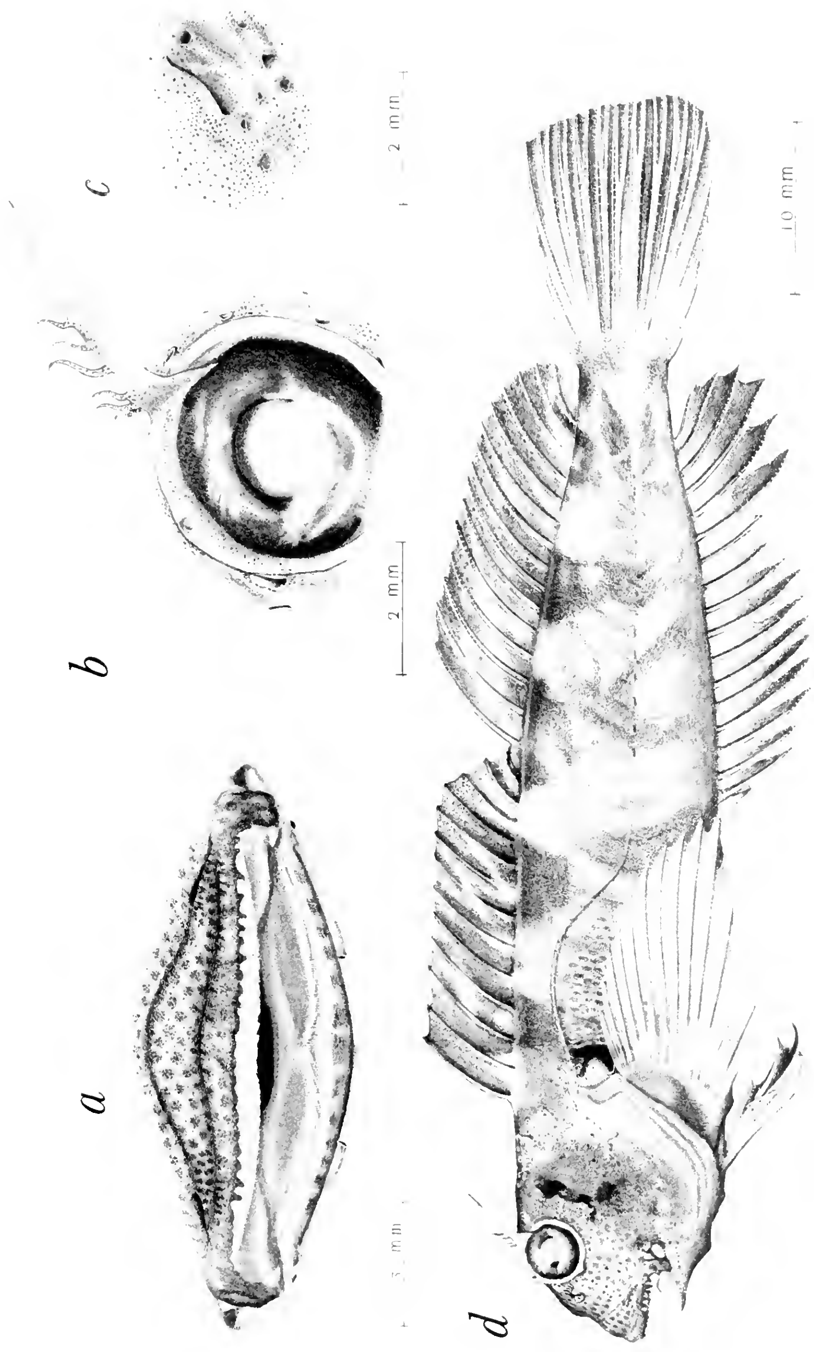
Entomacrodus epalzeocheilus, SU 14733, female, 69.8 mm SL, India: *a*, upper lip; *b*, left nape cirri; *c*, left supraorbital cirri; *d*, lateral view.



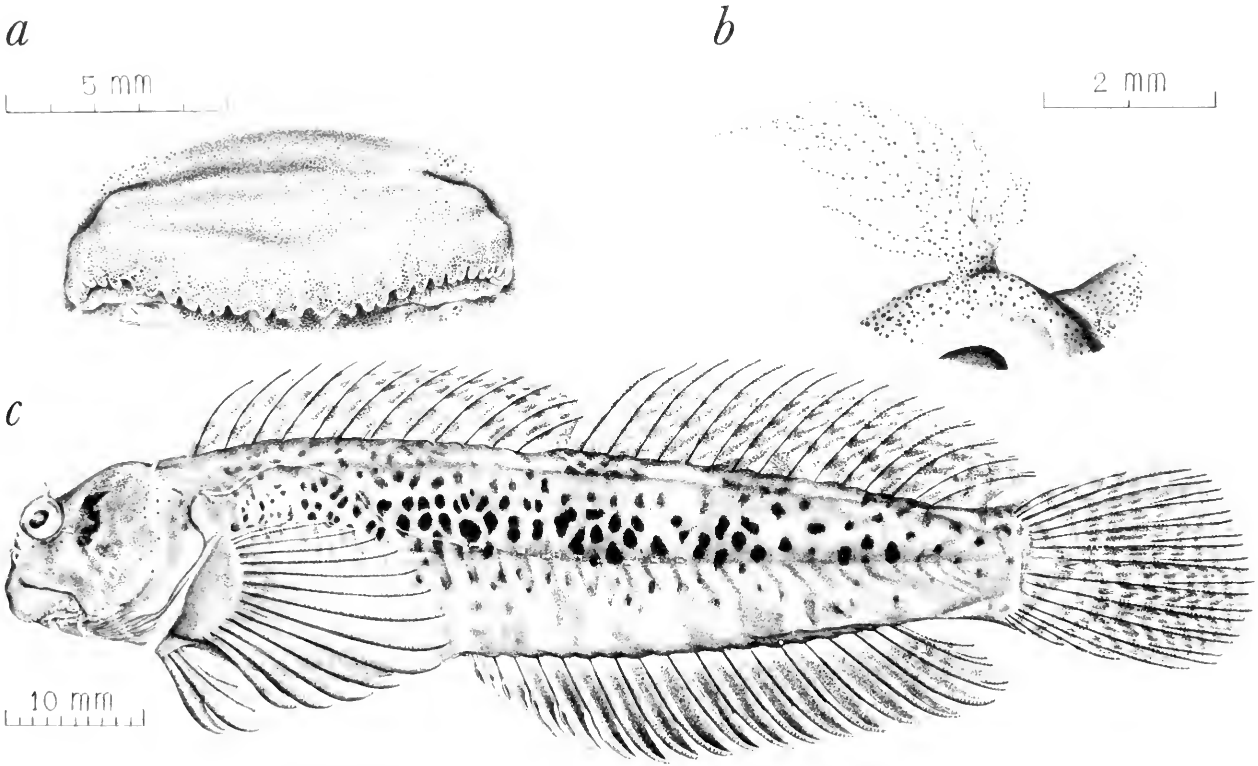
Entomacrodus niuafoouensis, UMMZ 144749, female, 83.5 mm SL, Bonin Islands: *a*, upper lip; *b*, left nuchal cirrus; *c*, left supraorbital cirri; *d*, lateral view.



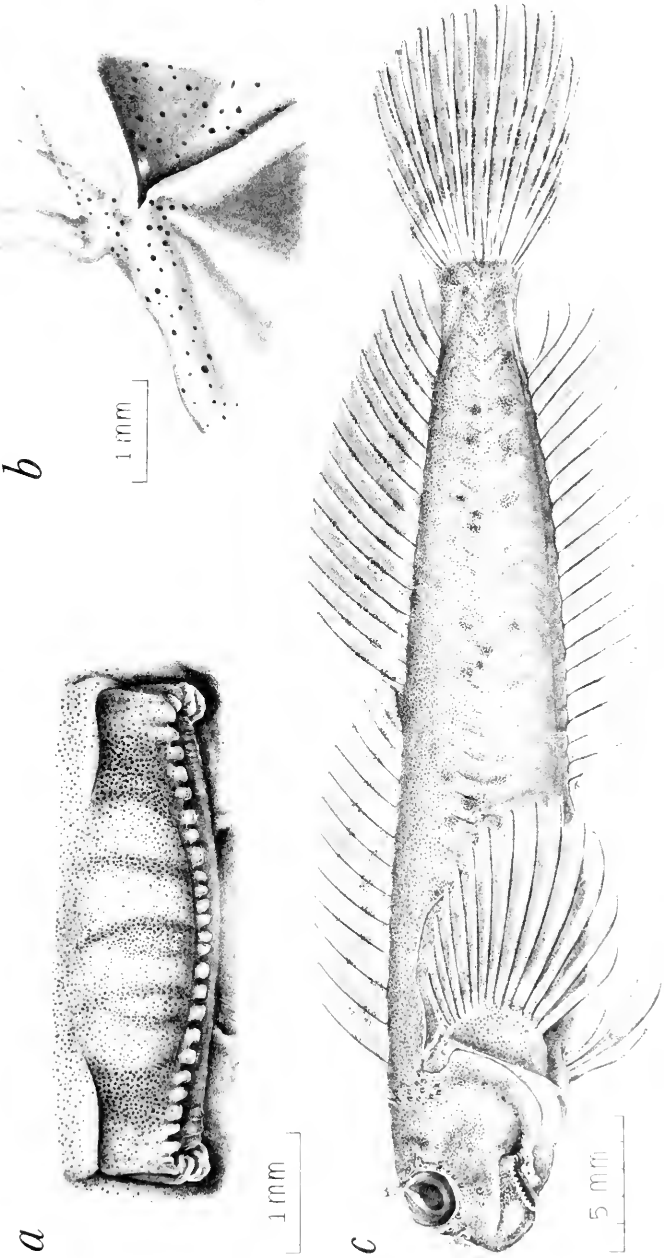
Entomacrodus epalzeocheilus, ANSP 102201, males, Seychelles: *a*, 104.5 mm SL; *b*, 99.2 mm SL. *E. niuafoouensis*, females, Tongatapu: *c*, UH 03083, 95.6 mm SL; *d*, UH 03084, 80.9 mm SL.



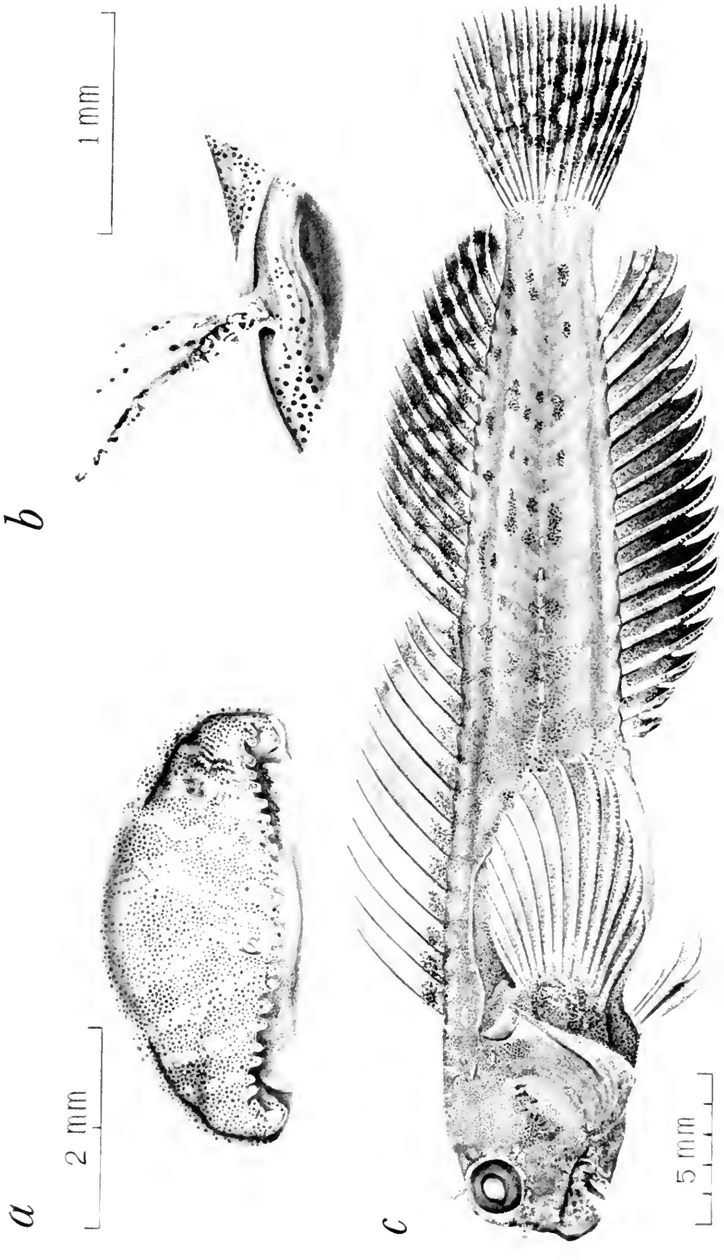
Entomacrodus randalli, SU 24522, female, about 58 mm SL, Nuku Hiva: *a*, upper lip; *b*, left supraorbital cirri; *c*, left nuchal cirrus; *d*, lateral view.



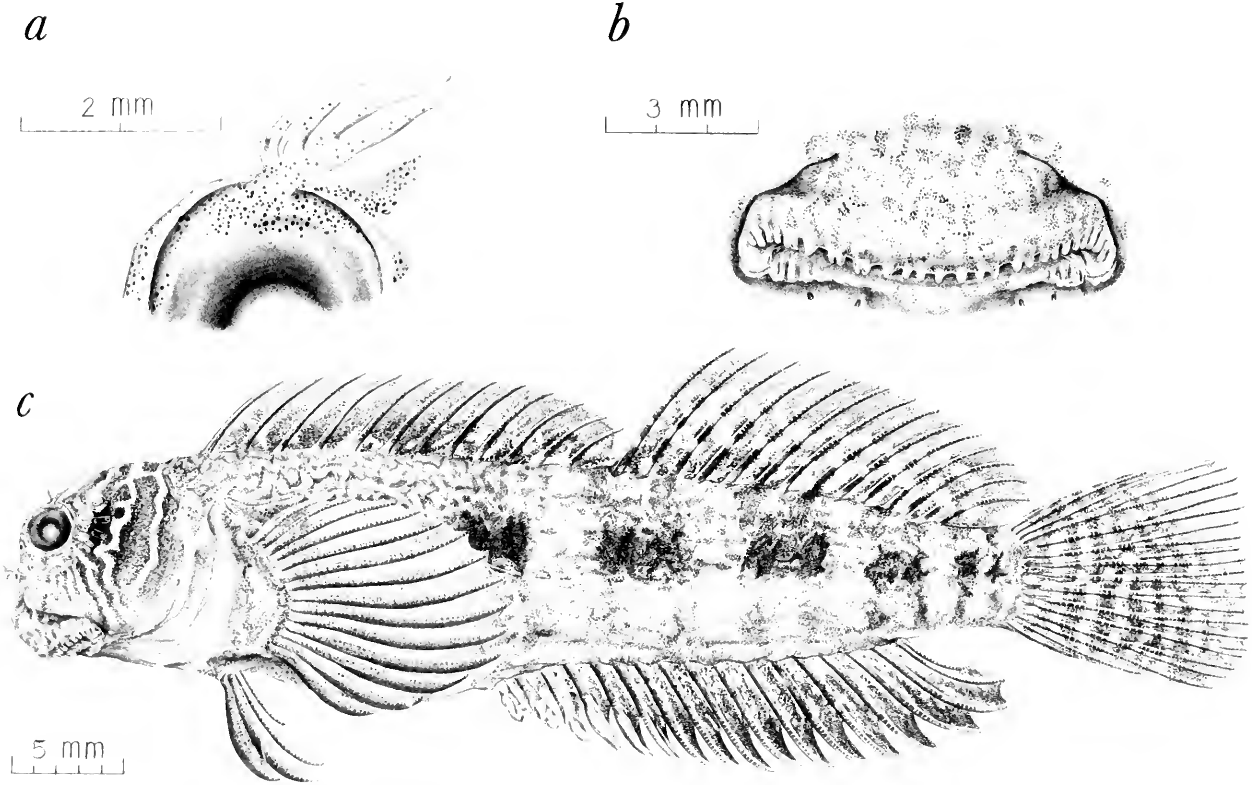
Entomacrodus striatus, USNM 115449, male, 72.6 mm SL, Phoenix Islands: *a*, upper lip; *b*, left supraorbital cirri; *c*, lateral view.



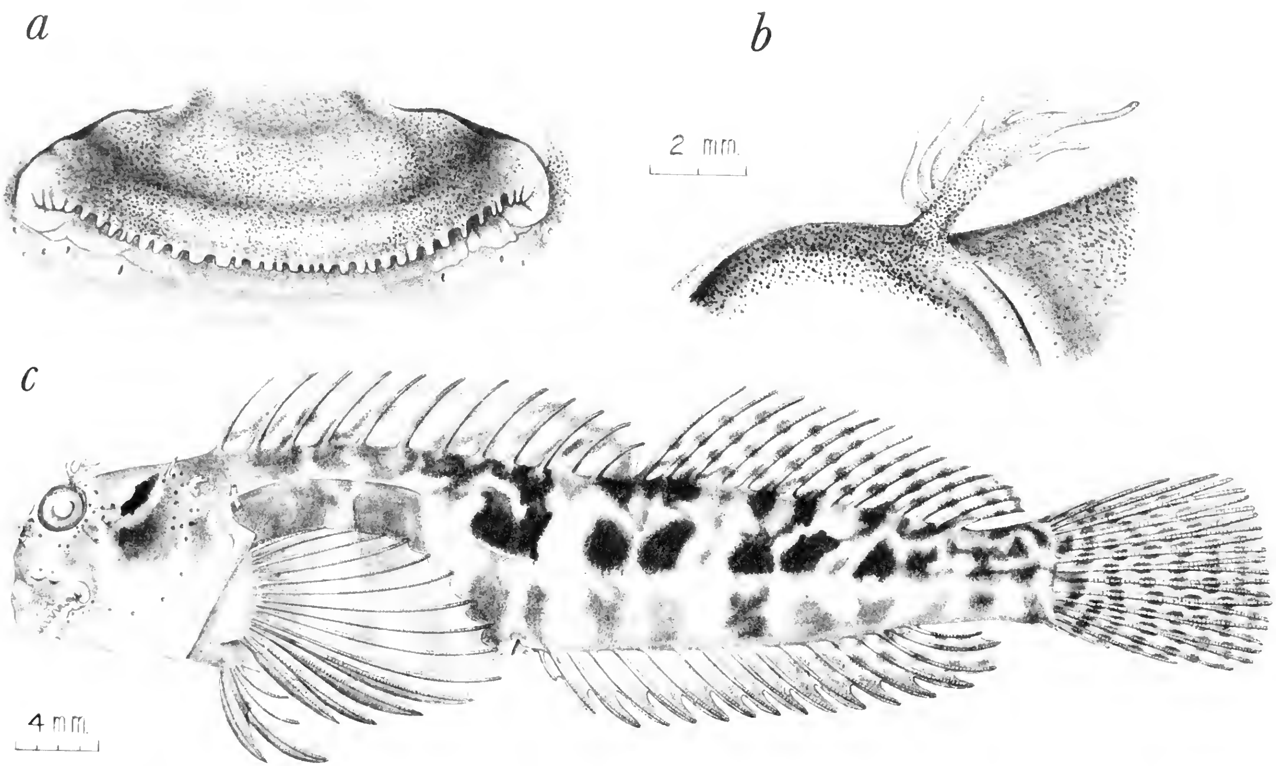
Entomacrodus rofeni, SU 62038, female, 36.4 mm SL, Raroia: *a*, upper lip; *b*, left supraorbital cirri; *c*, lateral view



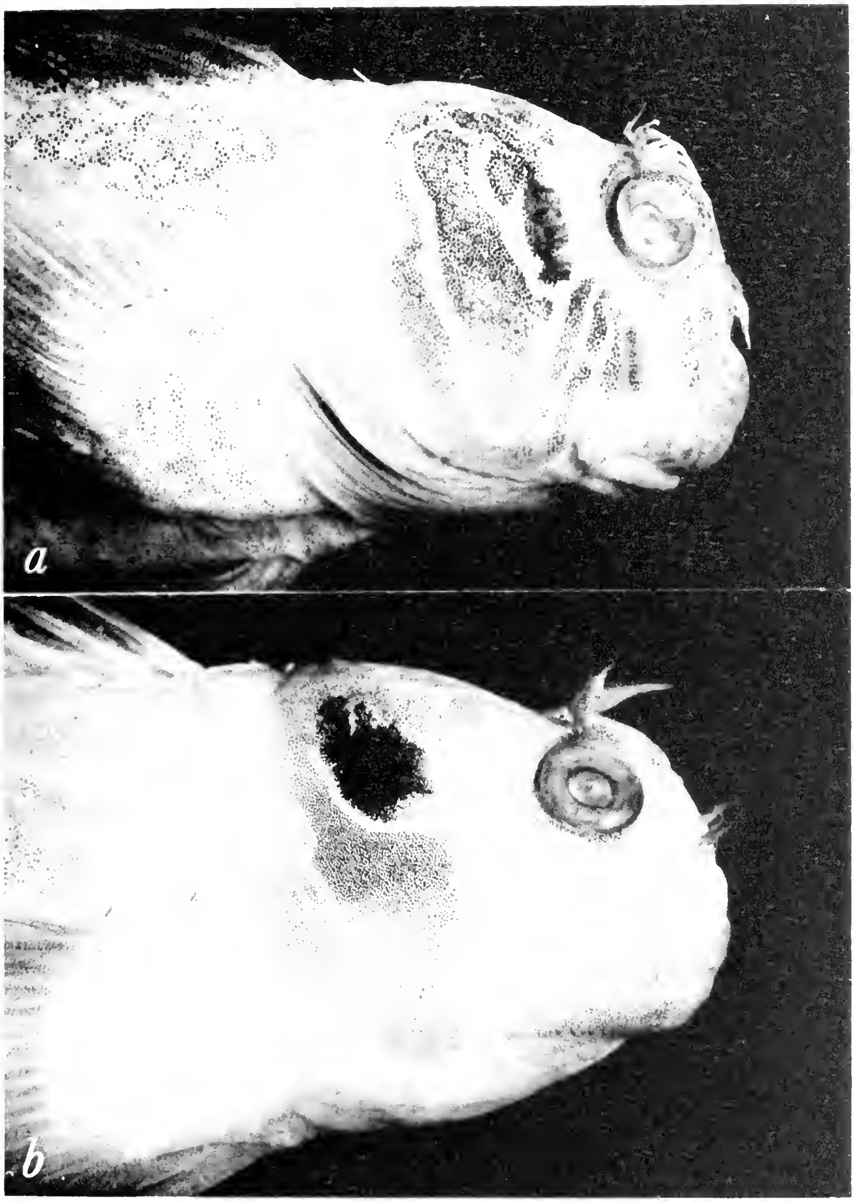
Entomacrodus strasburgi, USNM 179202, holotype, male, 35.0 mm SL, Oahu: *a*, upper lip; *b*, left supraorbital cirri; *c*, lateral view.



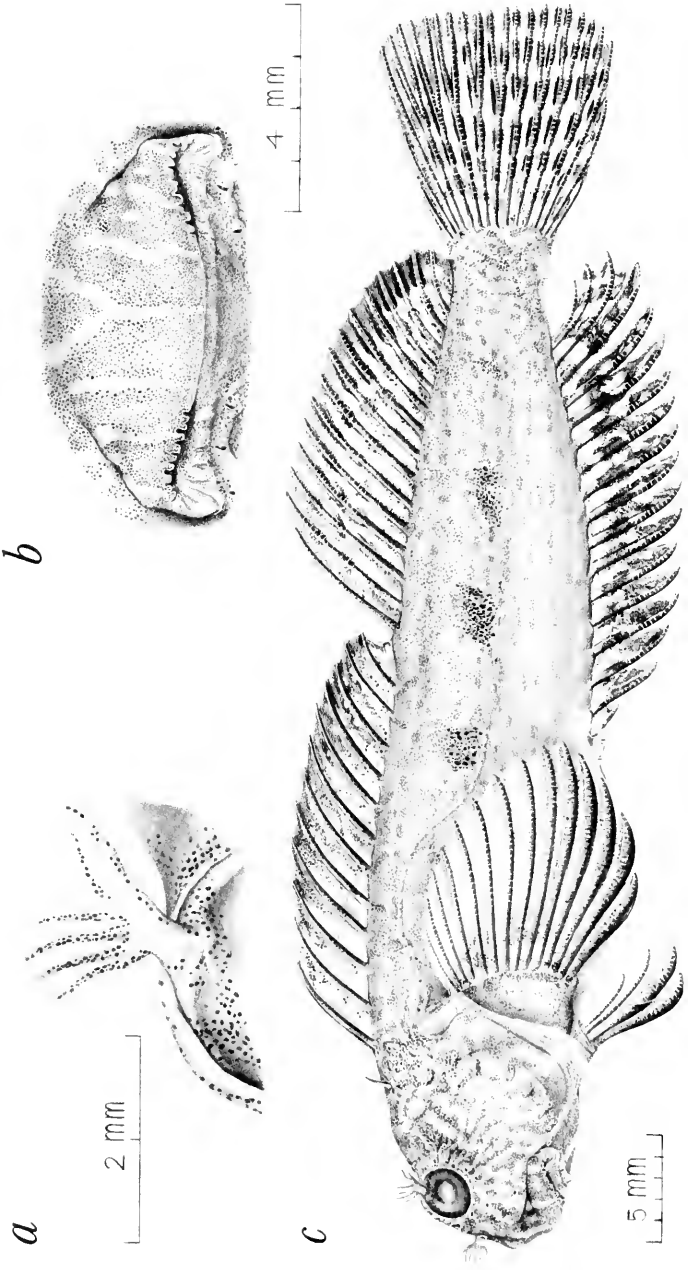
Entomacrodus cymatobiotus, USNM 198654, male, 45.8 mm SL, Jarvis Island: *a*, left supraorbital cirri; *b*, upper lip; *c*, lateral view.



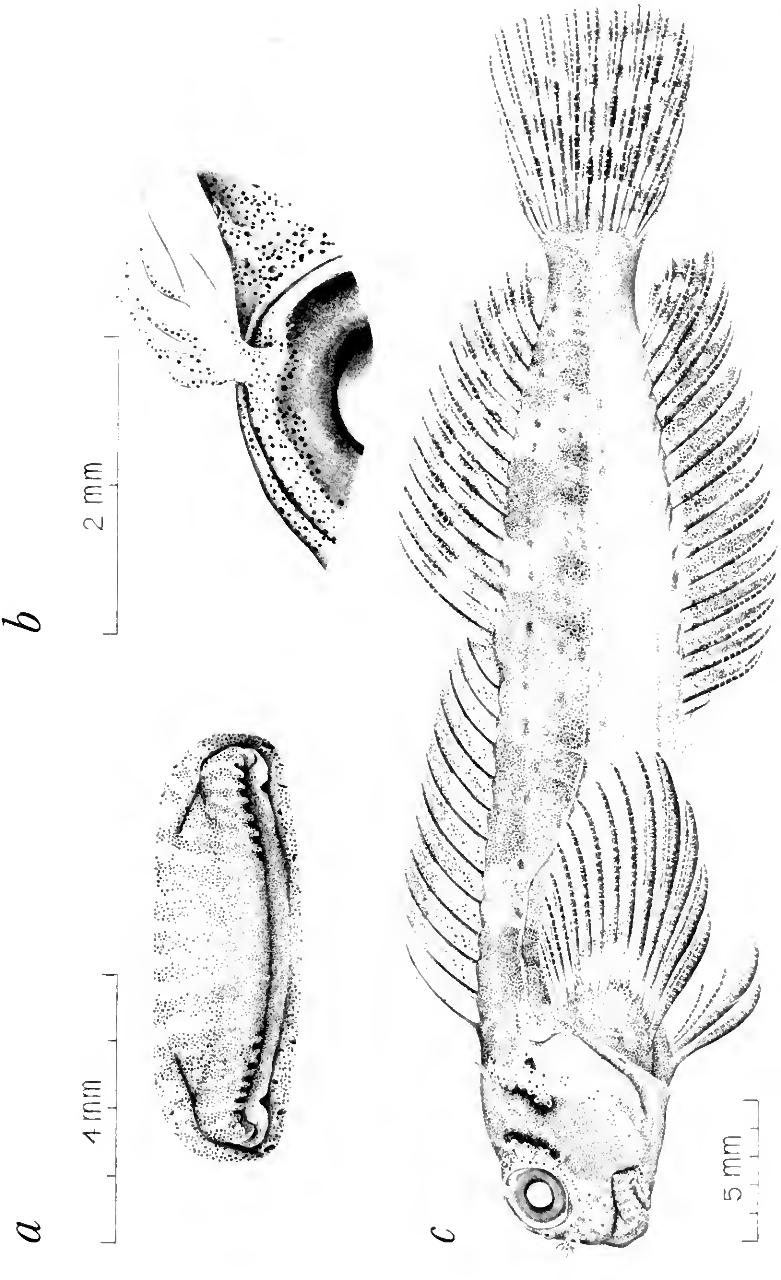
Entomacrodus chapmani, MCZ 29446, holotype, female, 52.5 mm SL, Easter Island: *a*, upper lip; *b*, left supraorbital cirri; *c*, lateral view.



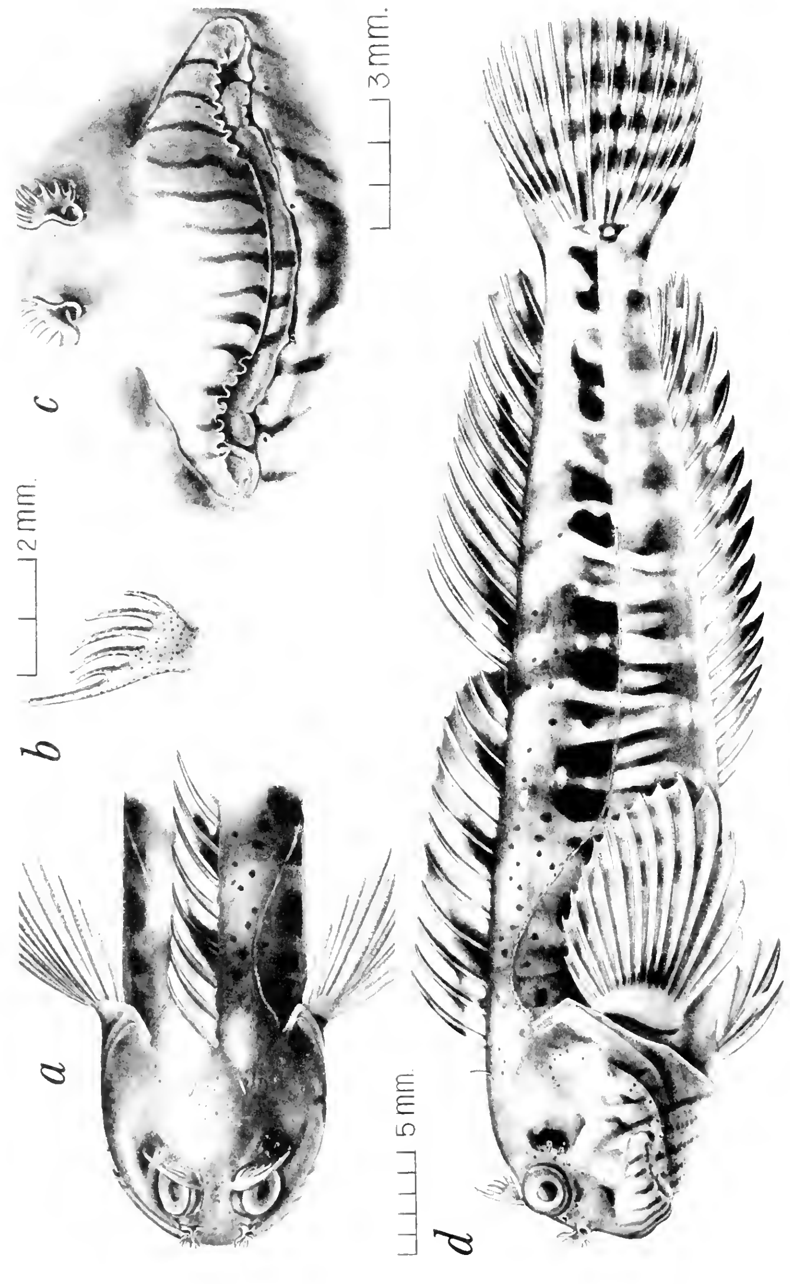
Entomacrodus cymatobiotus, USNM 198654, male, 45.8 mm SL, Jarvis Island: *a*, right side of head. *Entomacrodus chapmani*, UBC BC 65–449, male, 53.5 mm SL, Easter Island: *b*, right side of head.



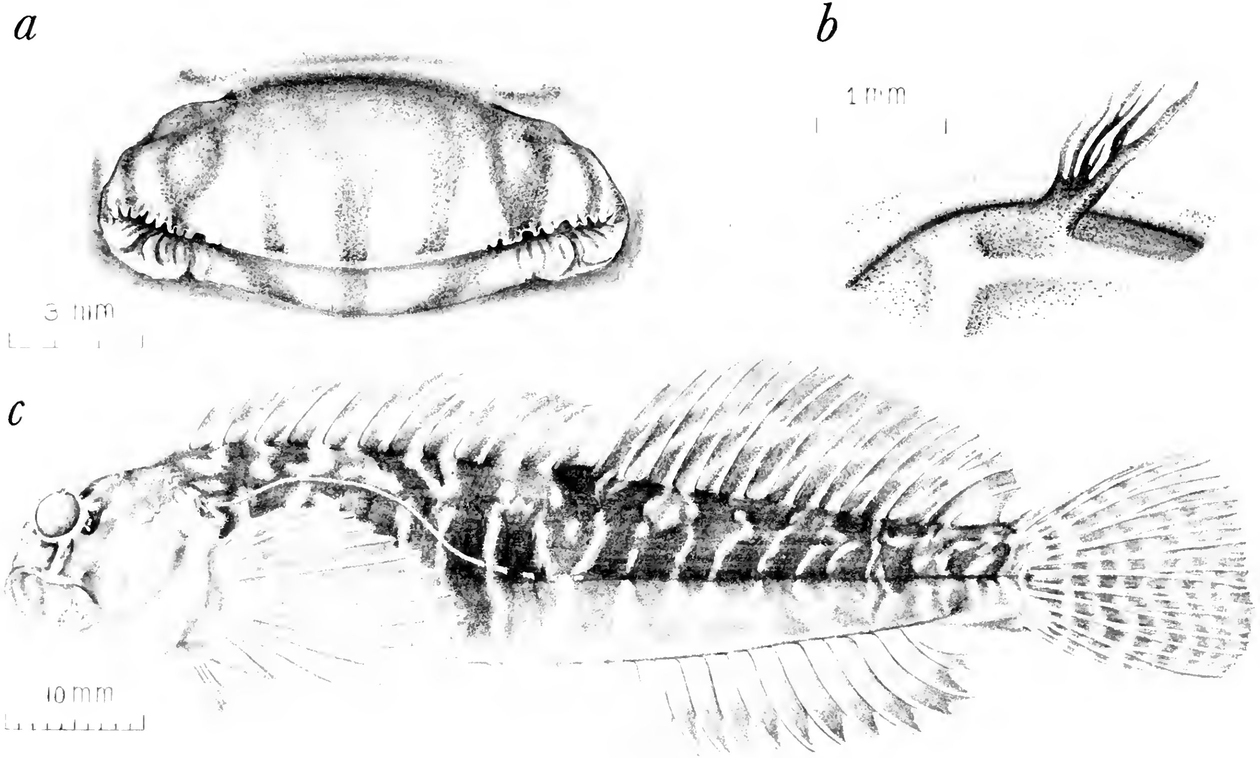
Entomacrodus sealei, USNM 198653, female, 47.2 mm SL, Jarvis Island: *a*, left supraorbital cirri; *b*, upper lip; *c*, lateral view.



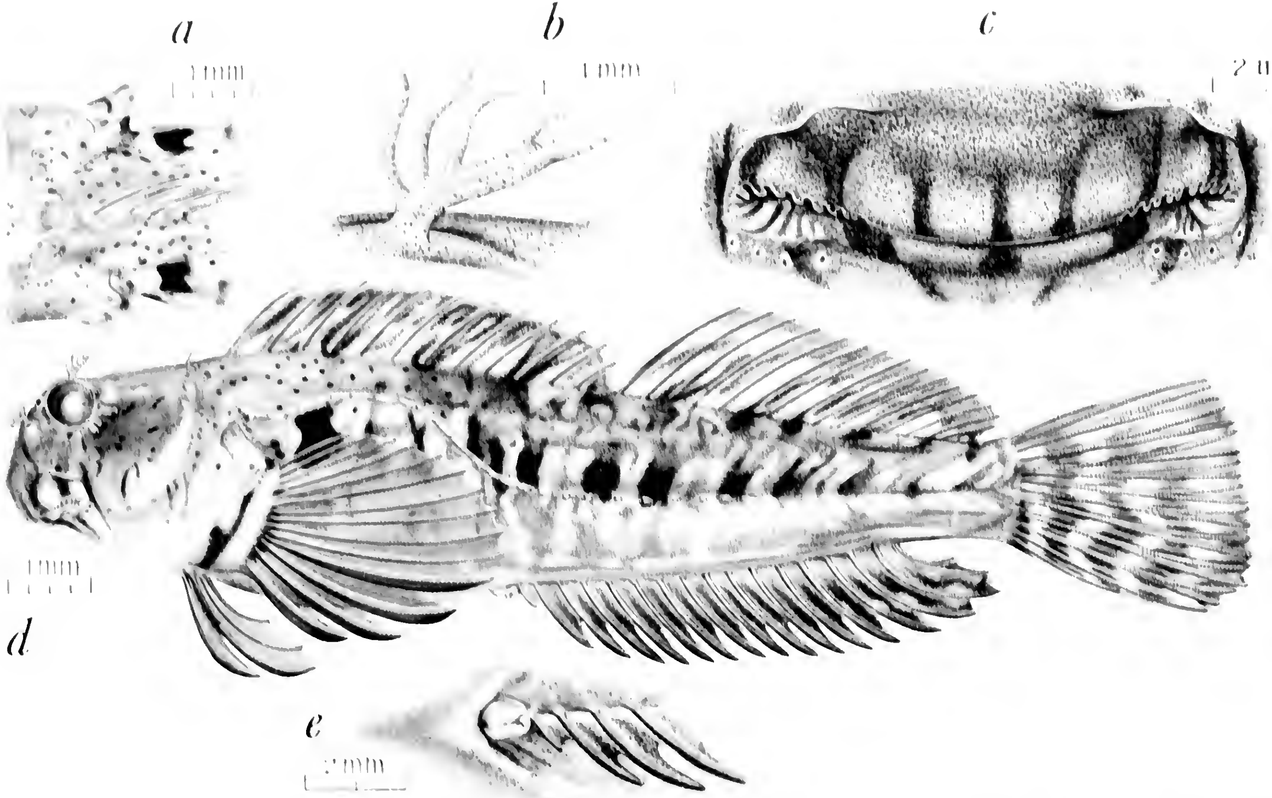
Entomacrodus corneliae, USNM 199991, female, 35.3 mm SL, Marquesas Islands: *a*, upper lip; *b*, left supraorbital cirri; *c*, lateral view.



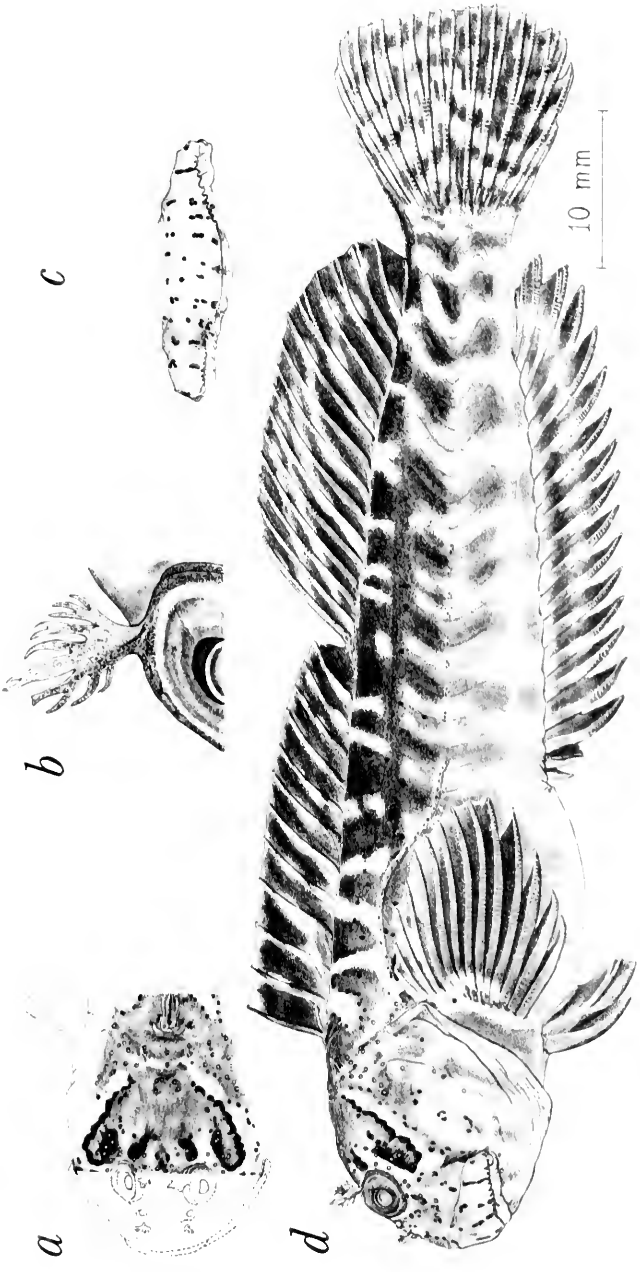
Entomacrodus chiostictus, SU 18973, male, 49.9 mm SL, Baja California: *a*, dorsal view of head; *b*, left supraorbital cirri; *c*, upper lip; *d*, lateral view.



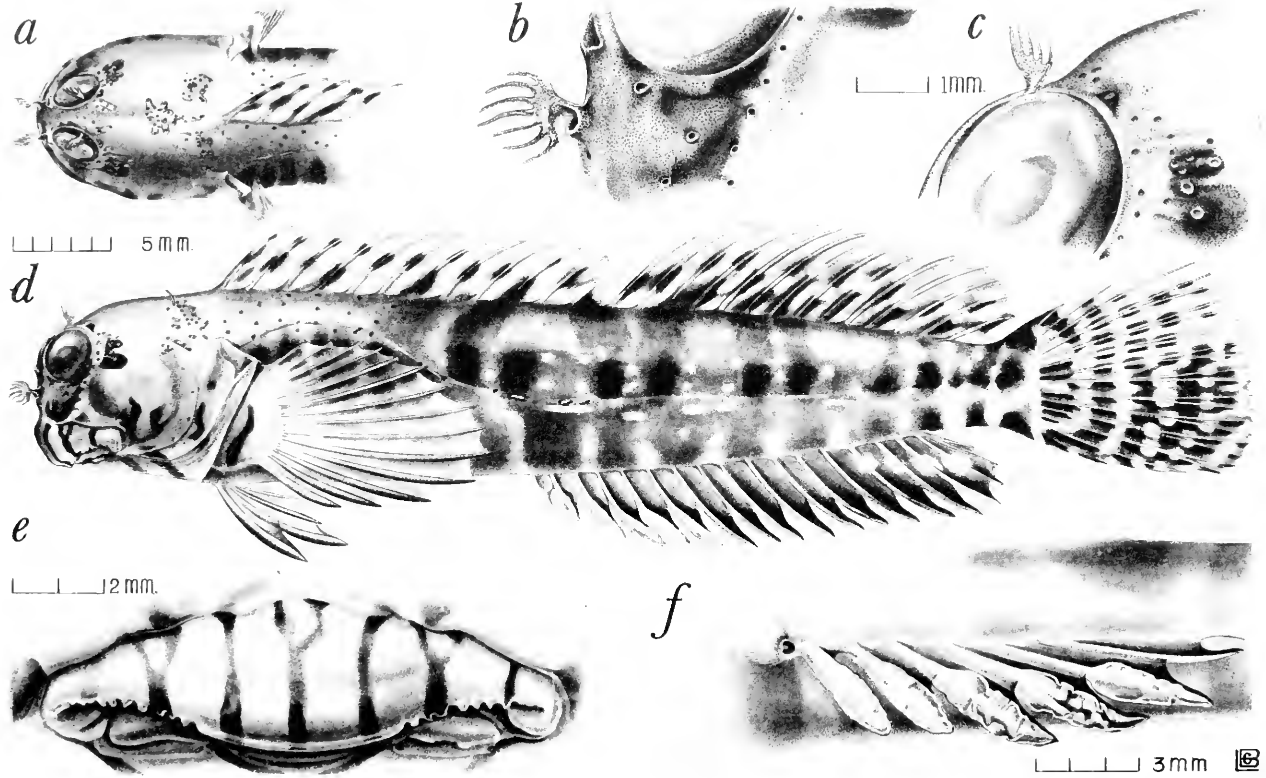
Entomacrodus vomerinus, USNM 43283, female, 73.7 mm SL, Brazil: *a*, upper lip; *b*, left supraorbital cirri; *c*, lateral view.



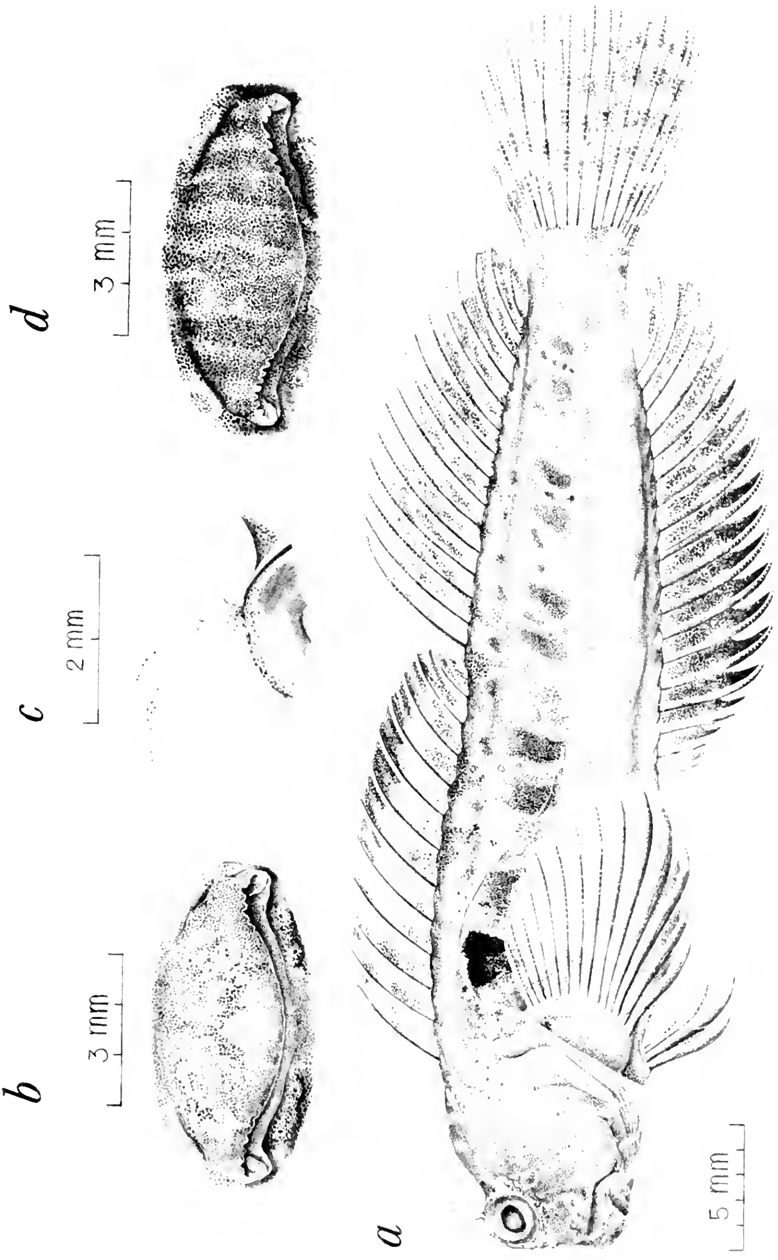
Entomacrodus textilis, BMNH 1960.3.1.45-60, female, 50.7 mm SL, St. Helena: *a*, dorsal view of humeral area; *b*, left supraorbital cirri; *c*, upper lip; *d*, lateral view; *e*, anal urogenital area and anterior anal fin elements.



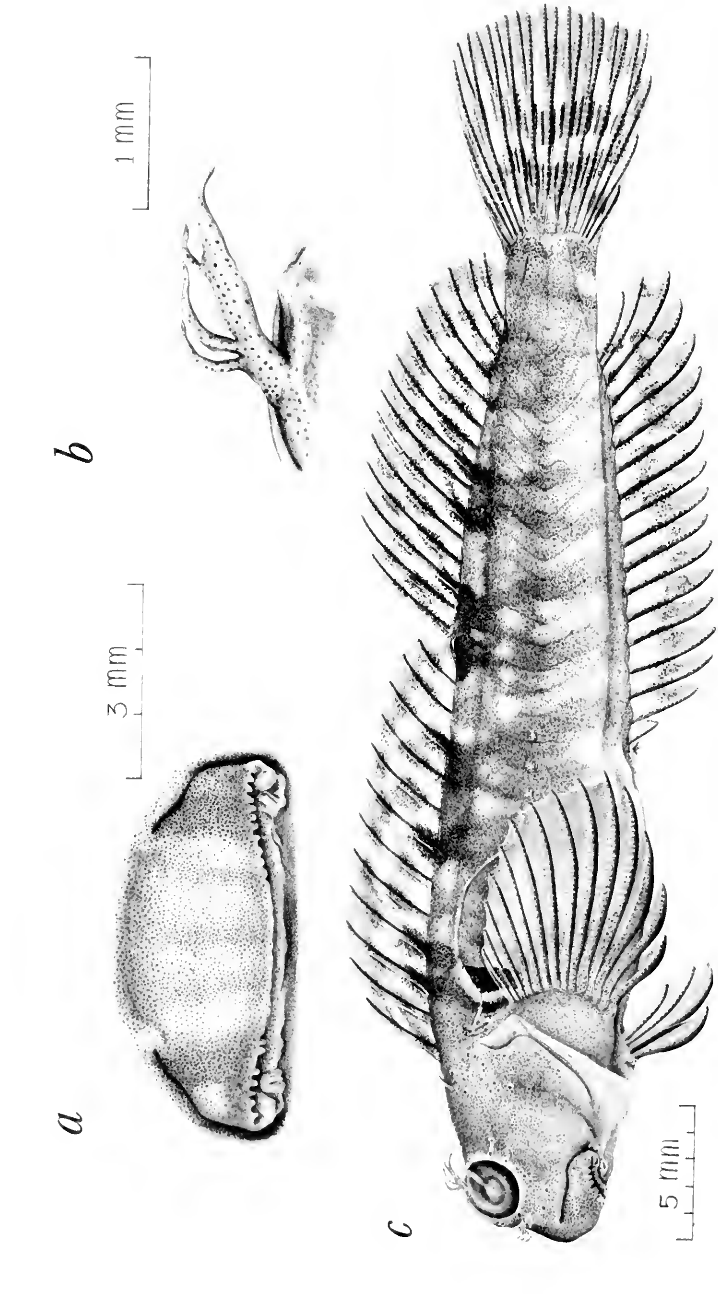
Entomacrodus cadenati, MNHN 1965-705, holotype, male, 64.0 mm SL, Senegal: *a*, top of head; *b*, left supraorbital cirri; *c*, upper lip; *d*, lateral view.



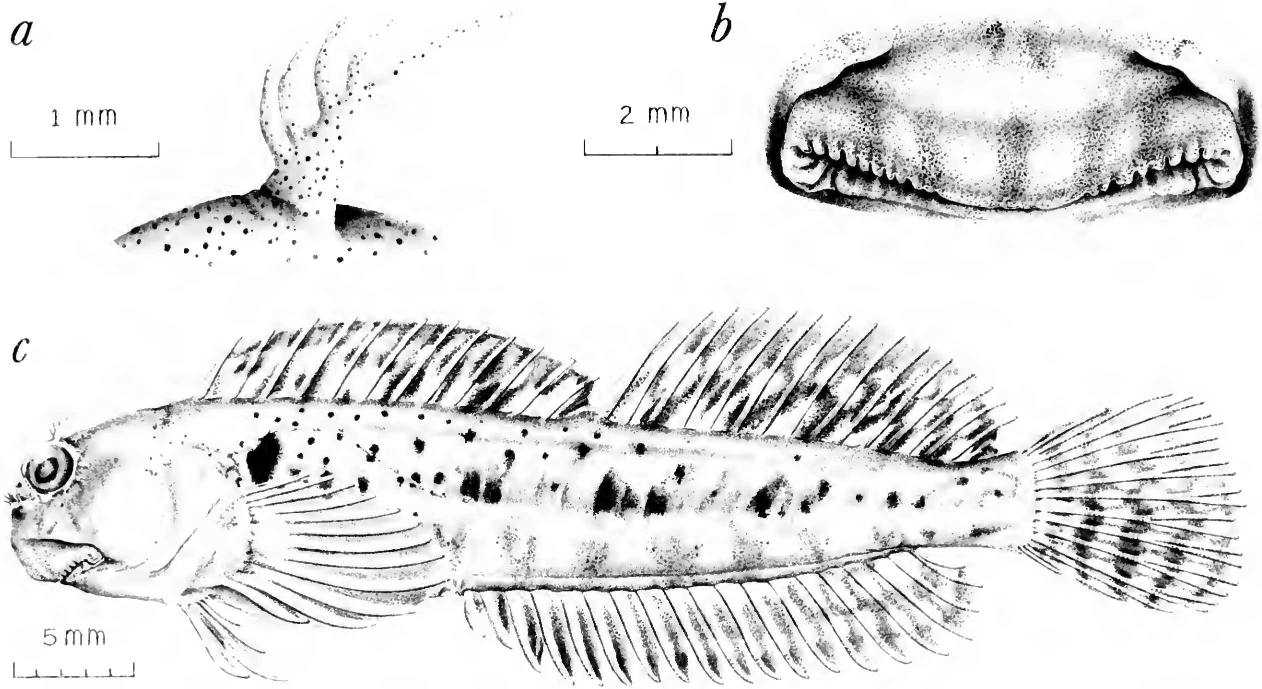
Entomacrodus nigricans, USNM 197324, male, 50.8 mm SL, Serrana Bank: *a*, top of head; *b*, left nasal cirri; *c*, left supraorbital cirri; *d*, lateral view; *e*, upper lip. Male, 48.5 mm SL: *f*, anal-urogenital area and anterior anal fin elements.



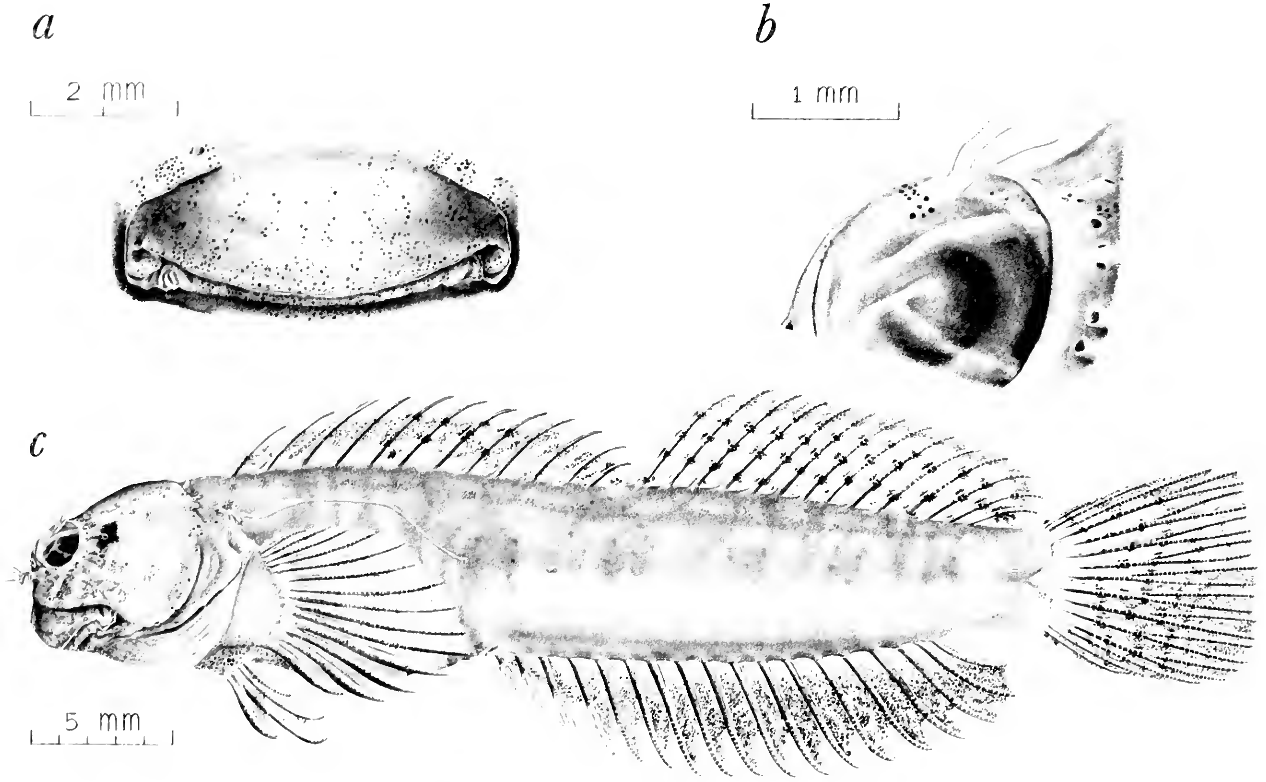
Entomacrodus caudofasciatus, males: USNM 198592, 41.7 mm SL, McKean Island: *a*, lateral view; *b*, upper lip; *c*, left supraorbital cirri. USNM 150586, 41.6 mm SL, Swains Island: *d*, upper lip.



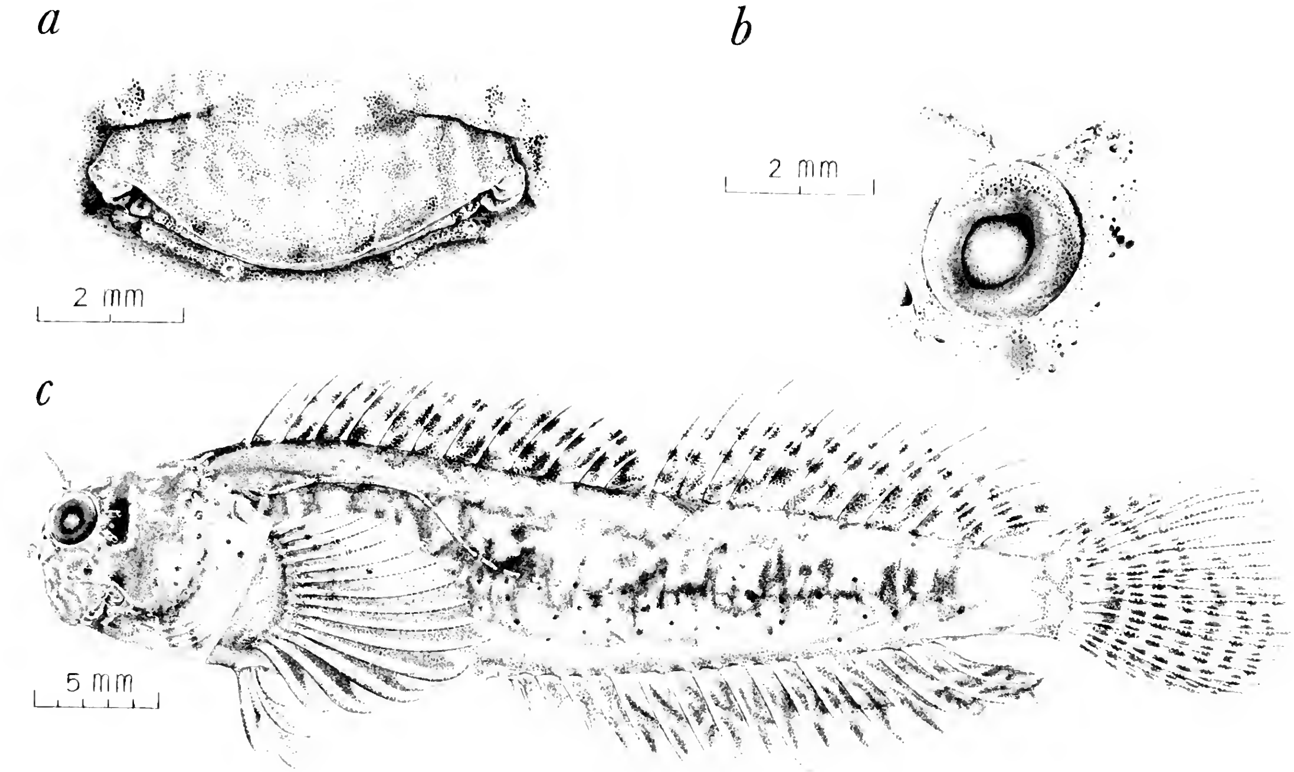
Entomacrodus caudofasciatus, UW 10320, female, 36.8 mm SL, Philippines: *a*, upper lip; *b*, left supraorbital cirri; *c*, lateral view.



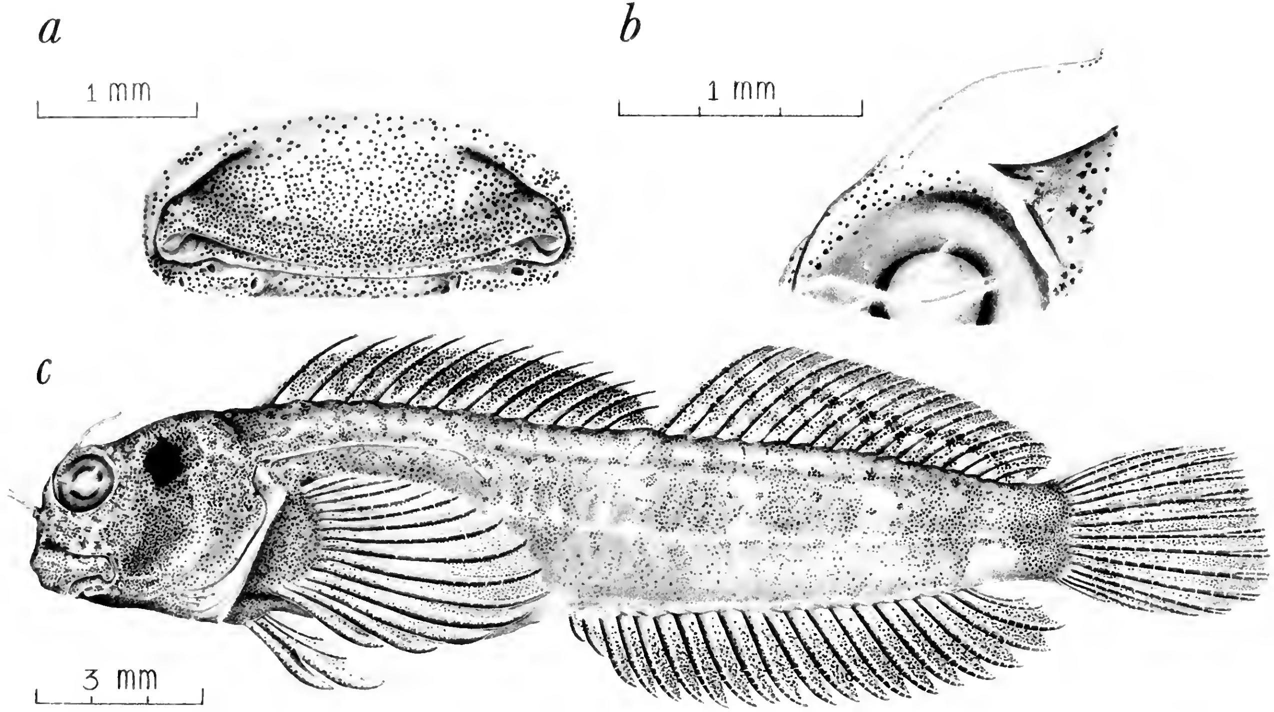
Entomacrodus caudofasciatus, SU 62070, male, 43.0 mm SL, New Britain: *a*, left supraorbital cirri; *b*, upper lip; *c*, lateral view.



Entomacrodus thalassinus thalassinus, USNM 198591, male, 36.8 mm SL, McKean Island: *a*, upper lip; *b*, left supraorbital cirri; *c*, lateral view.



Entomacrodus thalassinus longicirrus, SU 62089, holotype, male, 40.7 mm SL, Gulf of Thailand: *a*, upper lip; *b*, left supraorbital cirri; *c*, lateral view. (The nuchal cirrus is absent on the left side of this specimen; the cirrus from the right side has been illustrated in its place.)



Entomacrodus macrospilus, USNM 200279, holotype, male, 18.7 mm SL, Marquesas Islands: *a*, upper lip; *b*, left supraorbital cirrus; *c*, lateral view.

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BATHYPELAGIC CALANOID COPEPODS OF THE WESTERN INDIAN OCEAN[1]

By George D. Grice and Kuni Hulsemann[2]

The plankton and midwater trawl samples on which this paper is based were obtained during two cruises of R. V. *Anton Bruun* in 1963 and 1964, which, at that time, was participating in the Biological Program of the International Indian Ocean Expedition. The area in which the samples were collected extends from the northern Arabian Sea to approximately the latitude of the subtropical convergence in the southern Indian Ocean. The operation of the *Anton Bruun* in the Indian Ocean provided us with an opportunity to extend our studies on the systematics and the zoogeography of the bathypelagic calanoid copepods from the Atlantic to the Indian Ocean.

We would like to thank Misses Ann Mulcahy and Mary Ann Beecher for their help in sorting and counting the copepods of the plankton samples and Miss Cecilia Simons for inking the original figures. Mr. Bruce Rogers assisted in collecting the samples at sea.

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Methods and Materials

The area in the western Indian Ocean from where the 51 samples considered in this paper were obtained is bounded by latitude 18°N and 40°S and longitude 50°W and 80°W (fig. 1, table 1). Three types of collecting gear were used to sample the deep-living copepods:

Bé multiple plankton sampler: Six of the collections analyzed were collected by this sampler (described by Bé, 1962), hereafter designated the Bé net or sampler. The sampler was equipped with a number 3 net (.333 mm aperture), and the samples obtained between the 1000 and 2000 m depth interval on *Anton Bruun* Cruise 2 were studied. A total of 876 adult copepods (139 species) were identified in these samples. No volume measurements were made.

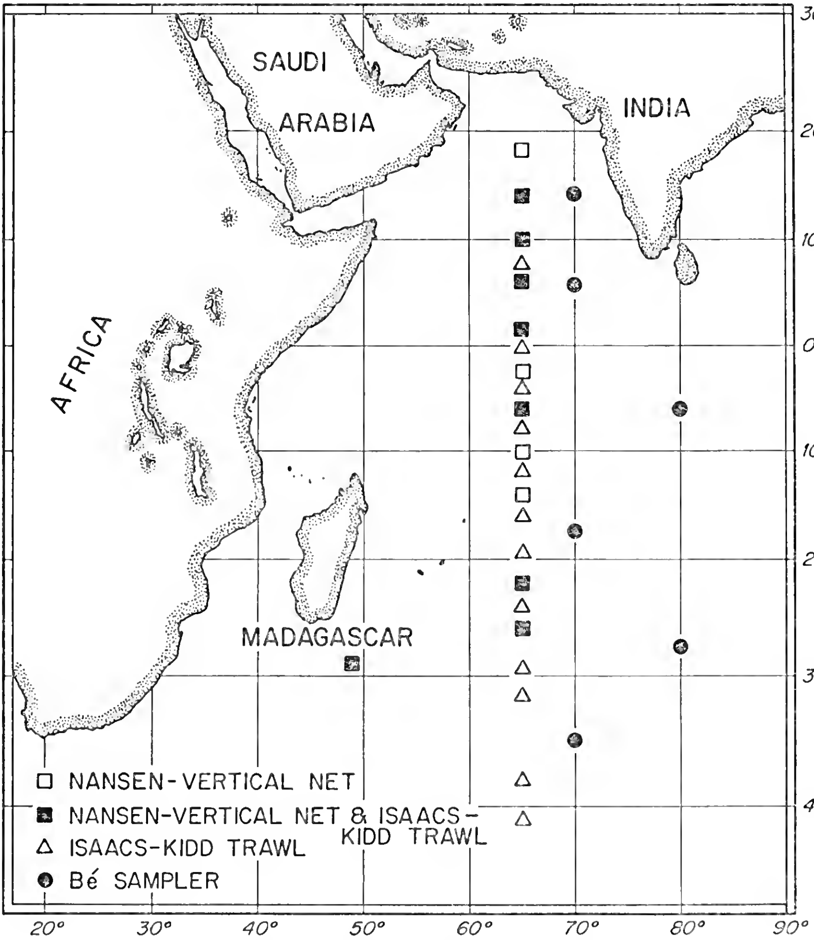

Figure 1.—Location of collection stations.

TABLE 1.—*Collection data* (blank space=volume not recorded, a=position at start of trawl, b=maximum depth from time-depth recorder (T) or wire angle (W))

Collection No.	Station No.	Date	Latitude	Longitude	Collection Depth (m)	Volume Plankton (cc)	No. Species Copepods
		Bé Sampler Collections (Cruise 2)					
1	108	25-V-63	13°50′N	70°07′E	2000-1000		40
2	112	29-V-63	05°48′N	70°03′E	2000-1000		50
3	123	10-VI-63	17°18′S	70°05′E	2000-1000		40
4	131	1-VII-63	35°09′S	69°59′E	2000-1000		41
5	134	6-VII-63	27°31′S	80°08′E	2000-1000		52
6	140	13-VII-63	05°53′S	79°57′E	2000-1000		53
		Isaacs-Kidd Midwater Trawl Collections (Cruise 6)					
7	330B	20-V-64	13°58′N [a]	65°02′E [a]	0-2750(T) [b]		3
8	332A	22-V-64	09°56′N	64°59′E	0-3250(W)		8
9	333A	23-V-64	07°55′N	64°55′E	350-2850(W)		21
10	333B	23-V-64	07°33′N	64°41′E	350- 940(W)		14
11	334B	24-V-64	05°48′N	64°57′E	275-2868(W)		17
12	336A	26-V-64	02°03′N	65°04′E	275- 817(W)		10
13	337B	28-V-64	00°14′S	65°03′E	275-2250(W)		26
14	339B	30-V-64	04°14′S	65°02′E	275-2080(W)		12
15	340A	31-V-64	05°55′S	65°10′E	275-2600(T)		21
16	341A	1-VI-64	08°00′S	65°00′E	0-3820(W)		8
17	343B	4-VI-64	12°11′S	64°11′E	225-1930(W)		17
18	345A	6-VI-64	15°57′S	64°46′E	0-2407(W)		7
19	346A	8-VI-64	19°24′S	65°30′E	225-2600(W)		18
20	347A	23-VI-64	22°11′S	64°53′E	350-2500(W)		21
21	348A	24-VI-64	24°03′S	65°00′E	350-3500(W)		17
22	349B	26-VI-64	26°24′S	65°02′E	350-1470(W)		26
23	351B	28-VI-64	29°45′S	64°58′E	350-1710(W)		25
24	351D	29-VI-64	31°45′S	65°08′E	350-1786(W)		16
25	353A	2-VII-64	37°59′S	64°56′E	350-2394(W)		22
26	354A	4-VII-64	40°48′S	65°03′E	0-1650(W)		18
27	355C	12-VII-64	29°29′S	48°43′E	0-3140(W)		22
		Nansen Vertical Net Collections (Cruise 6)					
28	328	17-V-64	18°02′N	65°08′E	2000- 750	1.5	37
29	328	17-V-64	18°02′N	65°08′E	3000-2000	1.0	18
30	330	20-V-64	13°36′N	65°03′E	1980-1050	1.0	40
31	332	22-V-64	10°04′N	64°59′E	2000-1002	0.7	40
32	332	22-V-64	10°04′N	64°59′E	3000-2000	0.5	19
33	332	22-V-64	10°04′N	64°59′E	4000-3000	0.5	8
34	334	24-V-64	06°01′N	64°59′E	2000-1078	0.7	9
35	334	24-V-64	06°01′N	64°59′E	3000-1894	0.5	16
36	336	27-V-64	01°30′N	65°09′E	2000-1000	1.0	41
37	336	27-V-64	01°30′N	65°09′E	3000-1940	0.7	21
38	338	29-V-64	02°38′S	65°01′E	2000-1000	1.0	41
39	338	29-V-64	02°38′S	65°01′E	3000-2000	0.3	26
40	340	31-V-64	06°00′S	65°10′E	1950-1015	1.0	41
41	340	31-V-64	06°00′S	65°10′E	2950-1990	0.5	28
42	342	2-VI-64	10°07′S	64°27′E	1970-1020	1.0	44
43	342	2-VI-64	10°07′S	64°27′E	3000-1980	0.7	32
44	344	5-VI-64	14°11′S	65°17′E	1980-1010	1.0	39
45	347	23-VI-64	22°06′S	64°55′E	2000-1000	0.3	33
46	349	25-VI-64	26°03′S	64°58′E	2000-1000	0.7	23
47	349	25-VI-64	26°03′S	64°58′E	3000-2000	0.5	8
48	349	25-VI-64	26°03′S	64°58′E	4000-3000	0.3	8
49	355	12-VII-64	29°38′S	49°23′E	2000-1000	0.5	11
50	355	12-VII-64	29°38′S	49°23′E	3000-2000	0.7	3
51	355	12-VII-64	29°38′S	49°23′E	4000-3000	0.7	8

Isaacs-Kidd midwater trawl: Twenty-one Isaacs-Kidd midwater samples (IK) collected on *Anton Bruun* Cruise 6 were examined and 10 to 70 copepods removed from each sample. The larger and deeper living species not usually collected in small vertical nets were selected from the trawl sample. The cod end of the trawl was made of number 2 mesh net (.366 mm). The maximum depth of trawling was determined from a time-depth recorder or calculated from measurements of length of wire-out vs. wire angle. Although a catch divider (Foxton, 1963) was attached to the end of the trawl, it apparently did not operate properly. Consequently, no attempt is made to discuss the vertical distribution of the species collected by the midwater trawl. A total of 797 adult copepods (113 species) were identified in these trawl samples.

Nansen vertical net: Twenty-four collections were also obtained on *Anton Bruun* Cruise 6 by a modified Nansen vertical net (NV). This net is similar to the one described by Currie and Foxton (1957) except that a flow-meter was mounted within the mouth of the net and a time-depth recorder (Benthos Mfg. Co., North Falmouth, Mass.) was attached to the weight below the cod end of the net. The net was made of number 6 mesh (.239 mm aperture). The samples from the following depth intervals are considered here: 2000–1000 m, 3000–2000 m, and 4000–3000 m. The time-depth recorder was equipped with a magnetic switch. Upon closure of the net, this switch activated a stylus that marked the recording chart. The maximum depth reached by the net and the depth of net closure was thus indicated on the chart. Since the speed of ascent of the net (60 m/min) and speed of descent of the messenger (200 m/min) that triggered the release and closure of the net was known, it was also possible to compute the depth of closing. In actual practice the depth of closing was clearly indicated in most cases by a severe jerk of the hydrographic wire when the throttling line pursed the net. When this occurred, the amount of wire out was recorded. Good agreement was found between the computed and actual depths of closure. The corrected depths are given in table 1. The method of measuring the volume of the NV samples and treating the copepods are the same as discussed in an earlier paper (Grice and Hulsemann, 1965). A total of 1740 adult copepods (194 species) were identified in these samples.

Contaminants: Twenty-six species of copepods collected by the NV net, which we feel may possibly have entered the net at shallower depths than those indicated, were found in many collections. These species, listed below, are in addition to those previously considered as contaminants in NV samples collected in the northeastern Atlantic Ocean (see Table II, Grice and Hulsemann, 1965). Species considered contaminants in samples collected with Nansen vertical net below 1000 m (in addition to those species listed by Grice and Hulsemann, 1965) are as follows:

Calanus tenuicornis
Canthocalanus pauper
Nannocalanus minor
Neocalanus gracilis
Undinula darwini
Acrocalanus longicornis
Acrocalanus monachus
Calocalanus pavo
Calocalanus plumulosus
Paracalanus denudatus?
Paracalanus nanus
Clausocalanus farrani
Euaetideus acutus
Scolecithricella maritima, new species
Scolecithricella species
Scolecithrix bradyi
Scolecithrix danae
Scolecithrix nicobarica
Temora discaudata
Undinella simplex
Lucicutia gaussae
Candacia catula
Paracandacia bispinosa
Paracandacia truncata
Labidocera detruncata
Acartia danae

In addition to the contaminant species recognized in the NV collections from the Indian Ocean, shallow-living species were also observed among the copepods in the six Bé net samples. To illustrate, 14 female *Metridia effusa* (a new species described below), a relatively large species (1.58–1.79 mm), were found in three Bé net samples that presumably sampled the 2000–1000 m depth interval; yet this species (18 females) also occured in five NV samples, all of which were collected in depth intervals between 1000 and 200 m. In none of the 12 NV collections obtained between 2000–1000 m was *M. effusa* observed. It was likewise absent from the 12 other NV collections obtained below 2000 m. These occurrence records for this species suggest that the depth data for species collected in the 2000–1000 m depth interval by the Bé net may not be reliable. For this reason we have included in the following discussion of vertical distribution only those species collected by the NV net as we are more familiar with the operation of this particular type of closing net.

Zooplankton and Copepod Abundance

The discussion in the following two sections is based on the analyses of the NV samples as only these collections were obtained quantitatively from several depth intervals in the water column and in the same manner as those collections previously analyzed by us from the northeastern Atlantic (Grice and Hulsemann, 1965).

Displacement volumes.—The displacement volumes of the samples collected by the NV net are shown in figure 2(A). The decrease in zooplankton concentration with increasing depth is clearly evident at all stations but one (station 355). In the depth intervals shown there appeared to be no region along the north-south transect of stations where there were significantly larger or smaller concentrations of zooplankton. On the contrary, omitting one station (station 347), there was no greater than a four-fold difference between the maximum and minimum concentration within the three depth intervals sampled. This is in contrast to our data (unpublished) on the zooplankton in the upper 1000 m, where differences in volumes within the same depth intervals frequently are much larger.

The mean volumes for each of the three depth intervals can be compared to those we obtained in the northeastern Atlantic between 30° and 40°N (Grice and Hulsemann, 1965). For the depth intervals 2000–1000, 3000–2000, and 4000–3000 m the mean zooplankton volume for the Indian Ocean were .004, .002, and .002 cc/m^3, respectively and for the Atlantic Ocean, .005, .002, and .001 cc/m^3, respectively. These data are certainly similar and indicate how small the zooplankton population is at great depths in the northeastern Atlantic and western Indian Oceans.

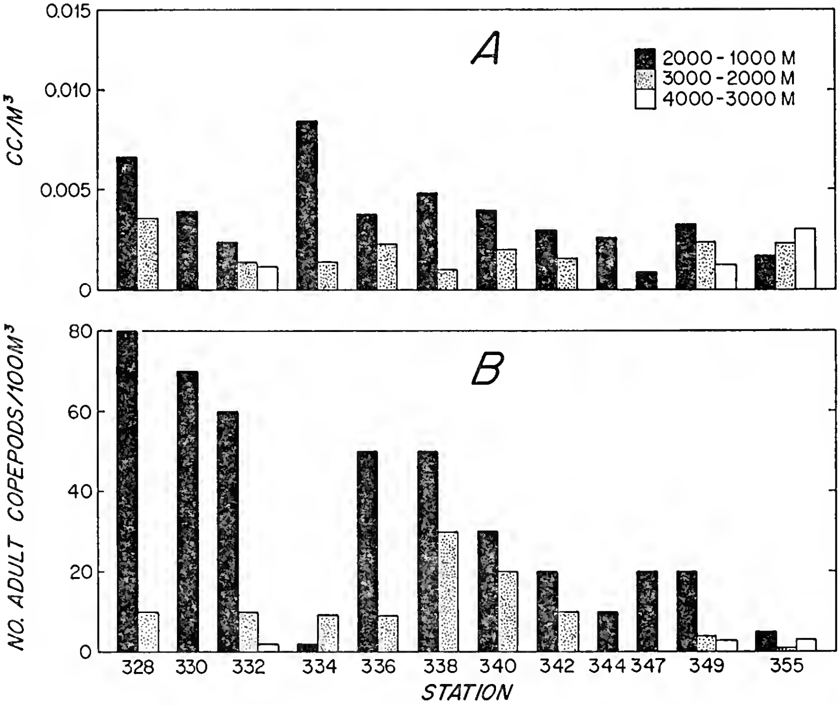

FIGURE 2.—Displacement volumes of the total zooplankton (A) and number of adult copepods excluding contaminant specimens (B).

COPEPOD ABUNDANCE.—The number of adult copepods per 100 cubic meter computed from the collections taken with the NV net are presented in figure 2(B). In general, the trends in copepod abundance are similar to those found for the total zooplankton. With but one exception the numbers of copepods within the 2000–1000 m interval were much larger than in the intervals below 2000 meters. In no case, however, did the numerical abundance exceed one copepod per cubic meter and generally the densities were considerably smaller, especially below a depth of 2000 m. The single exception referred to above, where small numbers of copepods were found in the 2000–1000 m interval, was at station 334. Interestingly, the volume of zooplankton at this station exceeded that of all other stations. A large number of contaminant specimens (i.e., copepods that inhabit shallower depths) were noted in this sample. It thus appears that a considerable quantity of zooplankton from the upper 1000 m might have entered the net and was then retained during its descent to 2000 m; or, possibly, material from the 1000–500 m interval, collected just prior to the collection of the 2000–1000 m sample, may have remained attached to the meshes of the net due to incomplete washing of the net. These animals may have been washed into the plankton during the washing of the net after the 2000–1000 m collection. The volume of zooplankton and number of copepods obtained in the 3000–2000 m collection at station 334 does not appear to be unusual.

The number of adult copepods found in the depth intervals below 1000 m in the Indian Ocean are comparable to that previously found by us between 30° and 40°N in the northeastern Atlantic Ocean (Grice and Hulsemann, 1965).

Vertical Occurrence of Copepods

Population mean size.—We have measured the total length of 1277 adult copepods from the NV samples amd computed the mean size of the animals, excluding the "contaminant" species, collected within each depth interval. The 4000–3000 m interval will not be considered as only 19 adults were found in the three samples obtained from this interval.

The mean size of the adult copepods between 2000 and 1000 m was 2.36 mm and between 3000 and 2000 m, 2.19 mm. The range of mean sizes in these same intervals at four stations between 30° and 40°N in the northeastern Atlantic (Grice and Hulsemann, 1965) was 2.26–3.04 mm (2000–1000 m) and 1.71–2.38 mm (3000–2000 m). The size of the Indian Ocean copepods living between 1000 and 3000 m are quite comparable to those of the Atlantic.

Species vertical distribution.—Since the present study is based on the analyses of only those NV samples collected in depths below 1000 m, the shallow living species and families are poorly represented. There were present 153 species, excluding contaminants, in 13 families.

The predominantly shallow living families Eucalanidae and Pseudocalanidae were together represented by only seven species. No species, excepting those considered contaminants, of Calanidae, Paracalanidae, Centropagidae, Pontellidae, or Acartiidae, also epipelagic families, were found in the NV samples collected below 1000 m.

The vertical range of many of the species in the 2000–1000 m interval extends into depths of less than 1000 m. Notably among these are species in the large families Aetideidae, Scolecithricidae, Lucicutiidae, and Augaptilidae. Each of these families is represented in our collections by 15 or more species.

Nine families of copepods had one-half or more of their species represented in depths below 2000 m. Only one family (Bathypontiidae) had more than one-half of its species (6 of 11) restricted to depths greater than 2000 m. The range of 9 of the 16 species in the family Spinocalanidae extended below 2000 m, but only 1 species was found exclusively below this depth. Species in these last two families are typical of collections made below 2000 m.

Concerning the 153 species, the largest number was found in the 2000–1000 m depth interval (122), an intermediate number in the 3000–2000 m interval (73), and the least number in the 4000–3000 m interval (13). A similar decrease in species diversity with increasing depth was noted by us (Grice and Hulsemann, 1965) in the northeastern Atlantic, where the decrease in diversity was as follows: 2000–1000 m (71), 3000–2000 m (59), and 4000–3000 m (28). In the Indian Ocean seven species were continually distributed from 1000 to 4000 m: *Mimocalanus cultrifer*, *Spinocalanus abyssalis*, *S. magnus*, *Metridia discreta*, *M. princeps*, *Lucicutia longiserrata*, and *Haloptilus longicornis*. Except for *L. longiserrata*, which we misidentified in our Atlantic samples (see Hulsemann, 1966), these species also occurred below 1000 m in the northeastern Atlantic. The first four we recorded in samples collected in excess of 4000 m.

Zoogeography

Geographic distribution of species.—Sewell (1948) has discussed the geographic distribution of copepods in some detail. His account represents an intensive analysis of the literature and attempts to relate the distribution of copepods to ocean currents. The discussion of the copepods in the Indian Ocean is based largely on his own numerous studies made there. A considerable section of his study is devoted to the deep-living copepods of the western Indian Ocean. We are mainly interested here in this discussion and that included in a recent paper by De Decker and Mombeck (1965) as these appear to be the only accounts concerning the zoogeography of the deep-living copepod species of the Indian Ocean.

Sewell (1948) recognized many North Atlantic Ocean species in the northern Indian Ocean. He indicated that these species may be carried southward from the North Atlantic by the North Atlantic

Intermediate water, then eastward into the southwestern Indian Ocean, and finally northward into the northern Indian Ocean by the Antarctic Intermediate water. Citing Sømme's (1933) view that the number of species in a current will decrease in the downstream direction, Sewell examined the occurrence of deep-water copepods at five stations in the Arabian Sea, the Gulf of Aden, and the Gulf of Oman. He indicated that the samples probably came from the Antarctic Intermediate water. He noted a gradual reduction of both deep-sea and North Atlantic copepods in a northward direction; i.e., the number of copepod species decreased from a maximum of 70 (including 56 North Atlantic species) to a minimum of 20 (12 North Atlantic species). The minimum number and the next to the minimum number of species were found in collections obtained in the Gulf of Aden and the Gulf of Oman, respectively. De Decker and Mombeck (1965) cited Sewell's Arabian Sea data and then applied Sewell's technique of examining the contribution of North Atlantic species to an even larger section of the Indian Ocean. These authors compared the number of Atlantic species (134) they found in the bathypelagic fauna of the southwest Indian Ocean with the number of Atlantic species found in the contents of six midwater trawl hauls (described by Sewell, 1929, 1932) made in the area between the Laccadive Sea and west of Andaman Island in the western part of the Bay of Bengal. De Decker and Mombeck pointed out that a gradual decrease of Atlantic species (20 to 0 species) occurred in a northerly and easterly direction.

Our transect of stations extending from approximately 18°N to 40°S along 65°E and 70°E, and one station at 29°S 49°E, in conjunction with the three different methods of collecting deep-water copepods has permitted us to sample a large number of deep-living calanoid species. We have specifically identified 269 species of calanoid copepods excluding the new species and those species found in two Bé net collections made in the eastern Indian Ocean (80°E). As we progressed in our taxonomic analyses of the samples, the similarity of the deep Indian Ocean copepod species to those of the Atlantic became clear. Of interest to us was the appearance of 13 of the 18 species we had recently described from the northeastern Atlantic (Hulsemann and Grice, 1963; Grice and Hulsemann, 1965).

Since our sampling program provided more systematic coverage of bathypelagic species than that of either Sewell (1929, 1932, 1947) or De Decker and Mombeck (1965), it is possible to look more closely into the occurrence of North Atlantic copepod species in the western Indian Ocean. For this analysis we have determined the number of copepod species in our samples in each of 10° latitude intervals from 20°N to 40°S. A comparison of species found in the western Indian Ocean and the North Atlantic is as follows:

latitude interval western Indian Ocean	*number western Indian Ocean species*[3]	*number species common to North Atlantic*[4]	*percent of species in common*
20°N–10°N	98	90	92
10°N– 0°	117	100	85
0° –10°S	96	95	99
10°S–20°S	120	105	88
20°S–30°S	103	92	89
30°S–40°S	70	55	79

It is quite clear from examination of this tabulation that very large numbers of so-called North Atlantic species are present at all latitudes and that no significant decrease is evident in either the number of species within each interval (north of 30°S) or in the number within each interval that are also present in the North Atlantic Ocean. Thus, Sewell's view of the "falling off" of deep sea copepods and especially the reduction of North Atlantic species northwards in the Antarctic Intermediate water in the northern Arabian Sea is not supported by our data. Since the two stations where Sewell found the least number of copepods are in the Gulf of Oman and Gulf of Aden, the reduction of diversity at these stations may be related to conditions present in these relatively constricted areas.

Other studies on the hydrography of the western Indian Ocean may not entirely support Sewell's interpretation of water mass distribution. Sewell's report of Antarctic Intermediate water in the Arabian Sea is based on an investigation of Mohamed (1940) of pH distribution. Sewell also cited the work of Möller (1929), which indicated that northward flowing subpolar water (500–2000 m) is traceable only to about 5°N (Möller referred only to the eastern Indian Ocean). Sverdrup et al. (1942) indicated that Antarctic Intermediate water and Bottom water flows north and mixes with the deep water in the region north of the Equator. These water masses then flow to the south. According to Ivanenkov and Gubin (1960), in the area between 10° and 16°S the upper part of the southward flowing North Indian Deep water mixes with northward flowing sub-Antarctic Intermediate water and the lower part of the North Indian Deep water mixes with Antarctic Bottom water. This mixing results in the formation of two water masses: the South Indian Deep water (1500–3500 m), which flows southward and North Indian Bottom water (a layer of 200–700 m), which flows northward. Most of the NV and Bé net samples considered in this paper, which were

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[3] Present in our samples.

[4] From Grice and Hulsemann (1965) and other literature records from North of 0°.

collected south of approximately 10°S, were probably obtained from within the South Indian Deep water. The midwater trawl (IK) also sampled this water during the greater part of each collection, The North Indian Deep water, formed in the northern Arabian Sea, is centered between 400 and 1500 m north of the Equator and between 800 and 2000 m south of the Equator. Most of our NV, Bé, and IK samples collected north of about 10°S were probably collected in this water mass.

It thus appears from Ivanenkov and Gubin's (1960) work that no sub-Antarctic water is present as such in the Arabian Sea. The continuity that apparently exists between the many species of copepods in the western Indian Ocean and the North Atlantic is apparently due to the transfer or movement of individuals from one water mass to another. Obviously this must be an extremely slow process, but as mentioned below, so might be the rate of speciation in these bathypelagic crustaceans.

Since De Decker and Mombeck's comments relate mostly to the occurrence of North Atlantic copepods (reported by Sewell, 1929, 1932, from six midwater trawl samples) mainly in the eastern Indian Ocean, where we have no samples, we are unable to compare their conclusions with our data. It may, however, be premature to conclude as De Decker and Mombeck did, that Atlantic Ocean copepods decrease in a northerly and easterly direction in the Indian Ocean. The midwater nets used by Sewell were made of "mosquito netting" and the number of copepod species collected in the six hauls was quoted by De Decker and Mombeck to be between only 1 and 54.

Rather than emphasize the decrease of Atlantic Ocean copepods, which our data fail to corroborate anyway, we wish to emphasize the extremely widespread distribution of bathypelagic copepods. The large number of our Indian Ocean species that are also common to the Atlantic (241 in all) is clear evidence for the effective dispersal of copepods by deep currents, slow and sluggish as these may be. Ninety-two percent of the deep-living species in the Arabian Sea, which is included in the northernmost interval (p. 10), are also found in the North Atlantic, some 8000 nautical miles distance. This high degree of similarity in copepod species may indicate a slow rate of speciation in these bathypelagic crustaceans, a suggestion that Day (1963) has already made for planktonic organisms.

Antarctic Species.—As indicated above, most of our collections contained species that are widely distributed in the deep waters. Certain of our collections obtained at the southern end of our sampling area, however, contained species we did not find elsewhere. Although few in number, these species have been included in a list of Antarctic and sub-Antarctic copepod species compiled by Vervoort (1965).

Three of the four collections in which we recognized Antarctic species were obtained from stations located between 35°S and 40°S, which is in the area of the subtropical convergence. The other collection where one Antarctic species occurred was obtained from 29°S.

The species in our collections that are especially indicative of Antarctic or sub-Antarctic waters and which have not been reported from elsewhere are *Calanus australis* Brodsky, *Euchaeta biloba* (Farran), and *Scolecithricella dentipes* Vervoort. *Rhincalanus gigas* Brady, a species much more important in the Antarctic because of its great abundance there, occurred in three of our collections made south of 35°S and in one collection made at 29°S. These four species were obtained in the Bé net and midwater trawl and were probably collected in the upper few hundred meters (see "Methods and Materials"). The occurrence of *R. gigas* at 29°S is considerably north of the subtropical convergence (approximately 40°S) and probably represents the northernmost distribution record for this species in the Indian Ocean. Thompson's (1900) report of *R. gigas* from 20°S has been questioned by Sewell (1929). *Metridia lucens* Boeck was also present in one sample (Bé net) from 35°S. It occurs in the North Atlantic and North Pacific Oceans and is also present in waters of high latitudes in the Southern Hemisphere. Thus, the above five species comprise the Antarctic element in our Indian Ocean copepod species.

INDIAN OCEAN SPECIES.—There are few species in the Indian Ocean including the epi-planktonic ones that are not found elsewhere. Out of a total of 310 species found by us, 40 are not found in the Atlantic Ocean. Of these 40, however, only 7—*Bradycalanus gigas* Sewell, *Amallothrix indica* Sewell, *Scottocalanus dauglishi* Sewell, *Lucicutia bella* Hulsemann, *L. pallida* Hulsemann, *L. rara* Hulsemann, *Euaugaptilus indicus* (Sewell)—are apparently restricted to the Indian Ocean. The remaining ones are also present in Pacific or Antarctic waters. The above 7 species are in addition to the 17 species indicated by Sewell (1947, p. 540) as being possibly endemic to the Indian Ocean. Actually, due to subsequently published distribution records, 3 of these 17 species have been reported from the Pacific: *Chirundina indica* (Grice, 1962), *Cornucalanus indicus* (Brodsky, 1950; Tanaka, 1960), *Lucicutia aurita* (Tanaka, 1963, as *L. maxima*). Further, *L. aurita* has been found in the Malay Archipelago (Scott, 1909) and near the island of South Georgia (Gunther and Hardy, 1935), both times reported as *L. maxima* (see Hulsemann, 1966).

Our list of 310 species includes 78 that have not hitherto been reported from the Indian Ocean. This is not unexpected since the bathypelagic species have not been studied as extensively as the epipelagic ones. The discovery of 17 new species, which are described in the present paper, is further indication of the paucity of prior taxonomic studies on the deep-water copepods of the Indian Ocean.

Taxonomy

One new genus, 17 new species, 8 previously unknown males, and 1 previously unknown female of calanoid copepods are described below. Systematic or distributional remarks are presented for 25 other species. Also included are descriptions and figures of 9 specimens which, because they may be referable to described species, are not recognized as new. Seven additional species of *Lucicutia* from these collections, which were not previously known from the Indian Ocean, are reported by Hulsemann (1966). In all, 310 species (300 were specifically identified) were found in the collections.

The forms of *Clausocalanus arcuicornis* (Dana) and *Microcalanus pygmaeus* (Sars) were not distinguished. The species designated *Euchaeta* species is being described elsewhere by Dr. Marion Fontaine.

In the description of the species the first to fifth thoracic segments refer to those to which the first to fifth pairs of feet are attached.

Holotype specimens have been deposited in the U.S. National Museum, Washington, D.C., and representative specimens of other species have been deposited in the Woods Hole Oceanographic Institution collections.

Species and collection numbers where they occurred are listed below. (The 78 species not previously known from the Indian Ocean are indicated by an asterisk. See table 1 for collecting data corresponding to collection number.)

CALANIDAE		
*1.	*Calanus australis* Brodsky, 1959	4
2.	*C. tenuicornis* Dana, 1849	5, 43–45
3.	*Canthocalanus pauper* (Giesbrecht, 1888)	6, 41
4.	*Nannocalanus minor* (Claus, 1863)	6, 31, 34, 43–45
5.	*Neocalanus gracilis* (Dana, 1849)	3, 5, 43
6.	*Undinula darwini* (Lubbock, 1860)	6, 29, 30, 42, 43
MEGACALANIDAE		
7.	*Bathycalanus bradyi* (Wolfenden, 1905)	7–11, 14, 15, 19, 20, 22–25
*8.	*B. princeps* (Brady, 1883)	24, 25
9.	*B. richardi* Sars, 1905	10, 15
*10.	*B. sverdrupi* Johnson, 1958	14, 19
11.	*Bradycalanus gigas* Sewell, 1947	15, 27
*12.	*B. sarsi* (Farran, 1939)	9, 15, 18, 21
*13.	*B. typicus* A. Scott, 1909	7, 8, 11
14.	*Megacalanus princeps* Wolfenden, 1904	8–15, 17, 18, 20, 21
EUCALANIDAE		
15.	*Eucalanus attenuatus* (Dana, 1849)	2, 16, 38, 45
16.	*E. crassus* Giesbrecht, 1888	38
17.	*E. elongatus hyalinus* (Claus, 1866)	4–6, 19–24, 45

18. *Mecynocera clausii* Thompson, 1888	41–44
19. *Rhincalanus cornutus* (Dana, 1849)	2, 3, 6, 36
20. *R. gigas* Brady, 1883	4, 25–27
21. *R. nasutus* Giesbrecht, 1888	3–6, 27, 36, 44, 46
PARACALANIDAE	
22. *Acrocalanus longicornis* Giesbrecht, 1888	44
23. *A. monachus* Giesbrecht, 1888	34, 42, 44
24. *Calocalanus contractus* Farran, 1926	48
25. *C. pavo* (Dana, 1849)	42, 43
26. *C. plumulosus* (Claus, 1863)	38
27. *C. styliremis* Giesbrecht, 1888	30–32, 34–43, 51
28. *Paracalanus aculeatus* Giesbrecht, 1888	28–30
29. *P. denudatus*? Sewell, 1929	30, 33, 34, 37, 42, 43
30. *P. nanus* Sars, 1907	37, 46, 51
PSEUDOCALANIDAE	
31. *Clausocalanus arcuicornis* (Dana, 1849)	4–6, 30, 39–46, 48, 49
32. *C. farrani* Sewell, 1929	38, 40–44
33. *C. furcatus* (Brady, 1883)	6, 28–31, 34, 38–41, 44, 45
34. *C. paululus* Farran, 1926	46–48, 51
35. *Ctenocalanus vanus* Giesbrecht, 1888	40, 42, 43, 45, 51
36. *Farrania frigida* (Wolfenden, 1911)	3, 39, 41
37. *Microcalanus pygmaeus* (Sars, 1900)	28, 30, 31, 36–40
SPINOCALANIDAE	
38. *Mimocalanus cultrifer* Farran, 1908	1, 2, 4–6, 28–32, 35–48
39. *M. inflatus*? Davis, 1949	36, 45
*40. *M. nudus* Farran, 1908	6, 31, 46
41. *Mimocalanus* species	39
42. *Monacilla tenera* Sars, 1907	30, 31, 40, 42, 45, 49
43. *M. typica* Sars, 1905	2-6, 34, 36, 38
*44. *Spinocalanus abruptus* Grice and Hulsemann, 1965	29, 31, 42, 45
45. *S. abyssalis* Giesbrecht, 1888	1-3, 5, 28, 30, 31, 35-39, 42, 43, 45, 46, 49
S. abyssalis var. *pygmaeus* Farran, 1926	1, 2, 4-6, 28-49
*46. *S. angusticeps* Sars, 1920	4, 6, 36, 40, 45
*47. *S. longipes* Tanaka, 1956	1, 28
48. *S. magnus* Wolfenden, 1904	1-6, 29, 33, 35, 37, 39, 43, 44
*49. *S. ovalis* Grice and Hulsemann, 1965	35, 51
50. *S. spinosus* Farran, 1908	1-3, 5, 6, 28, 30, 31, 36, 39, 40, 42-46, 50
*51. *S. validus* Sars, 1905	23, 45
52. *S. ventriosus*, new species	31, 32, 38, 41, 46
53. *Spinocalanus* species	46
*54. *Teneriforma naso*, new combination	28, 37, 38
AETIDEIDAE	
55. *Aetideopsis retusa*, new species	43
56. *Aetideus armatus* (Boeck, 1872)	5
*57. *Batheuchaeta lamellata* Brodsky, 1950	51
58. *Bradyetes florens*, new species	38
59. *Bradyidius bradyi* (Sars, 1902)	35
60. *Chiridiella macrodactyla* Sars, 1907	28, 38
61. *Chiridius poppei* Giesbrecht, 1892	2, 5
62. *Chirundina indica* Sewell, 1929	3, 13
63. *C. streetsi* Giesbrecht, 1895	5, 6, 16, 19-23, 27
*64. *Chirundinella cara* Tanaka, 1957	12

65. *Euaetideus acutus* (Farran, 1929)	44
66. *Euchirella amoena* Giesbrecht, 1888	13, 16
67. *E. bella* Giesbrecht, 1888	1, 2, 11, 21, 28, 30
68. *E. bitumida* With, 1915	22, 27
69. *E. curticauda* Giesbrecht, 1888	40
70. *E. formosa* Vervoort, 1949	20, 22, 23
71. *E. galeata* Giesbrecht, 1888	12, 13
72. *E. maxima* Wolfenden, 1905	1, 13, 16
73. *E. messinensis* (Claus, 1863)	19, 22, 27
74. *E. pulchra* (Lubbock, 1856)	2, 36, 40, 42, 44
75. *E. venusta* Giesbrecht, 1888	38
76. *Gaetanus antarcticus* Wolfenden, 1905	9, 13-15, 21-26
77. *G. armiger* Giesbrecht, 1888	2
*78. *G. brachyurus* Sars, 1907	4, 19, 21
79. *G. curvirostris* Sars, 1905	42
*80. *G. ferox* With, 1915	5
81. *G. kruppii* Giesbrecht, 1903	11, 21, 28
82. *G. latifrons* Sars, 1905	23
83. *G. minor* Farran, 1905	5
84. *G. pileatus* Farran, 1903	4, 32
*85. *Gaidius brevicaudatus* (Sars, 1907)	37
86. *G. minutus* Sars, 1907	36, 40
*87. *G. robustus* (Sars, 1905)	17, 22, 25
88. *G. tenuispinus* (Sars, 1900)	36
89. *Pseudeuchaeta brevicauda* Sars, 1905	4, 11, 13, 14, 17, 19, 22, 37
*90. *Pseudochirella divaricata* (Sars, 1905)	19
*91. *P. dubia* (Sars, 1905)	9, 50
*92. *P. gibbera* Vervoort, 1949	11, 13, 15, 24
93. *P. hirsuta* (Wolfenden, 1905)	24–26
94. *P. magna* (Wolfenden, 1911)	26
95. *P. obtusa* (Sars, 1905)	1, 13, 26
*96. *P. polyspina* Brodsky, 1950	25
*97. *P. pustulifera* (Sars, 1905)	22?, 24, 25
*98. *P. semispina* Vervoort, 1949	13
99. *P. squalida*, new species	23
*100. *P. tuberculata* Tanaka, 1957	16
101. *Undeuchaeta intermedia* A. Scott, 1909	6, 38
102. *U. major* Giesbrecht, 1888	17
103. *U. plumosa* (Lubbock, 1856)	2–4, 23, 44, 46
104. *Valdiviella brevicornis* Sars, 1905	11, 13, 15, 20, 36, 41
105. *V. insignis* Farran, 1908	7–17, 19, 21–27, 37, 38
106. *V. oligarthra* Steuer, 1904	15
EUCHAETIDAE	
107. *Euchaeta barbata* Brady, 1883	22, 24, 25
108. *E. biloba* (Farran, 1929)	4
109. *E. bisinuata* Sars, 1907	6, 20, 22, 36
*110. *E. calva* (Tanaka, 1958)	9, 10, 12, 13, 26
111. *E. dubia* Esterly, 1906	24–26
112. *E. exigua* Wolfenden, 1911	4
*113. *E. farrani* With, 1915	26
114. *E. gracilis* Sars, 1905	24, 27
115. *E. hanseni* With, 1915	11–13

116. *E. malayensis* (Sewell, 1929)	3, 26, 27
117. *E. marina* (Prestandrea, 1833)	29, 30, 39
*118. *E. robusta* Wolfenden, 1911	2
119. *E. sarsi* Farran, 1908	12, 17, 25
120. *E. scotti* Farran, 1908	8, 9, 20
121. *E. tonsa* Giesbrecht, 1895	22, 26, 40
122. *E. weberi* (A. Scott, 1909)	12, 13
123. *E. wolfendeni* A. Scott, 1909	44
124. *Euchaeta* species	24–26
PHAENNIDAE	
125. *Cornucalanus chelifer* (Thompson, 1903)	25
126. *C. indicus* Sewell, 1929	23
127. *C. simplex* Wolfenden, 1905	15
*128. *Heteramalla dubia* (T. Scott, 1894)	40
129. *Onchocalanus affinis* With, 1915	1
130. *O. magnus* (Wolfenden, 1906)	17, 23, 24
131. *O. trigoniceps* Sars, 1905	1
132. *Xanthocalanus greeni* Farran, 1905	10, 14
133. *X. hispidus*, new species	49
*134. *X. obtusus* Farran, 1905	47
SCOLECITHRICIDAE	
135. *Amallothrix arcuata* (Sars, 1920)	3
*136. *A. curticauda* (A. Scott, 1909)	5
137. *A. emarginata* (Farran, 1905)	2, 22, 23, 28, 43, 45, 46
138. *A. gracilis* (Sars, 1905)	1, 3
139. *A. indica* Sewell, 1929	1, 4, 28, 30, 31, 38, 40, 41
*140. *A. mollis* (Esterly, 1913)	2
*141. *A. obtusifrons* Sars, 1905	27, 32
142. *A. paravalida* Brodsky, 1950	3–6, 31, 38, 49
*143. *A. robustipes* Grice and Hulsemann, 1965	6, 40
144. *A. valida* (Farran, 1908)	2, 9, 11, 29, 38
145. *Lophothrix frontalis* Giesbrecht, 1895	20, 22, 23, 27, 49
146. *L. humilifrons* Sars, 1905	11, 13, 23, 27
*147. *L. insignis* Sars, 1920	15
*148. *Racovitzanus levis* Tanaka, 1961	5
*149. *R. porrectus* (Giesbrecht, 1888)	2, 28, 40
150. ?*Racovitzanus* species	29
151. *Scaphocalanus affinis* (Sars, 1905)	6, 19, 30, 44
*152. *S. bogorovi* Brodsky, 1955	43, 45
153. *S. brevicornis* (Sars, 1900)	1, 4, 6, 28, 30, 31, 45
*154. *S. curtus* (Farran, 1926)	5, 6, 36, 38
*155. *S. echinatus* (Farran, 1905)	3
156. *S. elongatus* A. Scott, 1909	1–3, 5, 29, 36, 38–40, 42, 44, 45
*157. *S. longifurca* (Giesbrecht, 1888)	1, 5, 36, 39, 41, 45
158. *S. magnus* (T. Scott, 1894)	3, 29, 36, 37, 39, 40
159. *S. major* (T. Scott, 1894)	3, 5, 41
160. *S. subbrevicornis* (Wolfenden, 1911)	1–6, 28, 30, 31, 36, 38, 40, 42, 43, 45
*161. *Scolecithricella auropecten* (Giesbrecht, 1892)	2, 31
162. *S. dentata* (Giesbrecht, 1892)	2, 5, 6
163. *S. dentipes* Vervoort,1951	4
164. *S. grata*, new species	4
*165. *S. laminata* (Farran, 1926)	36, 40, 42

166. *S. maritima*, new species	31, 40
167. *S. ovata* (Farran, 1905)	36
*168. *S. profunda* (Giesbrecht, 1892)	2
*169. *S. spinata* Tanaka, 1962	2, 6
*170. *S. timida* Tanaka, 1962	2, 3, 38, 40
*171. *S. unispinosa* Grice and Hulsemann, 1965	47
172. *Scolecithricella* species	36
173. *Scolecithrix bradyi* Giesbrecht, 1888	42, 43
174. *S. danae* (Lubbock, 1856)	34, 42, 43
*175. *S. fowleri* Farran, 1926	42
176. *S. nicobarica* Sewell, 1929	28, 30
177. *Scottocalanus dauglishi* Sewell, 1929	9
178. *S. helenae* (Lubbock, 1856)	26
THARYBIDAE	
*179. *Undinella brevipes* Farran, 1908)	31, 42
TEMORIDAE	
180. *Temora discaudata* Giesbrecht, 1889	41
181. *Temoropia mayumbaensis* T. Scott, 1894	28, 29, 31, 32, 35–39, 41, 44–47
METRIDIIDAE	
182. *Gaussia princeps* (T. Scott, 1894)	8–11, 14, 19, 25
183. *Metridia boecki* Giesbrecht, 1889	2, 4, 28, 37, 38, 44, 46
184. *M. brevicauda* Giesbrecht, 1889	1–6, 28, 30, 31, 35, 36, 40, 42, 49
*185. *M. discreta* Farran, 1946	1, 4, 29–33, 35, 39, 41, 43, 46, 48, 49
186. *M. effusa*, new species	1, 5, 6
187. *M. lucens* Boeck, 1864	4
188. *M. macrura* Sars, 1905	1, 3, 15, 21, 31, 32, 37, 41
189. *M. princeps* Giesbrecht, 1889	2, 6, 8, 10, 12, 13, 15, 17–28, 31, 35–37, 40 42, 46, 51
190. *M. venusta* Giesbrecht, 1889	2–6
191. *Pleuromamma abdominalis* (Lubbock, 1856)	2, 3, 5, 38
192. *P. gracilis gracilis* (Claus, 1863)	2, 4–6, 44
193. *P. indica* Wolfenden, 1905	1, 2, 5, 30, 31, 42
194. *P. piseki* Farran, 1929	31
195. *P. quadrungulata quadrungulata* (Dahl, 1893)	2, 6, 36, 40
196. *P. xiphias* (Giesbrecht, 1889)	2–6, 11, 13, 16, 18, 27, 38, 40
CENTROPAGIDAE	
197. *Centropages gracilis* (Dana, 1849)	6
LUCICUTIIDAE	
198. *Lucicutia aurita* Cleve, 1904	9, 13–17, 40, 44
199. *L. bella* Hulsemann, 1966	20, 21, 27, 46
200. *L. bicornuta* Wolfenden, 1905	17, 22, 27
201. *L. curta* Farran, 1905	2, 4–6, 30, 31, 36, 40, 43, 46
202. *L. flavicornis* (Claus, 1863)	3–5, 42, 45, 47
203. *L. formosa* Hulsemann, 1966	27, 51
204. *L. gaussae* Grice, 1963	3, 42, 43
205. *L. grandis* (Giesbrecht, 1895)	1, 2, 5, 21, 22, 25–28, 30, 31, 40
206. *L. intermedia* Sars, 1905	1, 30, 40–42, 44, 45
207. *L. longicornis* (Giesbrecht, 1889)	1, 2, 28, 30, 31
208. *L. longiserrata* (Giesbrecht, 1889)	3–6, 30, 31, 42, 44
209. *L. longispina* Tanaka, 1963	33, 38, 39
210. *L. lucida* Farran, 1908	6
211. *L. magna* (Wolfenden, 1903)	5

*212.	*L. major* Wolfenden, 1911	39
213.	*L. maxima* Steuer, 1904	11, 13, 15, 20, 27
214.	*L. ovalis* (Giesbrecht, 1889)	1–6, 30, 31, 36–38, 40–42, 44, 45, 49, 50
215.	*L. pallida* Hulsemann, 1966	3, 18, 23
216.	*L. parva* Grice and Hulsemann, 1965	5, 28–32, 35, 36, 38, 39, 41–47
217.	*L. polaris* Brodsky, 1950	38
218.	*L. rara* Hulsemann, 1966	22, 25, 27
219.	*L. sewelli* Tanaka, 1963	32, 41
220.	*L. wolfendeni* Sewell, 1932	4, 9, 13–15, 22, 25, 26, 42
HETERORHABDIDAE		
*221.	*Disseta minuta* Grice and Hulsemann, 1965	28, 30–32, 35, 36, 45, 46
222.	*D. palumboi* Giesbrecht, 1889	1, 2, 5, 6, 9–11, 13–15, 17, 18, 20, 22, 23, 30 36, 44
223.	*Hemirhabdus grimaldii* (Richard, 1893)	8, 9, 23, 24
*224.	*H. latus* Sars (1905)	17, 19, 44
225.	*Heterorhabdus abyssalis* (Giesbrecht, 1889)	2, 5, 6, 28–30, 32, 35–37, 40–42, 45
226.	*H. clausi* (Giesbrecht, 1889)	38, 40
227.	*H. compactus* (Sars, 1900)	1, 2, 4, 6, 30, 31, 38, 41, 43, 46, 49
228.	*H. norvegicus* (Boeck, 1872)	2–4, 6, 36, 38
229.	*H. papilliger* (Claus, 1863)	2, 6, 43, 44
*230.	*H. robustus* Farran, 1908	6
231.	*H. spinifrons* (Claus, 1863)	3, 4
232.	*Heterostylites longicornis* (Giesbrecht, 1892)	1, 28
233.	*H. major* (Dahl, 1894)	31
*234.	*Mesorhabdus brevicaudatus* (Wolfenden, 1905)	3
AUGAPTILIDAE		
235.	*Augaptilus glacialis* Sars, 1900	2, 5
*236.	*Centraugaptilus cucullatus* Sars, 1905	19
237.	*C. horridus* (Farran, 1908)	17, 21–23
*238.	*Disco inflatus* Grice and Hulsemann, 1965	3, 28, 30, 32, 36, 37, 39–42, 44, 45
*239.	*D. longus* Grice and Hulsemann, 1965	33, 36
*240.	*D. minutus* Grice and Hulsemann, 1965	28, 32
241.	*Disco* species	41
*242.	*Euaugaptilus brodskyi* Hulsemann, 1967	23, 36
243.	*E. bullifer* (Giesbrecht, 1889)	30, 31, 38, 42
244.	*E. curtus*, new species	1
245.	*E. elongatus* (Sars, 1905)	32, 44
246.	*E. facilis* (Farran, 1908)	30
*247.	*E. farrani* Sars, 1920	40
248.	*E. filigerus* (Claus, 1863)	1, 9
249.	*E. fundatus*, new species	1
*250.	*E. gracilis* (Sars, 1905)	32, 39
251.	*E. grandicornis* Sars, 1920	1, 2, 9, 30
*252.	*E. humilis* Farran, 1926	5, 28, 36
253.	*E. indicus* Sewell, 1932	14, 15, 30
254.	*E. laticeps* (Sars, 1905)	3, 9, 13, 19–22, 46
255.	*E. longimanus* (Sars, 1905)	1, 3, 15, 20, 28, 42
*256.	*E. longiseta* Grice and Hulsemann, 1965	28, 39
257.	*E. magnus* (Wolfenden, 1904)	1, 9–13, 15 17, 19, 21–25, 27, 30, 31, 35, 44, 49
258.	*E. malacus*, new species	5
*259.	*E. maxillaris* Sars, 1920	5

260. *E. nodifrons* (Sars, 1905)	1, 4, 5, 9, 17, 21, 23, 26, 28, 37, 38
261. *E. oblongus* (Sars, 1905)	1, 2, 10, 13, 29
262. *E. palumboi* (Giesbrecht, 1889)	1, 3, 5, 6
263. *E. penicillatus* Sars, 1920	3
264. *E. quaesitus*, new species	32
265. *E. rectus*, new species	13
*266. *E. rigidus* (Sars, 1907)	5, 38
267. *E. tenuispinus* Sars, 1920	28
268. *Euaugaptilus* species 1	28
269. *Euaugaptilus* species 2	6
270. *Euaugaptilus* species 3	20
271. *Haloptilus acutifrons* (Giesbrecht, 1892)	31, 42
272. *H. chierchiae* (Giesbrecht, 1889)	1, 2, 28
273. *H. longicornis* (Claus, 1863)	1–6, 30, 31, 36, 38, 40, 42–45, 48
274. *H. tenuis* Farran, 1908	40
275. *H. validus* Sars, 1920	10
*276. *Pachyptilus abbreviatus* (Sars, 1905)	9
277. *P. eurygnathus* Sars, 1920	20, 22, 23, 27
278. *P. pacificus* Johnson, 1936	15, 25
*279. *Pontoptilus mucronatus* Sars, 1905	9, 10, 20
*280. *P. robustus* Sars, 1905	10
281. *P. lacertosus*, new species	20
*282. *Pseudaugaptilus longiremis* Sars, 1907	42
ARIETELLIDAE	
283. *Arietellus simplex* Sars, 1905	17, 18, 20, 25, 26, 42
284. *Phyllopus aequalis* Sars, 1920	1
285. *P. bidentatus* Brady, 1883	19, 29
286. *P. helgae* Farran, 1908	5, 23
287. *P. impar* Farran, 1908	6, 28, 31
288. *P. muticus* Sars, 1907	45
CANDACIIDAE	
289. *Candacia catula* (Giesbrecht, 1889)	43
*290. *C. elongata* (Boeck, 1873)	4
291. *C. ethiopica* (Dana, 1849)	6
292. *C. longimana* (Claus, 1863)	5
293. *Paracandacia bispinosa* (Claus, 1863)	43, 44
294. *P. truncata* (Dana, 1849)	6, 44
PONTELLIDAE	
295. *Labidocera detruncata* (Dana, 1849)	44
BATHYPONTIIDAE	
*296. *Bathypontia elongata* Sars, 1905	2, 6, 17, 28
297. *B. major* (Wolfenden, 1906)	20
298. *B. regalis*, new species	39
*299. *B. sarsi* Grice and Hulsemann, 1965	37
*300. *B. similis* Tanaka, 1965	39
301. *B. spinifera* A. Scott, 1909	2, 3, 5, 6, 36, 42, 44, 46
*302. *Foxtonia barbatula* Hulsemann and Grice, 1963	35, 39, 43
303. *Rhinomaxillaris bathybia*, new genus and new species	30
*304. *Temorites brevis* Sars, 1900	2, 4, 6, 42
*305. *T. discoveryae* Grice and Hulsemann, 1965	32, 33, 35
*306. *Zenkevitchiella atlantica* Grice and Hulsemann, 1965	33
307. *Z. crassa*, new species	41

ACARTIIDAE	
308. *Acartia danae* Giesbrecht, 1889	38, 42, 45
309. *A. negligens* Dana, 1849	5, 31, 32, 34, 36, 38–40, 43–45, 48
INCERTAE SEDIS	
310. Male	41

Calanus australis Brodsky, 1959

Figure 3

Remarks: In dorsal view the slightly produced anterior end of the head and the narrow fifth thoracic segment make the specimen referable to Brodsky's *C. australis* var. *atlanticus*. Brodsky (1959) suggests that this is a species of temperate latitudes in the Southern Hemisphere. The single specimen was found in the Bé net sample at 35°09′ S, 69°59′ E. This is the first record of *C. australis* from the Indian Ocean.

Farrania frigida (Wolfenden, 1911)

Figures 4–15

Diagnosis (male): Fifth thoracic segment small and rounded. First antenna reaches to end of furca, segments 20–21 (fused) and 22 of right antenna each with patch of thick hair. Proximal end of first antenna highly setose and provided with aesthetasks. Fifth feet asymmetrical, right foot longer than left one. Right exopod 3-segmented, terminal segment provided with 2 terminal setae and subterminal hair. Endopod represented by small, bulblike protuberance. Left exopod 3-segmented. Two unequal spines on terminal segment and one spine on distal lateral corner of first segment. Endopod consists of small rounded protuberance. Total length 2.34 mm.

Remarks: The male of this species, not heretofore known, is distinguished from the male of *F. orbus* (Tanaka) by the rounded fifth thoracic segment and the structure of the fifth feet.

Mimocalanus inflatus? Davis, 1949

Figures 16–18

Remarks: As the swimming feet are broken off in both specimens examined it is not possible to determine whether the second endopodal segments are inflated as they are in Pacific and Atlantic specimens of *M. inflatus*. The Indian Ocean specimens have five setae on the second inner lobe and four setae on the second basal segment of the first maxilla. There are four setae and five setae on the corresponding structures of the second maxilla of the Atlantic Ocean specimen described by Grice and Hulsemann (1965). The total length of the present specimens is 1.76 and 2.01 mm. *Mimocalanus inflatus* has not previously been reported from the Indian Ocean.

Mimocalanus **species**

FIGURES 19–25

Remarks: We are tentatively assigning the two males to this genus. The fifth feet are uniramous and styliform. The terminal segments of the exopods each have a long spine. The fifth feet of *M. cultrifer* and *M. nudus* are not so elongate and the terminal segments of the exopods have short spines. The total length of both specimens is .78 mm.

Spinocalanus longipes **Tanaka, 1956**

FIGURES 26–27

Remarks: We are referring three male specimens to this species although, as Johnson (1963) points out, the fifth pair of feet is most unlike any described *Spinocalanus.* The total length of the three specimens ranges from 1.60 to 1.76 mm. *Spinocalanus longipes* has not previously been reported from the Indian Ocean.

Spinocalanus magnus **Wolfenden, 1904**

Remarks: Small differences were noted in the ornamentation (hair, spines) of the terminal exopodal segments of the fifth feet of the present male and that described by Tanaka (1956). The total length of our two male specimens is 2.00 mm.

Spinocalanus validus **Sars, 1905**

FIGURES 28–31

Diagnosis (male): Anterior end of head knoblike, lateral margin of third thoracic segment with protuberances. Exopods and endopods of fifth feet very elongate, second and third right exopodal segments pubescent. Total length 5.08 mm.

Remarks: The male of this species, heretofore unknown, is distinguished by its large size and details of the fifth feet. Our findings of *Spinocalanus validus* constitute a new record for the Indian Ocean.

***Spinocalanus ventriosus*,** **new species**

FIGURES 32–34

Occurrence: Station 332 NV, 2000 to 1002 m, 2 ♀♀; 332 NV, 3000 to 2000 m, 3 ♀♀; 338 NV, 2000 to 1000 m, 2 ♀♀; 340 NV, 2950 to 1990 m, 1 ♀; 349 NV, 2000 to 1000 m, 1 ♀.

Diagnosis (female): Head and first thoracic segment incompletely separated, fifth thoracic segment ends in rounded protrusions. First maxilla with four setae on second inner lobe, three on third inner lobe, four on second basal segment and nine on endopod. Total length 1.32–1.52 mm. Female from station 349 is holotype. Holotype: USNM 113513.

Remarks: The knoblike protrusions of the fifth thoracic segment and the number of setae on the first maxilla will distinguish this species from *S. polaris* Brodsky, a species it resembles.

***Spinocalanus* species**

FIGURE 35

Remarks: A single male specimen with fifth feet similar to *S. longipes* is here tentatively referred to the genus *Spinocalanus*. The left exopod is greatly elongate and the endopod is rudimentary. The right foot is small, 1-segmented, and does not exceed the second basal segment of the left foot. The total length of the specimen is 1.28 mm.

***Teneriforma*, new name**

***Teneriforma naso*, new combination**

FIGURES 36–38

Tanyrhinus naso Farran, 1936, pp. 86–87, text-fig. 4.

Diagnosis (male): Head and first thoracic segment separate, fourth and fifth thoracic segments separate. Furca approximately equal to combined length of fourth and fifth abdominal segments. Rostrum large and curved posteriorly. First antenna with 24 free segments (8 and 9 fused), reaching to end of furca. Fifth feet uniramous and asymmetrical. Left foot elongate and consisting of five segments. Right foot small and consisting of two segments. Total length .92 mm. USNM 113514.

Remarks: The male of this monotypic genus has not previously been described. Since the name *Tanyrhinus* has been used for a genus of insects (Coleoptera) by Mannerheim in 1852 (Bull. Soc. Imp. Nat. Moscou, vol. 25, no. 2, p. 349), the genus is here renamed *Teneriforma*. This is the first record of *Teneriforma naso* from the Indian Ocean.

***Aetideopsis retusa*, new species**

FIGURES 39–45

Occurrence: Station 342 NV, 3000 to 1980 m, 1 ♀.

Diagnosis (female): Head and first thoracic segment incompletely separate. Fourth and fifth thoracic segments separate. Rostrum distinct, rami separated by deep invagination. Frontal organ prominent and visible in dorsal view. Posterior lateral corner of fifth thoracic segment acutely pointed. First antenna exceeds furca by last two segments. Total length 1.96 mm. Holotype: USNM 113515.

Remarks: This species is distinguished from others in the genus by its small size and long first antenna.

Bradyetes florens, new species

FIGURES 46–54

Occurrence: Station 338 NV, 2000 to 1000 m, 1 ♀.

Diagnosis (female): Head and first thoracic segment incompletely separate, fourth and fifth thoracic segments separate. Fifth thoracic segment rounded. Rostrum absent. First antenna reaches to end of furca. Terminal five segments of maxilliped equal in length to second basal segment. First and second exopodal segments of first foot without external spines. Total length 1.10 mm. Holotype USNM 113516.

Remarks: This species differs from *B. inermis* Farran and *B. brevis* Farran, the only described species in this genus, by the relatively short first and second basal segments of the maxilliped, by the absence of a spine on the first exopodal segment of the first foot, and by its small size.

Chirundinella cara Tanaka, 1957

FIGURE 55

Remarks: The only difference between this specimen and the description given by Tanaka (1957) are 11 rather than 10 setae on the endopod of the first maxilla and 3 rather than 4 setae on the fifth lobe of the second maxilla. Our specimen measured 7.80 mm, Tanaka's measured 7.44 mm. This species has not heretofore been found in the Indian Ocean.

Gaetanus brachyurus Sars, 1907

Remarks: The female specimen from station 131 differs from the others and from the description of this species in having the exopod of the first foot consisting of two segments. Each segment has one external spine. The animal is also smaller (5.00 mm). The other two females found measured 6.17 and 6.42 mm. *Gaetanus brachyurus* has not previously been found in the Indian Ocean.

Gaetanus ferox With, 1915

FIGURES 56-59

Remarks: Although the right exopod of the fifth foot of the male is 3-segmented in our specimen (With, 1915, shows two segments), the terminal portion of the exopod is similar to With's figure. Possibly the suture separating the two terminal segments was not observed by him. Our specimen measured 3.55 mm; With's measured 3.4 mm. This species has not previously been reported from the Indian Ocean.

Gaidius robustus (Sars, 1905)

FIGURES 60-64

Gaetanus robustus Sars, 1905a, pp. 11-12.
Gaidius maximus Wolfenden, 1906, p. 35, pl. 11, figs. 1, 2.
Gaidius validus Farran, 1908, pp. 32-33, pl. 2, figs. 11-17.
Mesogaidius maximus (Wolfenden).—Wolfenden, 1911, pp. 224-226, pl. 26, figs. 3-6, text-fig. 13.
Pseudogaetanus robustus (Sars).—Brodsky, 1950, pp. 168-169, fig. 86.
not *Gaidius robustus* Vervoort, 1949, pp. 12-15, figs. 5, 6.

Remarks: Vervoort (1952a, 1952b) redefined the genera *Gaidius* Giesbrecht and *Gaetanus* Giesbrecht. Accordingly, the species Sars described in 1905 as *Gaetanus robustus* is here transferred to the genus *Gaidius*. Brodsky (1950) proposed a new genus, *Pseudogaetanus*, for this species. In our opinion, the characters given are insufficient for the erection of a new genus.

The paratype of *Gaidius robustus* Vervoort was kindly loaned to us for examination. We concur with Dr. Vervoort (in litt.) that the specimen is actually referable to *G. intermedius* Wolfenden, the latter species name having priority.

Gaidius robustus (Sars) has not previously been reported from the Indian Ocean.

Pseudochirella gibbera Vervoort, 1949

Remarks: None of the specimens had a spine on the right dorsal side of the fifth thoracic segment as described by Vervoort (1949) in the original description of the species. Our specimens varied in total length from 5.83 to 6.17 mm. Vervoort's single specimen measured 5.50 mm. The species has not been reported from the Indian Ocean.

Pseudochirella squalida, new species

FIGURES 65-70

Occurrence: Station 351B IK, 350 to 1710 m, 1 ♀.

Diagnosis (female): Rostrum strong and directed ventrally. Fifth thoracic segment rounded. First antenna reaches furca. Second endopodal segment of second antenna with seven setae on outer lobe and nine setae on inner lobe. First basal segment of fourth foot with six coarse spines. Genital segment slightly asymmetrical and hairy. Small rounded protuberances on each side. Total length 5.66 mm. Holotype: USNM 113517.

Remarks: This species resembles *P. obesa* Sars but may be distinguished from it by the protuberances on the genital segment. The genital segment of *P. obesa* has neither protuberances nor hair.

Euchaeta robusta (Wolfenden, 1911)

Remarks: Our female specimen differs from Wolfenden's (1911) original description by the absence of hair on the fifth thoracic segment and by a longer second abdominal segment. The first three abdominal segments have a relative length of 20:10:10. Wolfenden gave a ratio of 20:17:15 for his specimens. Our specimen measured 7.85 mm, Wolfenden's 7.8 mm.

Xanthocalanus hispidus, new species

FIGURES 71–79

Occurrence: Station 355 NV, 2000 to 1000 m, 1 ♀.

Diagnosis (female): Head and first thoracic segment fused, fourth and fifth thoracic segments incompletely separate. Ratio of cephalothorax to abdomen 4:1. Posterior lateral corner of fifth thoracic segment somewhat protruded and rounded. Rostral filaments present. First maxilla with two setae on second inner lobe, two setae on third inner lobe, two setae on second basal segment, eight setae on endopod and five setae on exopod. Second maxilla with sensory appendages, coarse setae broken off. Maxilliped setose. Spines on external margin of exopods of first foot long and seta-like. Exopods and endopods of second through fourth feet broken off. Fifth feet 2-segmented. Distal segment with three spines and one spinelike protrusion. Scattered spines on surface of segment and at junction of first and second segment. Total length 1.00 mm. Holotype: USNM 113518.

Remarks: This species resembles *X. paraincertus* Grice and Hulsemann, but the two may be distinguished by the segmentation and structure of the fifth feet. *X. hispidus* has 2-segmented fifth feet and two short outer spines on the terminal segment. *X. paraincertus* has 3-segmented fifth feet and two long outer spines on the terminal segment.

Amallothrix indica Sewell, 1929

FIGURES 80–82

Diagnosis (male): Left fifth foot nearly twice as long as abdomen. Basal segments of left foot very elongate, exopod 3-segmented, endopod 2-segmented. Right foot only slightly longer than first basal segment. Exopod 2-segmented, endopod 1-segmented. Total length 2.68–3.10 mm.

Remarks: The male of this species resembles *Amallothrix emarginata* (Farran) but the right exopod of the latter species exceeds the length of the left exopod. In *A. indica* the right exopod is quite short. The male of this species has not heretofore been described.

Amallothrix paravalida Brodsky, 1950

Figures 83–84

Diagnosis (male): The terminal segment of the left fifth foot has two rows of spines and a rounded lamella. Total length 2.30 mm.

Remarks: We are tentatively referring to this species a single male specimen found in a sample containing two female *A. paravalida*. The structure of the terminal segment of the left fifth foot of the male of *A. paravalida* will distinguish this species from *A. valida* (Farran).

Amallothrix robustipes Grice and Hulsemann, 1965

Remarks: The present specimens have 2 setae on the second inner lobe and 10 setae on the endopod of the first maxilla. The two Atlantic Ocean specimens described by Grice and Hulsemann (1965) have four setae on the second inner lobe and nine setae on the endopod of the first maxilla. There are no rostral filaments on the Indian Ocean specimens whereas there are two on the Atlantic Ocean ones. The total length of the specimens is 1.00 and 1.20 mm. This is the first record of *Amallothrix robustipes* in the Indian Ocean.

?*Racovitzanus* species

Figures 85–95

Diagnosis (male): Head and first thoracic segment separate, fourth and fifth thoracic segments separate. Posterior lateral corner of fifth thoracic segment indented. Abdominal segments elongate. Rostrum large, without filaments. First antenna exceeds furca by last segment. Segments 8–10 of right first antenna fused. First and second maxilla of the type present in family Scolecithricidae. Maxilliped greatly reduced and with few setae. Exopods of the fifth feet 3-segmented, endopods 1-segmented and pointed. Total length 1.92 mm.

Remarks: We are tentatively assigning this male to the genus *Racovitzanus* based largely on the shape of the rostrum. Since it may represent the undescribed male of a known species, we are not describing it as new species.

Scaphocalanus bogorovi Brodsky, 1955

Figures 96–99

Remarks: The present specimens agree with those collected by us in the North Atlantic (Grice and Hulsemann, 1965). The range of this species is here extended to the Indian Ocean.

Scolecithricella grata, new species

FIGURES 100–103

Occurrence: Station 131 Bé, 2000 to 1000 m, 1 ♀.

Diagnosis (female): Head and first thoracic segment fused, fourth and fifth thoracic segments fused. Rostral filaments present. First maxilla of usual scolecithricid structure. Second maxilla with four lobes each bearing setae and without terminal sensory appendages. Fifth feet consisting of one segment ending in a long spine. Total length 1.31 mm. Holotype: USNM 113521.

Remarks: This species differs from others in the genus by the structure of the fifth feet and the absence of sensory appendages on the second maxilla. In the latter respect it is similar to *Scolecithrix fowleri* Farran.

Scolecithricella maritima, new species

FIGURES 104–114

Occurrence: Station 332 NV, 2000 to 1002 m, 2 ♀♀; 340 NV, 1950 to 1015 m, 1 ♀.

Diagnosis (female): Head and first thoracic segment fused, fourth and fifth thoracic segments incompletely separate. Anterior margin of head broadly rounded. Rostral filaments absent. First antenna with 23 free segments (segments 8 and 9 fused), reaching to fifth thoracic segment. Mouth appendages of *Scolecithricella* type. Expods of first through fourth swimming feet 3-segmented, endopod of first foot 1-segmented, of second foot 2-segmented, of third and fourth feet 3-segmented. Scattered spines on terminal endopodal segments of second through fourth feet. Fifth feet 3-segmented with one terminal and one internal spine on distal segment. Total length .76–.77 mm. One female from station 332 is the holotype. Holotype USNM 113522.

Remarks: This species is similar to *S. ctenopus* (Giesbrecht), but the two may be distinguished by the structure of the fifth feet and by their size. *S. maritima* has no surface spines on the second and third segments of the fifth feet and the total length is less than 1 mm. *S. ctenopus* has numerous small spines in the second and third segments of the fifth feet and the total length is about 1.50 mm.

Scolecithricella timida Tanaka, 1962

FIGURES 115-123

Remarks: This species was originally described from Sagami Bay, Japan (Tanaka, 1962). Some additional figures are given here. The total length of the specimens varies from 1.50 to 1.76 mm. This species has not been reported from the Indian Ocean.

***Scolecithricella* species**

FIGURES 124–125

Diagnosis (male): Head and first thoracic segment fused, fourth and fifth thoracic segments separate. First antenna reaches end of second abdominal segment. Right fifth foot uniramous, 2-segmented. Left foot biramous, exopod 3-segmented, endopod 1-segmented. Total length .72 mm.

Remarks: The single male specimen is probably referable to a described female of this species. We therefore will not offer it as a new species.

***Scolecithrix fowleri* Farran, 1926**

FIGURES 126–129

Diagnosis (male): Head and first thoracic segment fused, fourth and fifth thoracic segments separate. Large, ventrally directed rostrum. Fifth feet biramous. Right foot with 3-segmented exopod, 2-segmented endopod. Left foot with 3-segmented exopod and 1-segmented endopod. Total length 1.62 mm.

Remarks: The male of this species has not been heretofore known. Our findings of *Scolecithrix fowleri* represent a new record for the Indian Ocean.

***Metridia boecki?* Giesbrecht, 1889**

FIGURES 130–133

Diagnosis (male): Head and first thoracic segment fused, fourth and fifth thoracic segments fused. Posterior lateral corner of fifth thoracic segment with small protuberance. First antenna reaches to end of second abdominal segment. First segment of left first foot with pubescent swelling. Total length 1.95–2.01 mm.

Remarks: The five male specimens here tentatively recognized as belonging to *M. boecki* differ slightly from *M. discreta* by the large swelling on the first segment of the left fifth foot.

***Metridia brevicauda* Giesbrecht, 1889**

Remarks: The fifth pair or feet of several female specimens were observed to have four rather than three segments. In other respects they agreed with *M. brevicauda.*

***Metridia effusa*, new species**

FIGURES 134–143

Occurrence: Station 108 Bé, 2000 to 1000 m, 1 ♀; 134 Bé, 2000 to 1000 m, 11 ♀♀, 6 ♂♂; 140 Bé, 2000 to 1000 m, 2 ♀♀.

Diagnosis (female): Head and first thoracic segment incompletely separate, fourth and fifth thoracic segments fused. Anterior end of head pointed, posterior lateral corner of fifth thoracic segment rounded.

Genital segment short, in dorsal view sides parallel. Furca longer than wide. First antenna reaches genital segment. First and second segments with prominent teeth. Fifth feet 3-segmented, with extremely small distal segment bearing a long seta. Penultimate segment with small distolateral spine. Total length 1.58–1.79 mm. Holotype: USNM 113525.

Diagnosis (male): Head and first thoracic segment fused, fourth and fifth thoracic segments fused. Anterior end of head with rounded knob. Posterior lateral corner of fifth thoracic segment rounded. Internal spine on second segment of right foot reaches just beyond middle of distal segment. Third segment of left foot with one seta and one spine on internal side. Total length 1.36–1.44 mm. Allotype: USNM 113526.

Remarks: The female of this species resembles *M. venusta* Giesbrecht and *M. brevicauda* Giesbrecht. From the former it is distinguished by the 3-segmented fifth feet and presence of one terminal seta on the distal segment. *M. venusta* has a 2-segmented fifth foot and four setae on the distal segment. From *M. brevicauda* it is distinguished by the spines on the first and second segments of the antenna; in addition, neither *M. venusta* nor *M. brevicauda* have pointed foreheads. The male is distinguished from these species by the rounded knob on the anterior margin of the head and the details of the fifth feet.

***Lucicutia major* Wolfenden, 1911**

FIGURES 144–147

Remarks: This species has not been reported since it was described by Wolfenden in 1911. The one female found differs from the description in that the first antenna exceeds the end of the furca by about the last four segments. Wolfenden stated that the antenna exceeds the furcae by the last two segments. Also, the left furca is only slightly longer than the right one instead of being considerably longer as mentioned in the original description. In all other points our specimen agrees with the description of Wolfenden. The present specimen measures 8.16 mm; Wolfenden's measured 8.0–8.2 mm. Since no figures of *Lucicutia major* have been published, we are presenting figures of this species here. This is the first record of *L. major* from the Indian Ocean.

***Disco inflatus* Grice and Hulsemann, 1965**

FIGURES 148–161

Diagnosis (male): Head and first thoracic segment separate, fourth and fifth thoracic segments fused. Anal segment longer than preceding segment, slightly shorter than furca. Rostrum absent. First antenna reaches to fourth segment of abdomen. Left antenna geniculate. Endopod of second antenna about equal in length to exopod. First endopodal segment of mandible with row of spines. Mandible palpus elongate, blade with two subequal teeth. First maxilla reduced, endopod (?) with two setae. Second maxilla and maxilliped with reduced number of setae. Exopods of swimming feet 3-segmented, endopod of first foot 2-segmented, of second to fourth feet 3-segmented. Spine of first exopodal segment of first foot large and elongate. Fifth feet biramous, exopods 3-segmented, endopods 2-segmented. Penultimate segment of left exopod indented on internal side. Total length 1.16 mm.

Remarks: The genus *Disco* was described by us (Grice and Hulsemann, 1965) on the basis of female specimens collected in the North Atlantic Ocean. *D. inflatus* has not been previously reported from the Indian Ocean.

Disco species

FIGURES 162–173

Diagnosis (male): Head and first thoracic segment incompletely separate, fourth and fifth thoracic segments fused. Anal segment longer than preceding segment and furca. Rostrum absent. Left antenna geniculate. Endopod of second antenna ⅔ the length of exopod. Mandible palpus elongate, blade with spinelike hairs and three spiniform teeth. First maxilla well developed, internal lobe bearing one seta, exopod with four setae, and second basal segment with one seta. Second maxilla and maxilliped with reduced number of setae. Exopods and endopods of first and second feet 3-segmented. Third and fourth feet broken off. Fifth feet biramous, exopods 3-segmented. Endopod of right foot 3-segmented, of left foot 2-segmented. Total length .80 mm.

Remarks: It appears that the present specimen is referable to the genus *Disco*, but probably not to either of the two described species (*D. longus*, *D. minutus*) in which the male is unknown. The present male differs from these two species in the absence of a rostrum and in the segmentation of the endopods of the first and second swimming feet. It seems preferable not to refer the male to either species as it may represent the male of an undescribed species of *Disco*.

Euaugaptilus brodskyi Hulsemann, 1967

FIGURES 174–179

Remarks: We found one female measuring 6.83 mm in length, which we believe is *Euaugaptilus brodskyi*. The mandible, first and second maxilla are figured here since Brodsky (1950) did not figure all of the appendages. In our specimen the exopod of the mandible palpus is reduced and bears four setae. The endopod is represented by one seta. Brodsky described this species as *E. mixtus*. The name was subsequently changed (Hulsemann, 1967) to *E. brodskyi* because it was preoccupied by a species described by Sars in 1905.

There was one male in the collection which measured 3.33 mm. In the structure of the mandible blade and the first maxilla it is closer to the female of *Euaugaptilus mixtus* Brodsky as described and figured by Tanaka (1964) than to the specimens originally described by Brodsky. In our specimen the mandible palpus is biramous. The number of setae on lobes 1–6 of the second maxilla is 1, 1, 2, 3, 2, 3, respectively, and that on lobes 1–5 of the maxilliped is 1, 3, 3, 2, 2, respectively. This male is identical to the one reported as *Euaugaptilus* species by Grice and Hulsemann (1965) from the northeastern Atlantic Ocean. *Euaugaptilus brodskyi* has not previously been reported from the Indian Ocean.

***Euaugaptilus curtus*, new species**

FIGURES 180–186

Occurrence: Station 108 Bé, 2000 to 1000 m, 1 ♀, 1 ♂.

Diagnosis (female): Body slender, head and first thoracic segment incompletely separate. Fourth and fifth thoracic segments fused, posterior lateral corners rounded. Abdomen 3-segmented, genital segment longer than the two following combined. Rostrum with two slender filaments. First antenna exceeds end of furca by about five segments. Exopod of second antenna consisting of eight segments, reaching to end of first endopodal segment. Mandible palpus uniramous composed of five segments, the last three each bearing one seta. Mandible blade with two strong double teeth and one smaller tooth adjacent to the seta. First inner lobe of first maxilla with six spines, second and third inner lobes rudimentary. Fused second basal segment and endopod with one seta. Exopod carrying one very long and one small terminal seta and one slender subterminal seta. External lobe with two setae. Number of setae on lobes 1–6 of second maxilla: 3, 2, 2, 3, 2, 3, respectively; 7 setae on the endopod. Maxilliped bearing 1, 3, 3, 2, 2 setae on the lobes of the basipod. Exopods and endopods of first to fifth pair of swimming feet 3-segmented. Total length 2.81 mm. Holotype: USNM 113528.

Diagnosis (male): Differs from female in the following: Abdomen consisting of five segments. Left first antenna geniculate. Segmentation of mandible palpus incomplete. First inner lobe of first maxilla with five spines. Fifth feet as in figure 186. Total length 2.49 mm. Allotype: USNM 113529.

Remarks: *Euaugaptilus curtus* resembles *E. longiseta* Grice and Hulsemann. The former species differs from the latter, however, in having two teeth on the mandible blade, a uniramous mandible palpus, and a more reduced first maxilla.

***Euaugaptilus fundatus*, new species**

FIGURES 187–192

Occurrence: Station 108 Bé, 2000 to 1000 m, 1 ♀.

Diagnosis (female): Head and first thoracic segment separate, fourth and fifth thoracic segments fused. Posterior lateral corner of fifth thoracic segment rounded. Abdomen 3-segmented. Genital segment longer than the two following combined. Rostral filaments slender, broken short. First antenna exceeding end of furca by about last three segments. Exopod of second antenna 8-segmented. Mandible palpus biramous, endopod small, ending in one setae. Mandible blade with two strong teeth, each with a small side tooth, and one large seta. First inner lobe of first maxilla with four spines; second and third inner lobes absent; fused second basipodal segment and endopod with one seta; exopod with five setae, the two terminal ones largest; external lobes with five setae, the middle one being the largest. Number of setae on lobes 1–6 in the second maxilla: 3, 2, 2, 2, 2, 1, respectively. Two setae each on lobes 3–5 of the maxilliped. Exopod of first swimming foot consisting of three segments, endopod of two segments. Groups of small hairs near base of external spines of second and third exopodal segments. Exopods and endopods of second to fifth swimming feet 3-segmented. Total length 3.64 mm. Holotype: USNM 113530.

Remarks: *Euaugaptilus fundatus* resembles *E. longiseta* Grice and Hulsemann and *E. curtus.* It is distinguished from these by the structure of the mandible blade and palpus, and the development of the first and second maxilla.

***Euaugaptilus humilis* Farran, 1926**

Remarks: These specimens agree in those details discussed by Grice (1963): presence of rostral filaments, symmetrical furcae, symmetrical genital segment, and the presence of a second inner lobe on the first maxilla. *Euaugaptilus humilis* has not previously been reported from the Indian Ocean.

***Euaugaptilus longiseta* Grice and Hulsemann, 1965**

FIGURES 193–195

Diagnosis (male): Rostrum small with slender filaments. Right furca shorter than left. First antenna exceeds end of furca by last four segments. Exopod of second antenna 7-segmented. Mandible palpus biramous, blade as in female. First maxilla with one seta on fused second basal segment and endopod, five setae on exopod. Number of setae on lobes 1–6 of second maxilla: 2, 2, 2, 3, 2, 1 respectively. Number of setae on lobes 1–5 of maxilliped: 1, 2, 3, 2, 2. Exopods and endopods of fifth feet 3-segmented, terminal segments with one long seta and one short spine. Total length 1.82 mm.

Remarks: Although the first maxilla of the male has no second inner lobe and fewer setae on the fused second basal segment and endopod (one rather than three setae as in the female), the other head appendages agree well with those of the female. The male has not heretofore been described. Our findings of *Euaugaptilus longiseta* represent a new record for the Indian Ocean.

***Euaugaptilus malacus*, new species**

Figures 196–200

Occurrence: Station 134 Bé, 2000 to 1000 m, 1 ♀.

Diagnosis (female): Head and first thoracic segment separate, fourth and fifth thoracic segments fused. Posterior lateral corner of fifth thoracic segment rounded, set off by a slight indentation. Abdomen 3-segmented. Rostral filaments very slender. First antenna exceeds end of furca but broken off at segment 22. Exopod of second antenna 8-segmented, shorter than endopod. Mandible blade obliquely cut bearing two strong double-teeth and two slender, shorter teeth. Endopod of mandible palpus rudimentary. First inner lobe of first maxilla with six rather slender and elongate spines, second inner lobe with one seta, third inner lobe lacking; fused second basal segment and endopod with one seta; exopod with two strong and one weak seta; external lobe with three setae. Number of setae on lobes 1–6 of second maxilla: 0, 1, 2, 2, 2, 1, respectively. Number of setae on first five lobes of maxilliped: 1, 2, 3, 2, 2, respectively. Endopods and exopods of first through fifth pair of swimming feet 3-segmented. Total length 3.29 mm. Holotype: USNM 113532.

Remarks: *Euaugaptilus malacus* resembles *E. facilis* (Farran). The obliquely cut mandible blade, the rudimentary endopod of the mandible palpus, the lack of a blunt process on the outer margin of the second and third exopodal segments of the third and fourth swimming feet, and the small size of *E. malacus* will distinguish it from *E. facilis.*

***Euaugaptilus nodifrons* (Sars, 1905)**

Figures 201–203

Remarks: A dorsal view of the body, rostrum, and mandible blade of the male are illustrated for the first time. Other appendages of the male are shown by Sars (1924–25) and Sewell (1929).

Euaugaptilus oblongus (Sars, 1905)

Augaptilus oblongus Sars, 1905b, pp. 11–12.
Augaptilus rostratus Esterly, 1906, p. 73, pls. 9 (fig. 19), 11 (fig. 42), 12 (figs. 57, 63), 13 (fig. 75).
Augaptilus subfiligerus Wolfenden, 1911, p. 343.
Euaugaptilus oblongus (Sars).—Sars, 1924–1925, pp. 266–267, pl. 81.
Euaugaptilus rostratus (Esterly).—Brodsky, 1950, pp. 374–375, fig. 264.

Remarks: Close examination of two females of *Euaugaptilus rostratus* (loaned to us by Scripps Institution of Oceanography) on which Esterly (1906) probably based the description of that species indicates that *E. rostratus* (Esterly) is identical to *E. oblongus* (Sars, 1905). A comparison of the description of *Augaptilus subfiligerus* Wolfenden, 1911, with *E. oblongus* (Sars) shows that these two species are also identical.

The synonymy of the three species extends the size range of *Euaugaptilus oblongus* to 4.65–7.4 mm.

Euaugaptilus quaesitus, new species

FIGURES 204–209

Occurrence: Station 332 NV, 3000 to 2000 m, 1 ♀.

Diagnosis (female): Head and first thoracic segment separate, fourth and fifth thoracic segments fused. Posterior lateral corner of fifth thoracic segment rounded. Abdomen 3-segmented. Genital segment longer than the two following combined. Rostrum consisting of two points, rostral filaments absent. First antenna barely reaching furca. Exopod of second antenna 8-segmented, segments seven and eight incompletely separated; exopod and endopod of equal length. Mandible blade with two widely separated strong teeth and one slender tooth near the seta. First inner lobe of first maxilla with four spines; second and third inner lobes absent; fused second basipodal segment and endopod with one seta; exopod with five setae, the two terminal ones largest; external lobe with three setae of equal length. Number of setae on lobes 1–6 of the second maxilla: 2, 2,1, 2, 2, 1, respectively. Number of setae on lobes 1–5 of the maxilliped: 0, 3, 3, 2, 2, respectively. Exopod of first swimming foot consisting of three segments, endopod of two segments. Exopods and endopods of second through fourth pair of swimming feet 3-segmented. Exopod and endopod of fifth pair 2-segmented. Total length 1.40 mm. Holotype: USNM 113533.

Remarks: *Euaugaptilus quaesitus* resembles *E. fundatus* in the structure of the mandible blade, the first maxilla, and the 2-segmented endopod of the first swimming foot. The two species can be sepaby the smaller size of *Euaugaptilus quaesitus* and by its lack of rostral filaments, its shorter first antenna, and its 2-segmented exopod and endopod of the fifth feet. *E. quaesitus* is also close to *Euaugaptilus hecticus* (Giesbrecht), but the shorter first antenna in *E. quaesitus* and the more developed mandible palpus and blade distinguish these two species. Finally, *E. quaesitus* differs from *E. humilis* Farran in its shorter first antenna and the structure of the mandible blade and the first maxilla.

Euaugaptilus rectus, new species

FIGURES 210–214

Occurrence: Station 337B IK, 275 to 2250 m, 1 ♀.

Diagnosis (female): Head and first thoracic segment separate, fourth and fifth thoracic segments fused. Posterior lateral corner of fifth thoracic segment rounded. Rostrum consisting of two short and stout cones. No rostral filaments. Exopod of second antenna 8-segmented. Mandible palpus with well-developed rami. Mandible blade obliquely terminated. First maxilla with one seta on second inner lobe, no seta on third inner lobe, three setae on fused second basal segment and endopod, and four setae on exopod. Second maxilla with following setae number on lobes 1–6: 2, 1, 1, 3, 2, 3. Number of setae on lobes 1–5 of maxilliped: 1, 3, 3, 2, 2. Exopod of first foot with one external spine on first segment, one external spine on second segment and two external spines on third segment. Total length 7.98 mm. Holotype: USNM 113534.

Remarks: This species is similar to *E. angustus* (Sars) but the two may be separated by the structure of the rostrum (2-pointed in *E. rectus*, rounded in *E. angustus*), and first foot (two external spines in *E. rectus*, one spine in *E. angustus*).

Euaugaptilus species 1

FIGURES 215–224

Diagnosis (female): Head and first thoracic segment separate, fourth and fifth thoracic segments fused. Genital segment more than one-half the length of the abdomen. Rostral filaments small and fine. First antenna exceeds furca by last five segments. Exopod of second antenna 8-segmented. Mandible palpus without rami. First maxilla with one seta on second inner lobe, no seta on third inner lobe, one seta on fused second basal segment and endopod, and four setae on exopod. Number of setae on lobes 1–6 of the second maxilla: 2, 2, 2, 3, 2, 3, respectively. Number of setae on lobes 1–5 of maxilliped: 1, 3, 3, 2, 2. Maxilliped with indented knob on posterior side. Exopods and endopods of first through fourth feet 3-segmented. Third exopodal segment of third foot cup shaped with two rudimentary spines on external margin and five setae on internal margin. Fifth feet with 3-segmented exopods and endopods and with a small spine on the inne side of the second exopodal segment. Total length 4.87 mm.

Remarks: There is reasonably good agreement between the present specimen and *E. facilis* (Farran), a species also found in these collections. They differ chiefly in the structure of the mandible (no rami in *Euaugaptilus* species 1, biramous in *E. facilis*), first maxilla (three large and one small setae on the exopod in *Euaugaptilus* species 1, three large setae on exopod of *E. facilis*), and third pair of feet (enlarged terminal exopodal segments in *Euaugaptilus* species 1, usual type of terminal segment in exopods in *E. facilis*). The present specimen could possibly be an abnormally developed *E. facilis* and we have therefore not considered it a new species.

***Euaugaptilus* species 2**

FIGURES 225–230

Diagnosis (male): Head and first thoracic segment separate, fourth and fifth thoracic segments fused. Posterior lateral corner of fifth thoracic segment rounded. Abdomen consisting of five segments, anal segment very long, longer than furca. Large rostrum rounded. Rostral filaments slender. Right first antenna reaching anal segment; left first antenna geniculate. Exopod of second antenna 8-segmented, small, extending to two-thirds of first segment of endopod. Mandible blade with four strong and one slender tooth of about the same length, seta small. Mandible palpus biramous. First maxilla much reduced; first endopodal lobe with one spine, second endopodal lobe with one spine, third lobe absent; fused second basal segment and endopod with one seta; exopod with two rather strong setae; external lobe without setae. Number of setae on lobes 1–6 of second maxilla: 1 and a small process, 1 (?), 2, 2, 2, 1, respectively. Number of setae on first 5 lobes of maxilliped: 1, 1, 2, 2, 2, respectively. Exopods and endopods of first to fifth pair of swimming feet 3-segmented. Seta on second basipodal segment of fifth foot short; inner margin of second exopodal segment of right fifth foot with process near proximal corner; external spines of first and second exopodal segments with small knoblike protrusions apically near their base. Total length 3.7 mm.

Remarks: The structure of the mandible and the first maxilla as well as the relatively long genital segment suggest a close relationship of *Euaugaptilus* species 2 to *E. affinis* Sars. The one male specimen found differs from Sars' description (1924–25) of the female in a reduced number of spines or setae, respectively, on the first inner lobe and the outer lobe of the first maxilla, second maxilla and the maxilliped. Also, this male (total length 3.77 mm) is smaller than the female of *E. affinis* (5.40 mm). The male of *E. affinis* is undescribed.

The characteristics pointed out by Brodsky (1950) to distinguish his *Euaugaptilus pseudaffinis* from *E. affinis*—i.e., differences in the length of the first and second antenna and the structure of the fifth pair of feet—seem insufficient to distinguish *E. pseudaffinis* Brodsky from *E. affinis* Sars. No difference is obvious between Brodsky's and Sars' figure of the fifth feet of the female.

Euaugaptilus **species 3**

FIGURES 231–240

Diagnosis (male): Head and first thoracic segment fused, fourth and fifth thoracic segments fused. Anal segment twice the length of the preceding segment. Rostrum knoblike , with two short filaments. First antenna exceeds furca by last two segments, left antenna geniculate. Endopod of second antenna about four times longer than exopod. Mandible palpus small, uniramous. First maxilla much reduced. Distal setae of second maxilla and maxilliped with numerous "buttons." Swimming feet with 3-segmented exopods and endopods. Total length 6.16 mm.

Remarks: We are unable to refer this male to a described species but it may be the undescribed male of a known species. The head appendages resemble those of the female of *E. rigidus* (Sars), but the size of the present male exceeds that of the female.

Pachyptilus abbreviatus **(Sars, 1905)**

FIGURES 241–247

Remarks: Figures of the female of this species, not previously known from the Indian Ocean, are given here. The total length is 5.52 mm.

Pachyptilus pacificus **Johnson, 1936**

Pachyptilus eurygnathus Sars.—Sewell, 1947, p. 239, text-fig. 65.

Remarks: The species reported by Sewell (1947) as *P. eurygnathus* is referable to *P. pacificus*. Sewell's specimen has a 2-segmented exopod on the first feet, which is the same number found in *P. pacificus*.

Pontoptilus robustus **Sars, 1905**

FIGURES 248–258

Diagnosis (female): Head and first thoracic segment separate, fourth and fifth thoracic segments fused, posterior lateral corner of fifth thoracic segment protruded. Rostrum absent. First antenna consisting of 25 free segments, exceeding furca by last 3 segments. Structure and setation of head and thoracic appendages similar to *P. muticus* Sars. Total length 8.51 mm.

Remarks: Although closely resembling *P. muticus*, *P. robustus* is distinguished by its larger size, long antenna, and protruding fifth thoracic segment. The female has not been described heretofore. The male was described by Sars in 1905 and later illustrated by him

(Sars, 1924–25). This is the first record of *Pontoptilus robustus* in the Indian Ocean.

Pontoptilus lacertosus, new species

Figures 259–265

Occurrence: Station 347A, IK, 350 to 2500 m, 1 ♀.

Diagnosis (female): Head and first thoracic segment fused, fourth and fifth thoracic segments fused. Fifth thoracic segment rounded. Rostrum robust with a single point. First antenna exceeding furca by about five segments. Mandible palpus with three setae. Blade resembling that of *P. ovalis* Sars. First maxilla with five setae on second inner lobe, four setae and a small spine on the endopod, two setae on the second basal segment, five setae on the endopod, three setae on the exopod and one seta on a lobe located just ventrad of the exopod. Setae on lobes 1–5 of the second maxilla as follows: 8, 3, 3, 3, 3, respectively. First to fourth swimming feet with 3-segmented exopods and endopods. Fifth feet with 3-segmented exopods, 2-segmented endopods. Total length 7.17 mm. Holotype: USNM 113535.

Remarks: *P. lacertosus* differs from *P. ovalis* Sars, a species it resembles, in the presence of a rostrum and additional setae on the second basal segment, endopod and exopod of the first maxilla.

Phyllopus muticus Sars, 1907

Figures 266–270

Remarks: A very large female (total length 7.21 mm) was found at one station. Figures of this specimen including illustrations of some appendages not heretofore figured are given here.

Bathypontia elongata Sars, 1905

Figures 271–274

Remarks: Several figures of the male are given here. The rostrum of the male is rounded and unlike that found in the female. Total length 4.68 mm. *Bathypontia elongata* has not previously been reported from the Indian Ocean.

Bathypontia regalis, new species

Figures 275–280

Occurrence: Station 338 NV, 3000 to 2000 m, 1 ♂.

Diagnosis (male): Head and first thoracic segment separate, fourth and fifth thoracic segments separate. Posterior lateral corner of fifth thoracic segment broadly rounded. Rostrum robust and rounded. Exopods of first through fourth feet 3-segmented, endopods of first foot 2-segmented, of second through fourth feet 3-segmented.

Left fifth foot 5-segmented with hair on internal margin of second and third segments. Right fifth foot 5-segmented. Total length 2.32 mm. Holotype: USNM 113537.

Remarks: This species resembles the male of *B. major* (Wolfenden) but the small size of the present specimen and the inflated and pubescent second segment of the left fifth foot will distinguish it from *B. major*.

***Rhinomaxillaris*, new genus**

Type-species: *Rhinomaxillaris bathybia*, new species.

***Rhinomaxillaris bathybia*, new species**

FIGURES 281–292

Occurrence: Station 330 NV, 2000 to 1000 m, 1 ♀.

Diagnosis (female): Head and first thoracic segment incompletely separate, fourth and fifth thoracic segments incompletely separate. Abdomen 4-segmented. Anal segment longer than preceding segment and furca. Rostrum large and obtuse. First antenna reaching to fifth thoracic segment. Segments 8 and 9, 24 and 25 fused. Exopod of second antenna consisting of seven segments, about twice the length of the endopod. Mandible palpus with two setae. First maxilla with two setae on second inner lobe, five setae on endopod and two setae on exopod. Second maxilla with 5 lobes bearing 1, 1, 3, 3, and 2 setae, respectively. Maxilliped large, with long and coarse setae distally. First foot with 3-segmented exopod and 1-segmented endopod. First and second exopodal segments of first foot without external spines. Exopods of second through fourth feet broken off. Endopods of second foot 2- or 3-segmented, of third and fourth feet 3-segmented. Third endopodal segments of third and fourth feet with six setae. Total length 1.12 mm. Holotype: USNM 113538.

REMARKS.—We found one female specimen of a calanoid copepod for which we establish a new genus and species. It was difficult to assign this species to an existing family. Characteristics of this specimen can be found in the genera of the family Bathypontiidae Brodsky: *Bathypontia* Sars, *Temorites* Sars, *Zenkevitchiella* Brodsky, and *Foxtonia* Hulsemann and Grice . The last two of these genera were tentatively placed in this family.

The large, blunt rostrum of *Rhinomaxillaris* is similar to that found in *Bathypontia*. There are 23 free segments in the first antenna of all four genera mentioned except in the species *Temorites discoveryae* Grice and Hulsemann. Segments 24 and 25 are fused in all species in the family. In general, the second maxilla and the maxilliped resemble those in the other genera in the family with respect to their compact form and the strong, spinelike setae on the endopods. The first and second exopodal segments of the first foot lack external spines as is the case in *Bathypontia*, *Temorites*, and *Foxtonia*. The absence of fifth feet is common to the female of *Foxtonia*.

The new genus *Rhinomaxillaris* is distinguished from *Bathypontia* and *Temorites* by the long exopod in the second antenna, the shape and arrangement of the teeth on the mandible blade, and the absence of fifth feet. *Rhinomaxillaris* differs from *Zenkevitchiella* and *Foxtonia* in the long exopod of the second antenna, the mandible blade, and the peculiar rostrum. From *Zenkevitchiella*, *Rhinomaxillaris* is further distinguished by the absence of external spines on the first and second exopodal segments of the first foot, and the absence of fifth feet. It differs from *Foxtonia* in the increased number of segments in the endopods of the second and third feet and in the absence of spinelike setae between the bases of the first antenna. *Rhinomaxillaris* also resembles certain genera in the family *Pseudocalanidae*. The large and blunt rostrum, the fused 24th and 25th segments in the first antenna, and the absence of external spines on the first and second exopodal segments of the first foot prevent *Rhinomaxillaris* from being placed in this family.

Until a female with intact swimming feet and a male are found, it is not possible to establish the true familial relationship of *Rhinomaxillaris*. In the meantime we have tentatively placed it in the family Bathypontiidae with the full realization that until this family is critically studied it may represent a composite of unrelated genera.

Until additional species are discovered, the genus *Rhinomaxillaris* cannot be diagnosed.

Zenkevitchiella atlantica Grice and Hulsemann, 1965

Remarks: In the single specimen found segments seven and eight of the first antenna are fused as is shown in figure 22(a) in our description of this species from North Atlantic specimens (Grice and Hulsemann, 1965) and not segments eight and nine as stated in the text. Segments 24 and 25 are fused and not segments 23 and 24 as also stated in the text. The distal end of the first antennae are broken off in the Indian Ocean specimen. It may be added here that in the male of *Zenkevitchiella atlantica* described by us (1965), segments seven and eight of the first antenna are fused. No male of this species has yet been found in the Indian Ocean. The occurrence of a female of *Zenkevitchiella atlantica* represents a new record for the Indian Ocean.

Zenkevitchiella crassa, new species

FIGURES 293–305

Occurrence: Station 340 NV, 2950 to 1990 m, 1 ♂.

Diagnosis (male): Head and first thoracic segment incompletely separate, fourth and fifth thoracic segments separate. Posterior lateral corner of fifth thoracic segment rounded. Rostrum 2-pointed, each point with a filament. Right first antenna geniculate, fifth segment from end with two rounded knobs. Endopod of second antenna about two-thirds the length of exopod. Mandible with two setae on palpus. First maxilla with one seta on second inner lobe, two setae on third inner lobe, one seta on second basal segment, endopod absent, exopod with five setae. Second maxilla with five well-defined lobes bearing 3, 2, 1, 3, 2 setae, respectively. Long and coarse setae on distal lobe and on end of appendage. Maxilliped with coarse setae distally. Exopods of first through fourth feet 3-segmented. Endopods of first foot 1-segmented, of second through fourth feet 3-segmented. Second basal segment of third foot with distolateral spinelike protrusion. Fifth feet with right exopod 2-segmented, left exopod 1-segmented. Right endopod a small knob, left endopod large and bearing a large spine distally. Total length .84 mm. Holotype: USNM 113539.

Remarks: This species is different from *Z. atlantica* Grice and Hulsemann in the structure of the endopods of the fifth feet. In *Z. atlantica* the endopods are bulbous, and neither bears a spine. The male of *Z. abyssalis* Brodsky is not known. It is unlikely that the present specimen is the male of *Z. abyssalis* as this is a relatively large species (2.37 mm).

Unidentified Male

FIGURES 306–319

Diagnosis (male): Head and first thoracic segment separate, fourth and fifth thoracic segments fused. Abdomen 5-segmented, anal segment longer than preceding, equal in length to furca. Rostrum robust, broadly rounded at tip. Left first antenna geniculate, numerous aesthetasks on proximal segments. Endopod of second antenna about two-thirds the length of exopod. Endopod of mandible about two-thirds the length of exopod. Palpus devoid of setae. Blade with one large and two small teeth, distal end covered with numerous small spines. First maxilla with one seta on second inner lobe, three setae on third inner lobe, two setae on second basal segment, nine setae on endopod, and seven setae on exopod. Second maxilla with five lobes bearing 4, 3, 3, 3, and 1 setae, respectively. Maxillipeds broken off distally. Swimming feet broken off. Fifth feet uniramous, each ramus 5-segmented. Distal segment of left foot with 2 spinelike protrusions terminally. Total length .72 mm.

Remarks: In most respects the present male is similar to the males of the two *Disco* species (family Augaptilidae) described earlier. However, the uniramous fifth feet of the present male apparently preclude its referral to the genus *Disco* and the family Augaptilidae. Until females are discovered, we will not attempt a family designation or generic description.

Summary

Calanoid copepods were identified in 51 samples collected by Bé multiple sampler, Isaacs-Kidd midwater trawl, and modified Nansen vertical net at stations located in the western Indian Ocean between the northern Arabian Sea and approximately the subtropical convergence. The Bé net collections were obtained between 2000 and 1000 m, the midwater trawl samples between the surface and a maximum depth of 3820 m, and the Nansen vertical net samples between 2000 and 1000, 3000 and 2000, and 4000 and 3000 m.

The displacement volumes of the zooplankton and numerical density and size of the copepods collected by the Nansen net were determined and compared to similar collections made in the northeastern Atlantic. In general, the total zooplankton as well as the copepods were more abundant in the 2000–1000 m depth interval than in intervals below 2000 m. The mean size of the animals was larger in the 2000–1000 m interval than in the 3000–2000 m interval. The values obtained for the displacement volumes, numerical abundance, and mean size were similar to those in comparable depth intervals in the northeastern Atlantic.

The greatest number of species in the Nansen vertical collections were found between 2000 and 1000 m (122), a lesser number between 3000 and 2000 m (73), and the least number between 4000 and 3000 m (13). This decrease in diversity with increasing depth is similar to that found in the northeastern Atlantic.

The distribution of 269 species found in the western Indian Ocean was discussed and compared to previous discussions of the geographic distribution of Indian Ocean bathypelagic copepods and to water mass distribution. The very widespread distribution of the bathypelagic species was indicated by the great similarity in species composition between the North Atlantic and western Indian Oceans. Eighty-six percent of the western Indian Ocean species are also present in the North Atlantic. Five typically Antarctic species were found in four samples collected in the southern Indian Ocean near the subtropical convergence.

Included in the 310 species found are 1 new genus, 17 new species, 8 previously unknown males, and 1 previously unknown female. Seventy-eight of the 310 species excluding the newly described ones have not been previously reported from the Indian Ocean. Seven species are apparently known only from the Indian Ocean.

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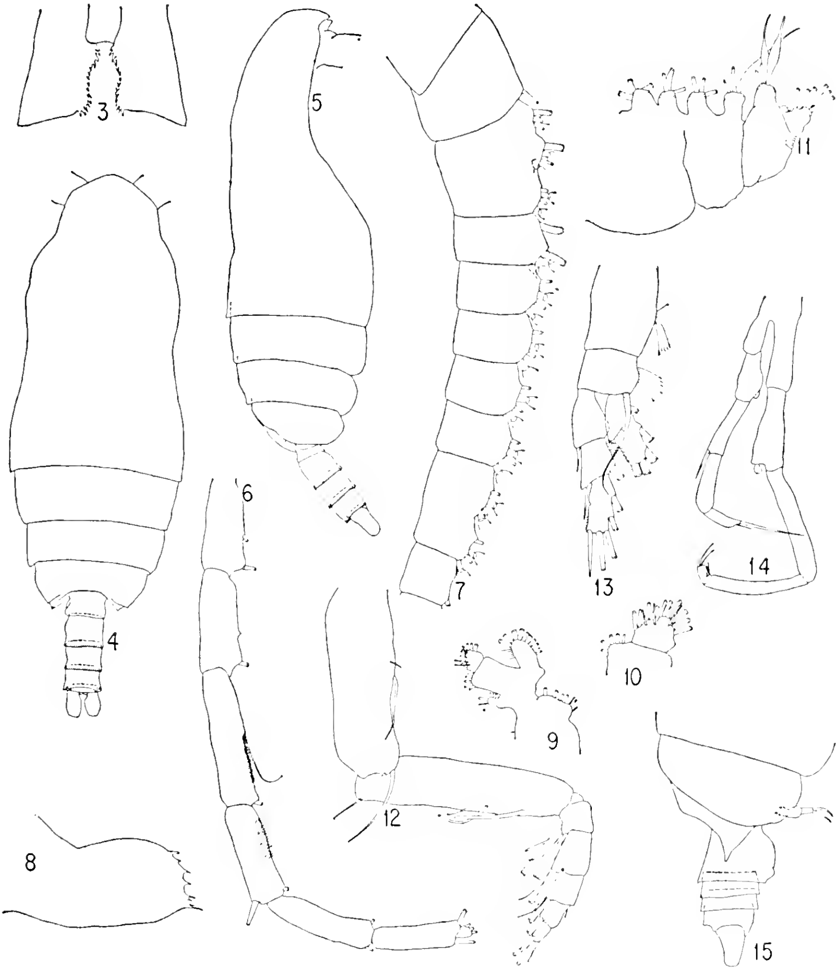
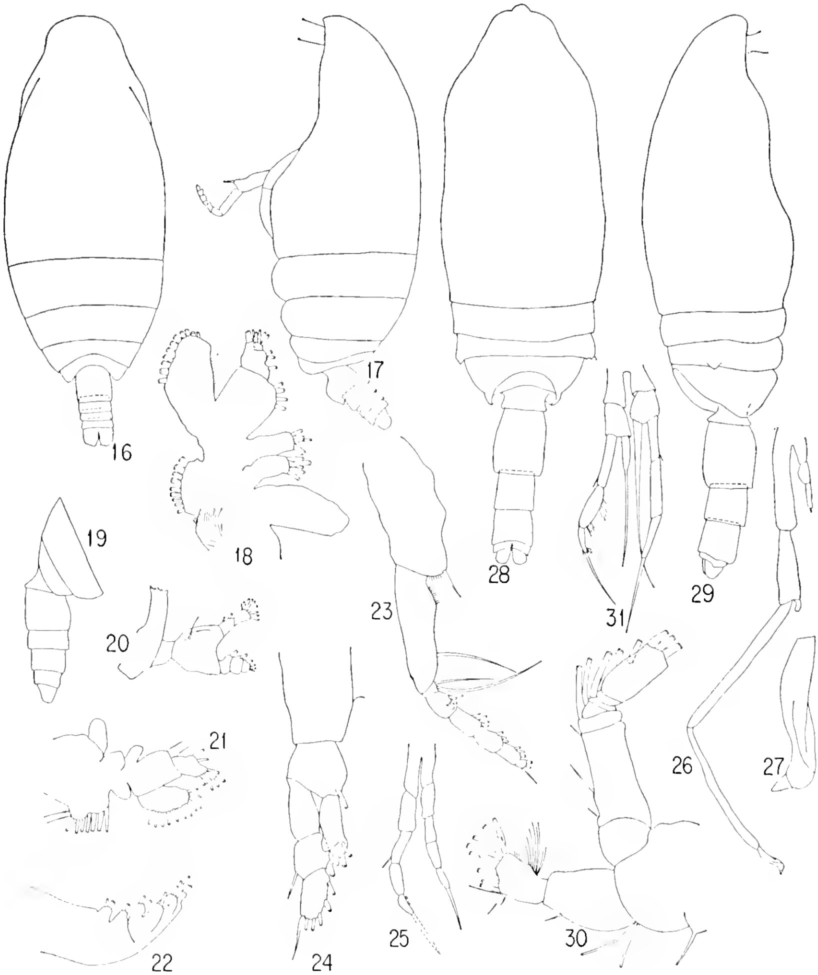
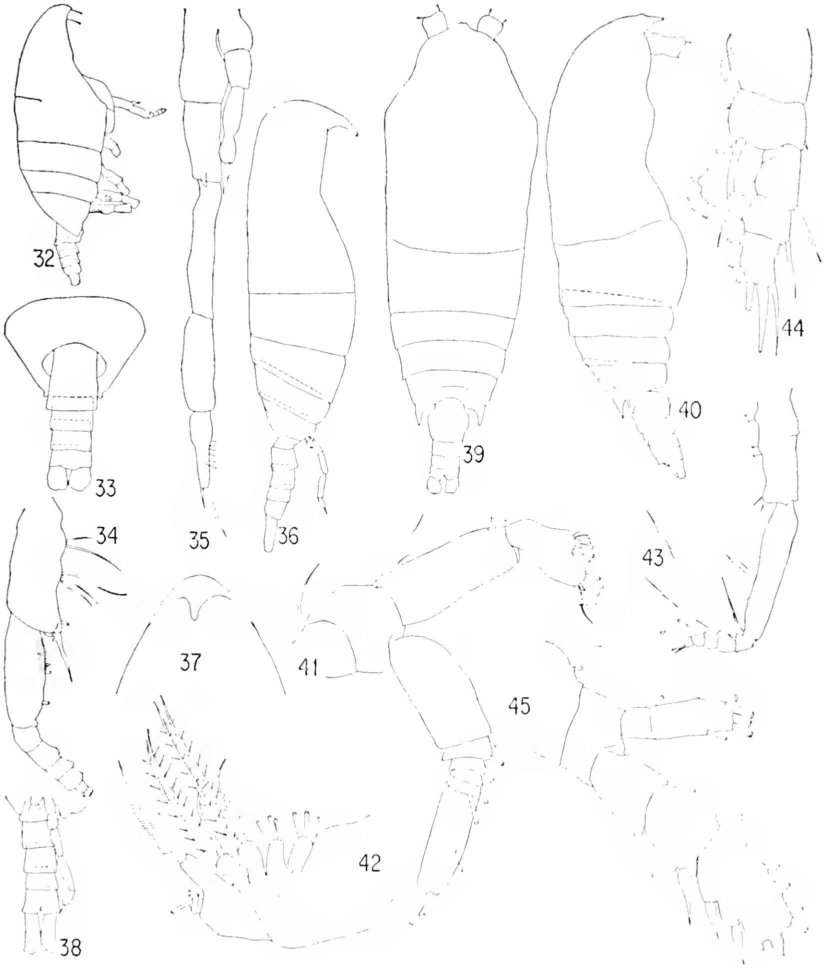


FIGURES 3-15.—*Calanus australis*, female: 3, first basipodal segments of fifth feet. *Farrania frigida*, male: 4, dorsal view; 5, lateral view; 6, distal end of right first antenna; 7, proximal end of right first antenna; 8, mandible blade; 9, first maxilla (first inner lobe omitted); 10, second basal segment and endopod of first maxilla; 11, second maxilla; 12, maxilliped; 13, first foot; 14, fifth foot; 15, female, posterior end of thorax and abdomen.



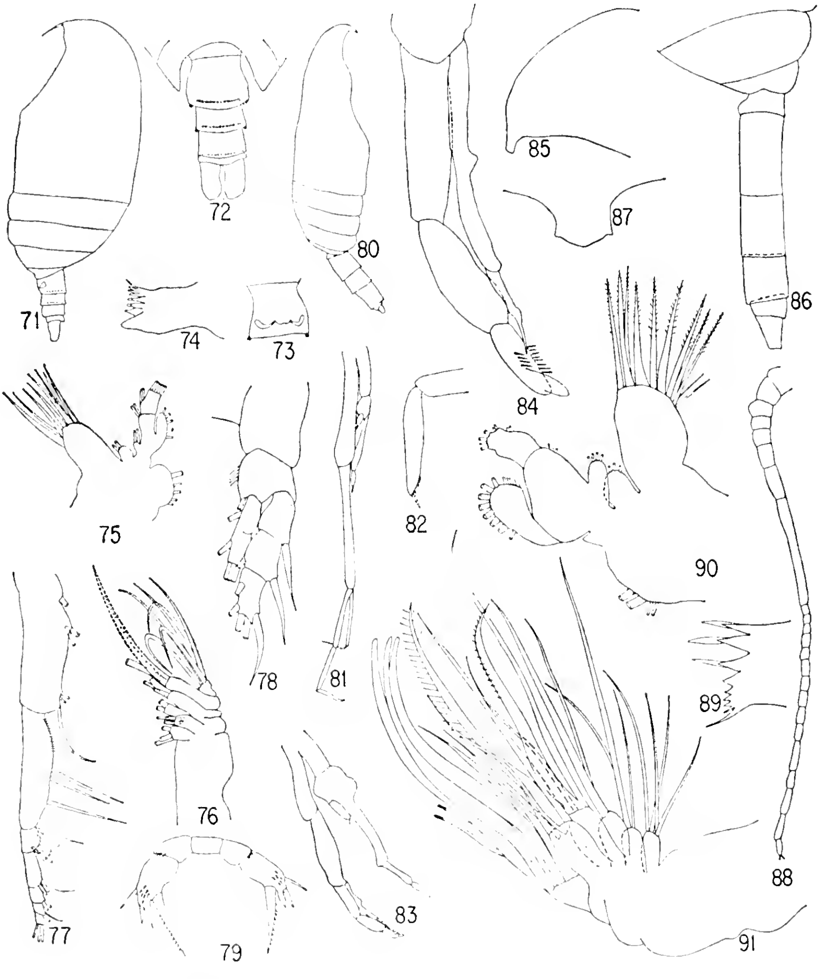
FIGURES 16–31.—*Mimocalanus inflatus?*, female: 16, dorsal view; 17, lateral view; 18, first maxilla (spines on inner lobe omitted). *Mimocalanus* species, male: 19, posterior end of thorax and abdomen, lateral view; 20, mandible; 21, first maxilla; 22, second maxilla; 23, maxilliped; 24, first foot; 25, fifth feet. *Spinocalanus longipes*, male: 26, fifth feet; 27, terminal segment of left fifth foot. *Spinocalanus validus*, male: 28, dorsal view; 29, lateral view; 30, second antenna; 31, fifth feet.



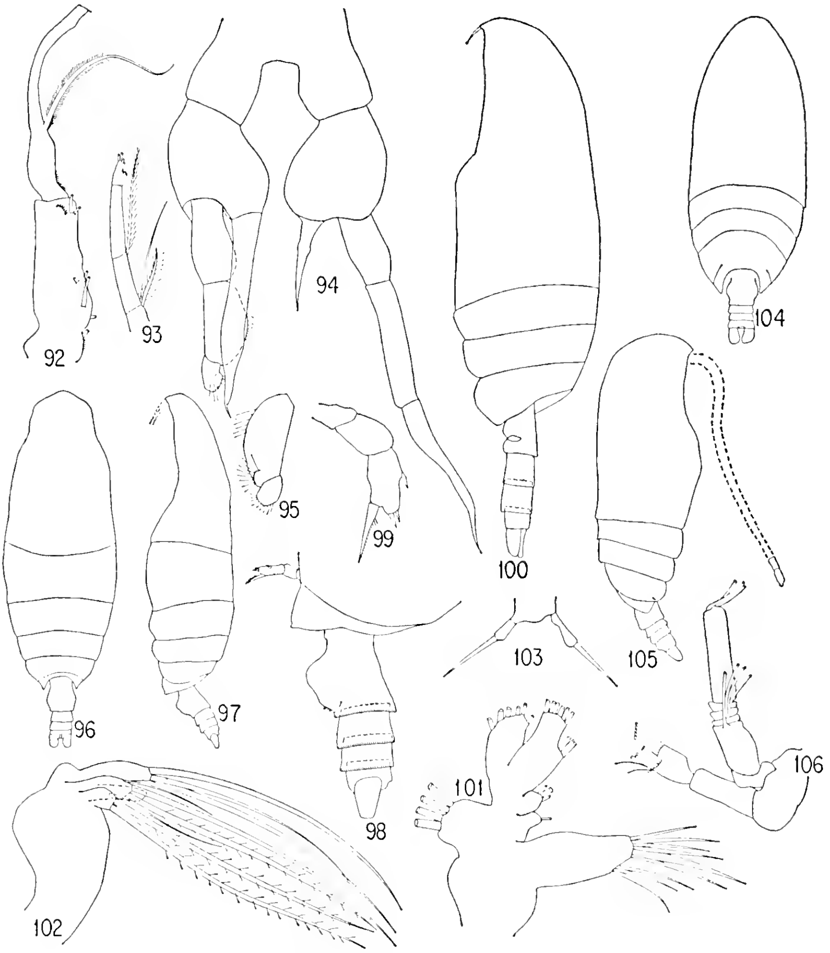
FIGURES 32-45.—*Spinocalanus ventriosus*, new species, female: 32, lateral view; 33, fifth thoracic segment and abdomen, dorsal view; 34, maxilliped (setae on distal segments omitted). *Spinocalanus* species, male: 35, fifth feet. *Teneriforma naso*, male: 36, lateral view; 37, anterior end of head, ventral view; 38, fifth feet and abdomen, ventral view. *Aetideopsis retusa*, new species, female: 39, dorsal view; 40, lateral view; 41, second antenna; 42, second maxilla; 43, maxilliped; 44, first foot; 45, second foot (terminal spine on exopod broken off).

FIGURES 46–55.—*Bradyetes florens*, new species, female: 46, dorsal view; 47, lateral view; 48, second antenna; 49, mandible palpus; 50, mandible blade; 51, first maxilla; 52, second maxilla; 53, maxilliped; 54, first foot. *Chirundinella cara*, female: 55, head, lateral view.

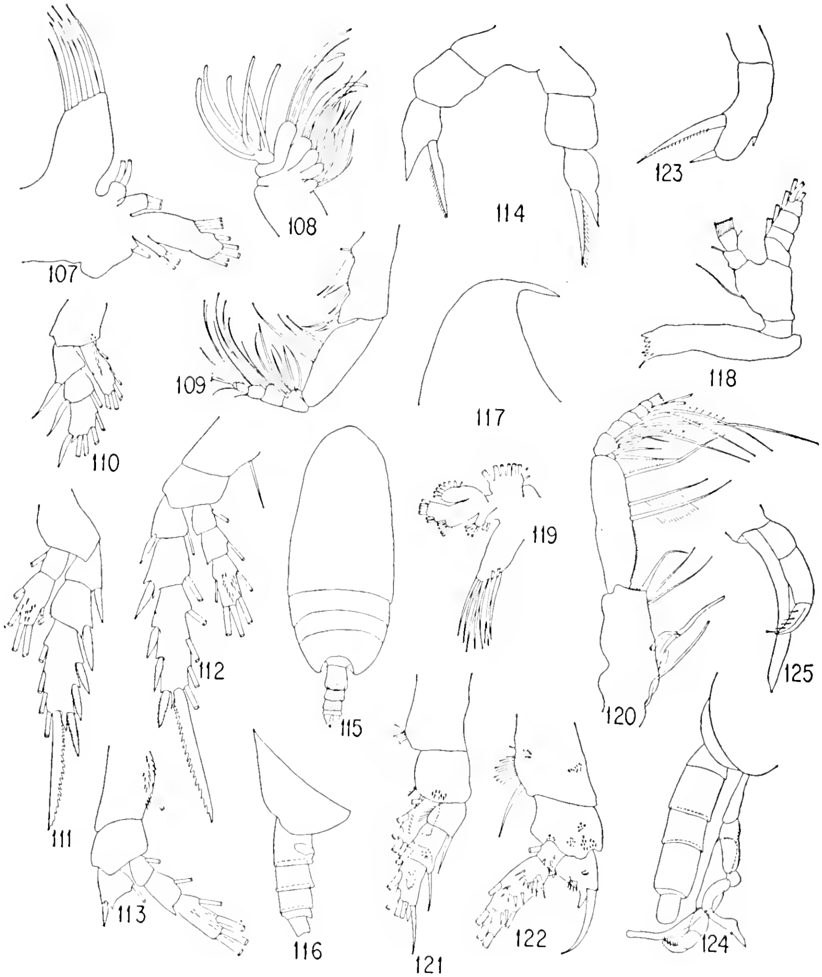
Figures 56–70.—*Gaetanus ferox*, male: 56, fifth thoracic segment and abdomen, dorsal view; 57, anterior end of head, lateral view; 58, anterior end of head, ventral view; 59, fifth feet. *Gaidius robustus*, male: 60, fifth thoracic segment and abdomen, dorsal view; 61, fifth thoracic segment and abdomen, lateral view; 62, anterior end of head, lateral view; 63, fifth feet; 64, distal end of left fifth foot. *Pseudochirella squalida*, new species, female: 65, anterior end of head, lateral view; 66, abdomen, lateral view; 67, genital segment, dorsal view; 68, genital segment, left side; 69, second antenna; 70, fourth foot.



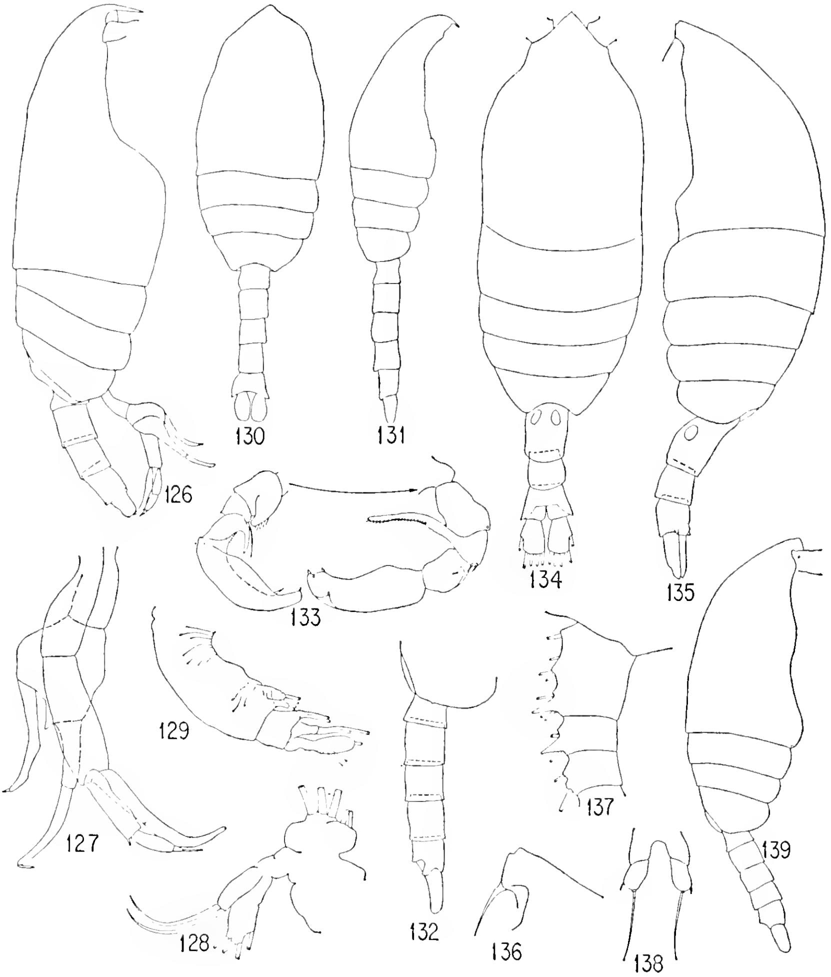
FIGURES 71–91.—*Xanthocalanus hispidus*, new species, female: 71, lateral view; 72, fifth thoracic segment and abdomen, dorsal view; 73, genital segment, ventral view; 74, mandible blade; 75, first maxilla; 76, second maxilla; 77, maxilliped; 78, first foot; 79, fifth feet. *Amallothrix indica*, male: 80, lateral view; 81, fifth feet; 82, distal end of left fifth foot. *Amallothrix paravalida*, male: 83, fifth feet; 84, left fifth foot. ?*Racovitzanus* species, male: 85, anterior end of head, lateral view; 86, posterior end of thorax and abdomen, lateral view; 87, rostrum, ventral view; 88, right first antenna; 89, mandible blade; 90, first maxilla; 91, second maxilla.



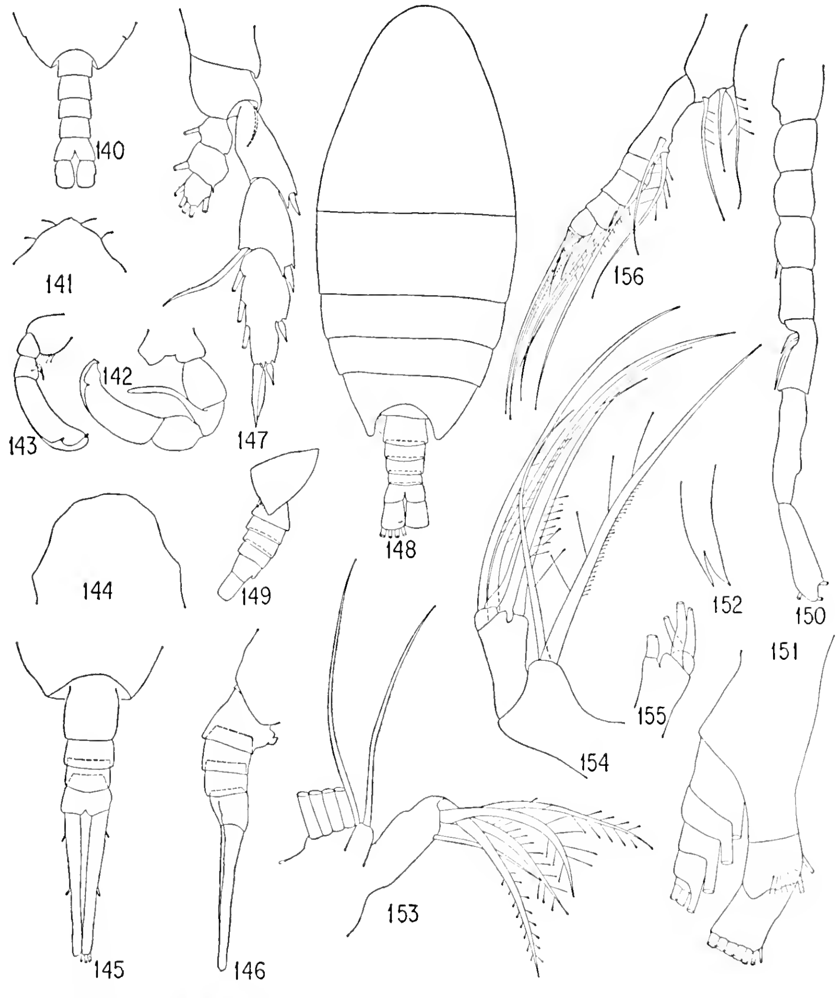
FIGURES 92–106.—?*Racovitzanus* species, male: 92, basipodal segments of maxilliped; 93, distal segments of maxilliped (enlarged); 94, fifth feet; 95, distal segments of left fifth foot. *Scaphocalanus bogorovi*, female: 96, dorsal view; 97, lateral view; 98, fifth thoracic segment and abdomen, lateral view; 99, fifth foot. *Scolecithricella grata*, new species, female: 100, lateral view; 101, first maxilla; 102, second maxilla; 103, fifth feet. *Scolecithricella maritima*, new species, female: 104, dorsal view; 105, lateral view; 106, second antenna.



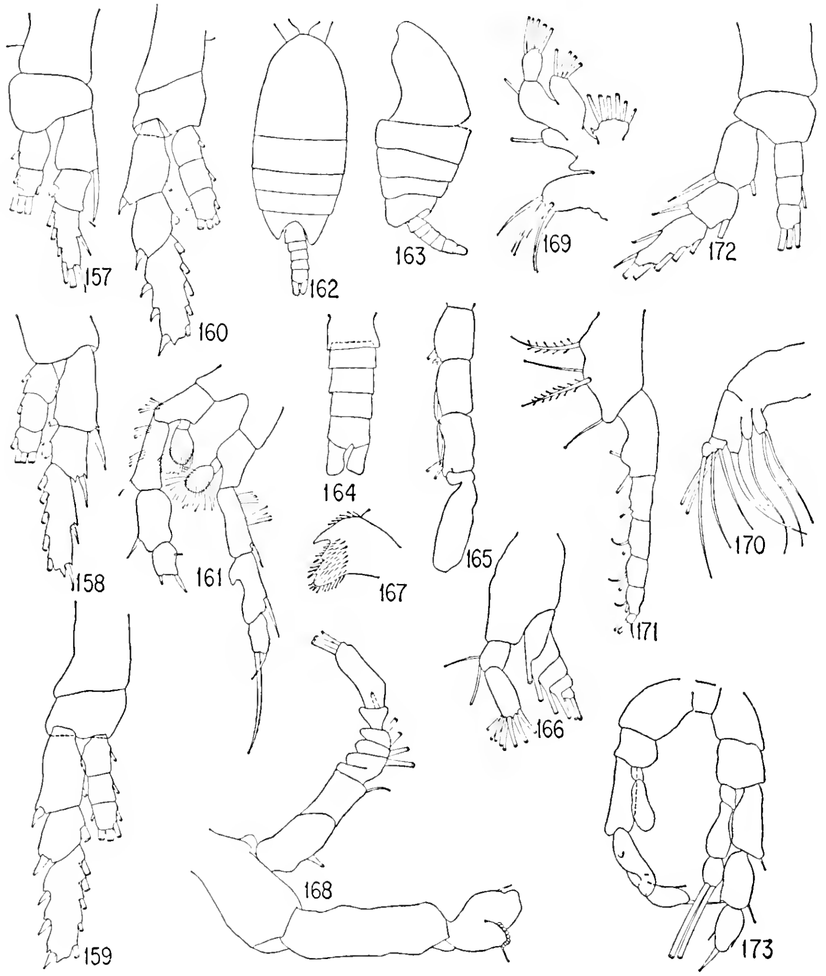
Figures 107–125.—*Scolecithricella maritima*, new species, female: 107, first maxilla; 108, second maxilla; 109, maxilliped; 110, first foot; 111, second foot; 112, third foot; 113, fourth feet (second and third exopodal segments broken off); 114, fifth feet. *Scolecithricella timida*, female: 115, dorsal view; 116, fourth and fifth thoracic segments and abdomen, lateral view; 117, anterior end of head, lateral view; 118, mandible; 119, first maxilla; 120, maxilliped; 121, first foot; 122, second foot (second and third exopodal segments broken off); 123, fifth foot. *Scolecithricella*, species, male: 124, abdomen and fifth feet, lateral view; 125, distal end of left fifth foot (enlarged).



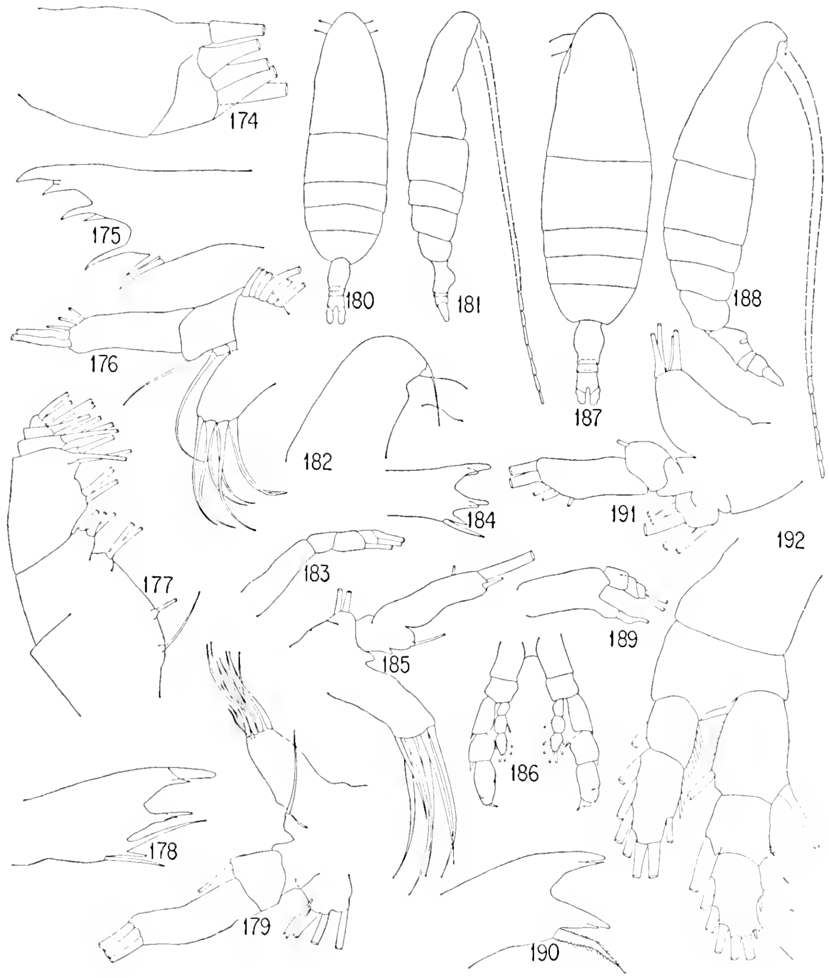
FIGURES 126–139.—*Scolecithrix fowleri*, male: 126, lateral view; 127, fifth feet; 128, first maxilla; 129, second maxilla. *Metridia boecki?*, male: 130, dorsal view; 131, lateral view; 132, fifth thoracic segment and abdomen, lateral view; 133, fifth feet. *Metridia effusa*, new species, female: 134, dorsal view; 135, lateral view; 136, anterior end of head, lateral view; 137, proximal end of first antenna; 138, fifth feet; 139, male, lateral view.



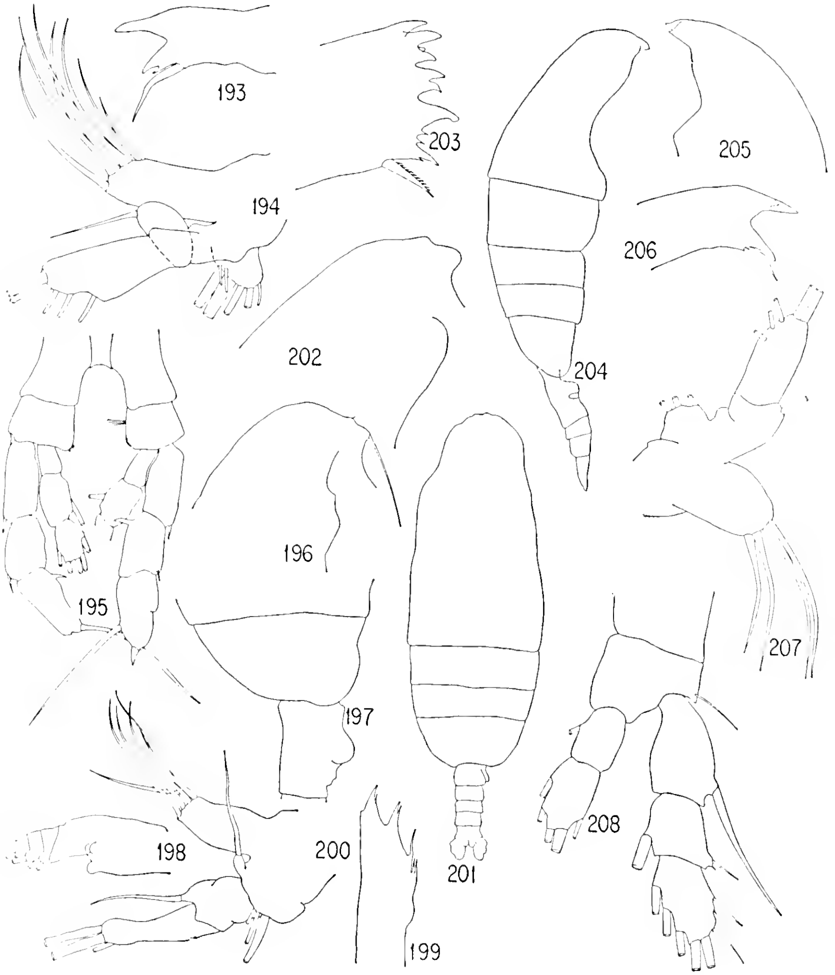
Figures 140–156.—*Metridia effusa*, new species, male: 140, fourth and fifth thoracic segments and abdomen, dorsal view; 141, anterior end of head, dorsal view; 142, right fifth foot; 143, left fifth foot. *Lucicutia major*, female: 144, anterior end of head, dorsal view; 145, fifth thoracic segment and abdomen, dorsal view; 146, fifth thoracic segment and abdomen, lateral view; 147, fifth foot. *Disco inflatus*, male: 148, dorsal view; 149, fifth thoracic segment and abdomen, lateral view; 150, distal segments of left first antenna; 151, mandible palpus; 152, mandible blade; 153, first maxilla; 154, second maxilla; 155, distal end of second maxilla, other side; 156, maxilliped.



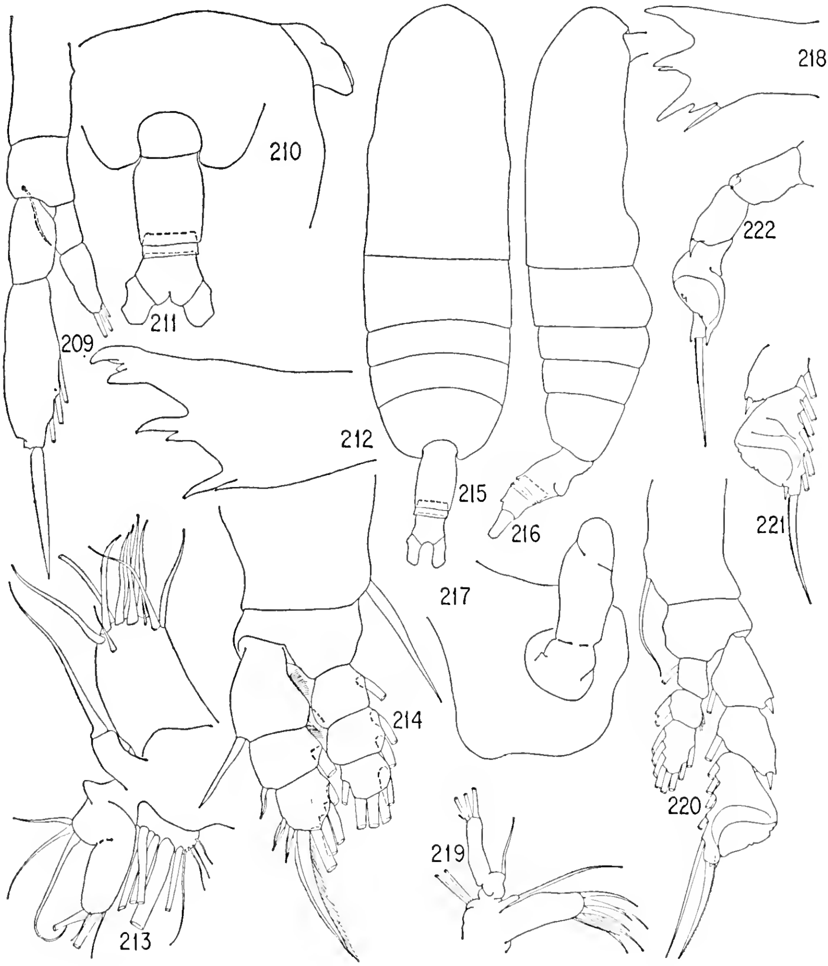
Figures 157–173.—*Disco inflatus*, male: 157, first foot; 158, second foot (terminal spine broken off); 159, third foot (terminal spine broken off); 160, fourth foot (terminal spine broken off); 161, fifth feet. *Disco* species, male: 162, dorsal view; 163, lateral view; 164, abdomen dorsal view; 165, segments 15–18 of left first antenna; 166, mandible palpus; 167, mandible blade; 168, second antenna (distal setae of endopod broken off); 169, first maxilla; 170, second maxilla; 171, maxilliped; 172, first foot; 173, fifth feet.



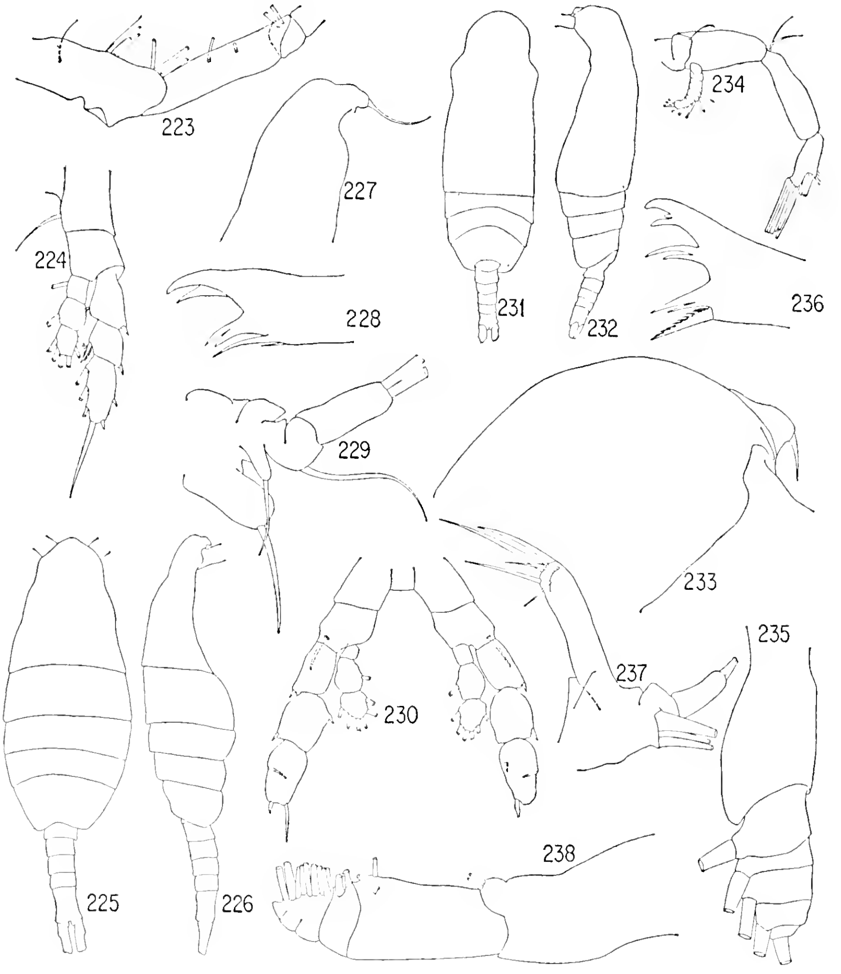
Figures 174–192.—*Euaugaptilus brodskyi*, female: 174, mandible palpus; 175, mandible blade; 176, first maxilla; 177, second maxilla; 178, male, mandible blade; 179, first maxilla. *Euaugaptilus curtus*, new species, female: 180, dorsal view; 181, lateral view; 182, anterior portion of head, lateral view; 183, mandible palpus; 184, mandible blade; 185, first maxilla; 186, male, fifth feet. *Euaugaptilus fundatus*, new species, female: 187, dorsal view; 188, lateral view; 189, mandible palpus; 190, mandible blade; 191, first maxilla; 192, first foot.



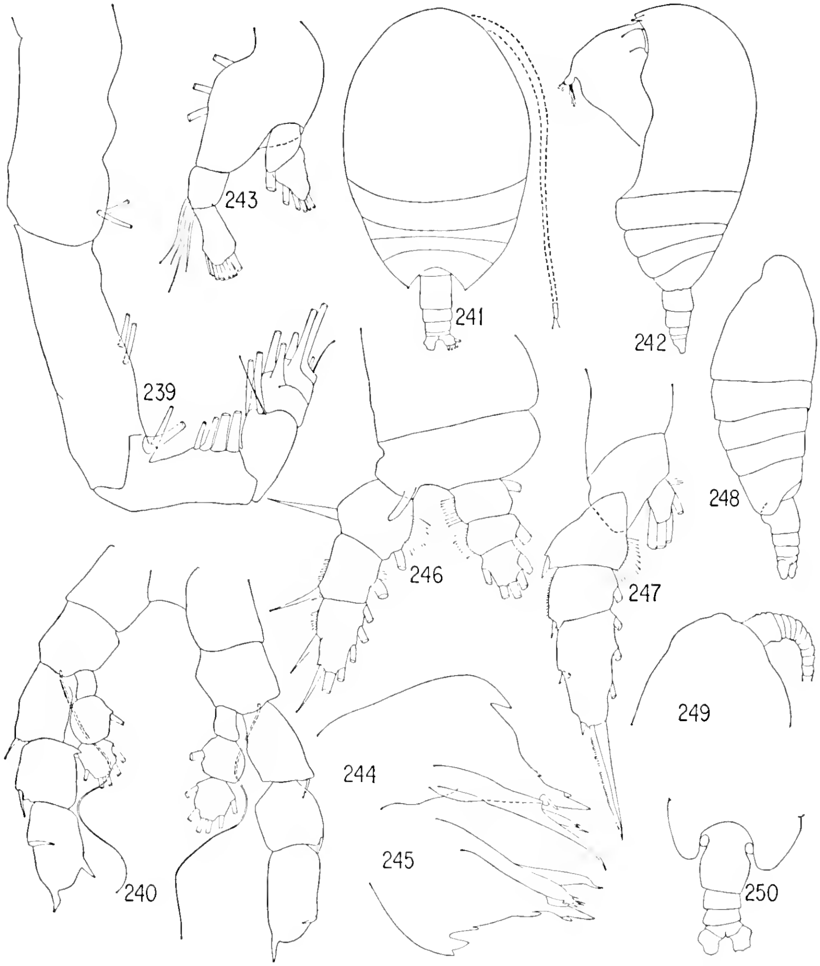
FIGURES 193–208.—*Euaugaptilus longiseta*, male: 193, mandible blade; 194, first maxilla; 195, fifth feet (terminal segment of right endopod incomplete). *Euaugaptilus malacus*, new species, female: 196, anterior portion of head, lateral view; 197, fifth thoracic segment and genital segment; 198, mandible palpus; 199, mandible blade; 200, first maxilla. *Euaugaptilus nodifrons*, male: 201, dorsal view; 202, anterior portion of head, lateral view; 203, mandible blade. *Euaugaptilus quaesitus*, new species, female: 204, lateral view; 205, anterior portion of head, lateral view; 206, mandible blade; 207, first maxilla; 208 first foot.



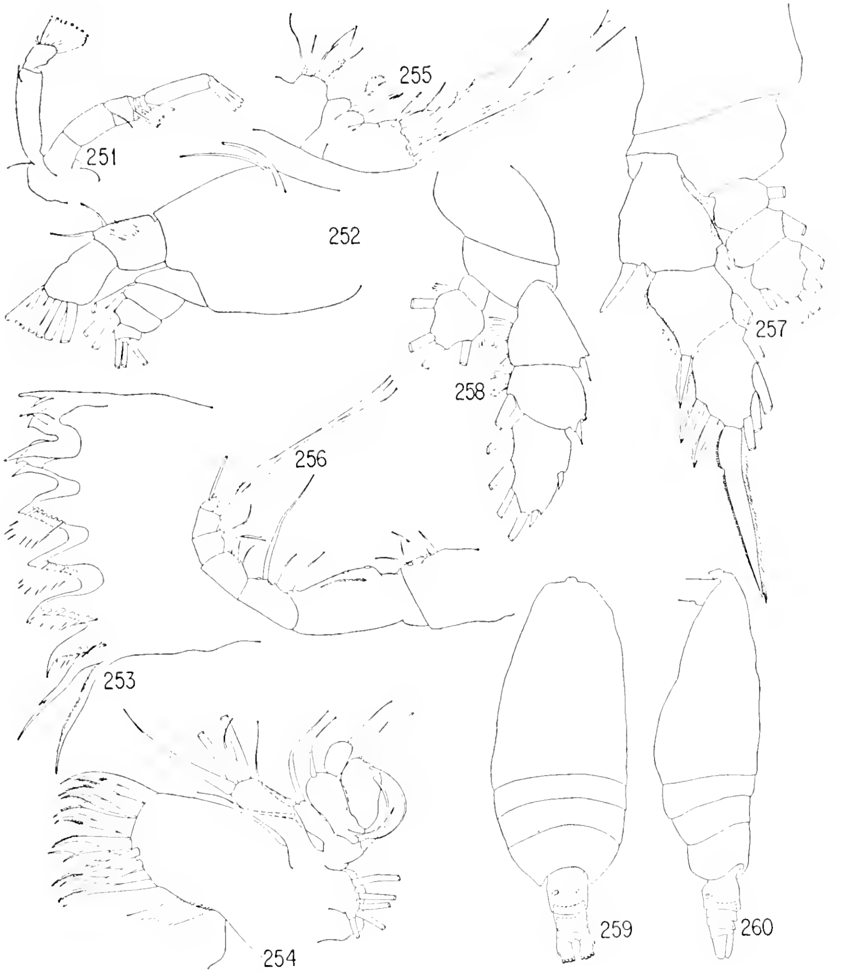
FIGURES 209–222.—*Euaugaptilus quaesitus*, new species, female: 209, fifth foot. *Euaugaptilus rectus*, new species, female: 210, anterior portion of head, lateral view; 211, abdomen, dorsal view; 212, mandible blade; 213, first maxilla; 214, first foot. *Euaugaptilus* species 1, female: 215, dorsal view; 216, lateral view; 217, mandible palpus with basis of mandible blade; 218, mandible blade; 219, first maxilla; 220, third foot, anterior side; 221, second and third exopodal segments of third foot, posterior side; 222, exopod of left third foot, external side.



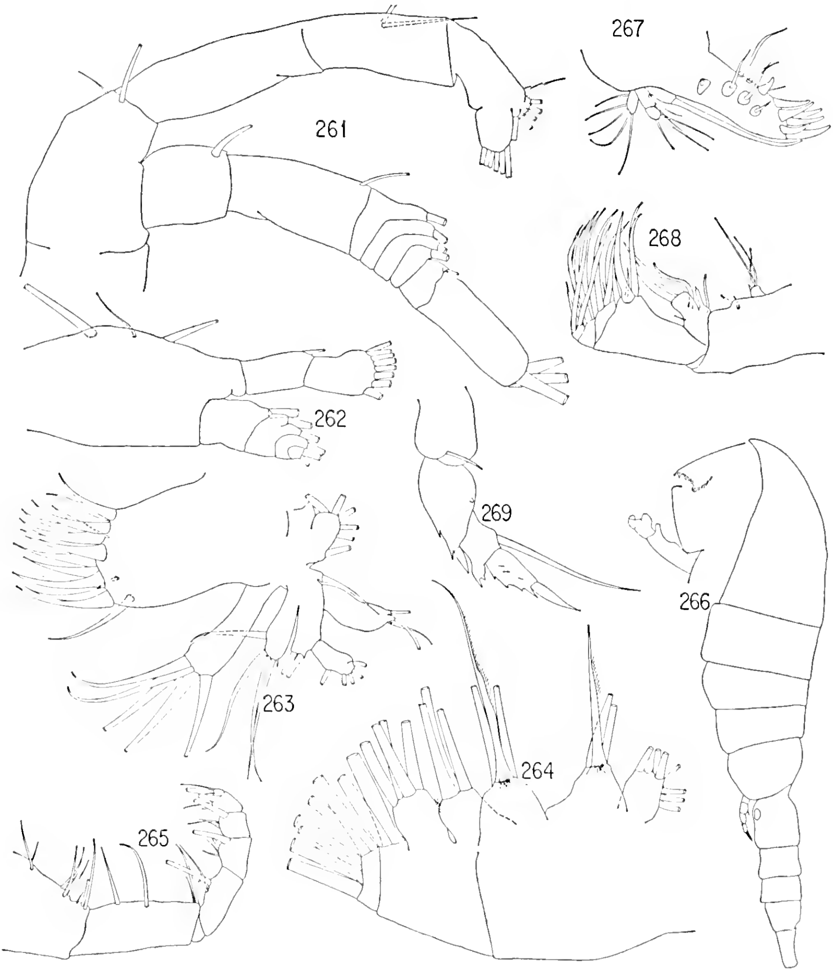
FIGURES 223–238.—*Euaugaptilus* species 1, female: 223, basipodal segments of maxilliped; 224, fifth foot. *Euaugaptilus* species 2, male: 225, dorsal view; 226, lateral view; 227, anterior portion of head, lateral view; 228, mandible blade; 229, first maxilla; 230, fifth feet. *Euaugaptilus* species 3, male: 231, dorsal view; 232, lateral view; 233, anterior portion of head, lateral view; 234, second antenna; 235, mandible palpus; 236, mandible blade; 237, first maxilla; 238, second maxilla.



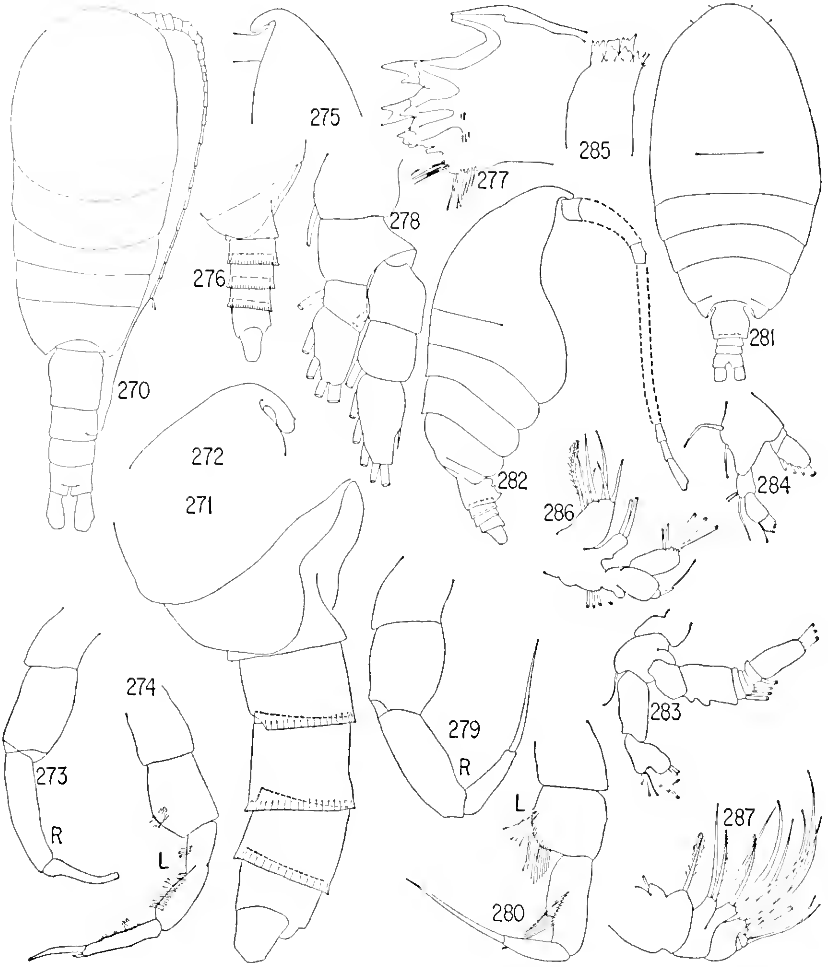
FIGURES 239–250.—*Euaugaptilus* species 3, male: 239, maxilliped; 240, fifth feet. *Pachyptilus abbreviatus*, female: 241 dorsal view; 242, lateral view; 243, mandible palpus; 244, mandible blade; 245, mandible blade, another view; 246, first foot; 247, fifth foot. *Pontoptilus robustus*, female: 248, lateral view; 249, anterior portion of head, dorsal view; 250, fifth thoracic segment and abdomen, dorsal view.



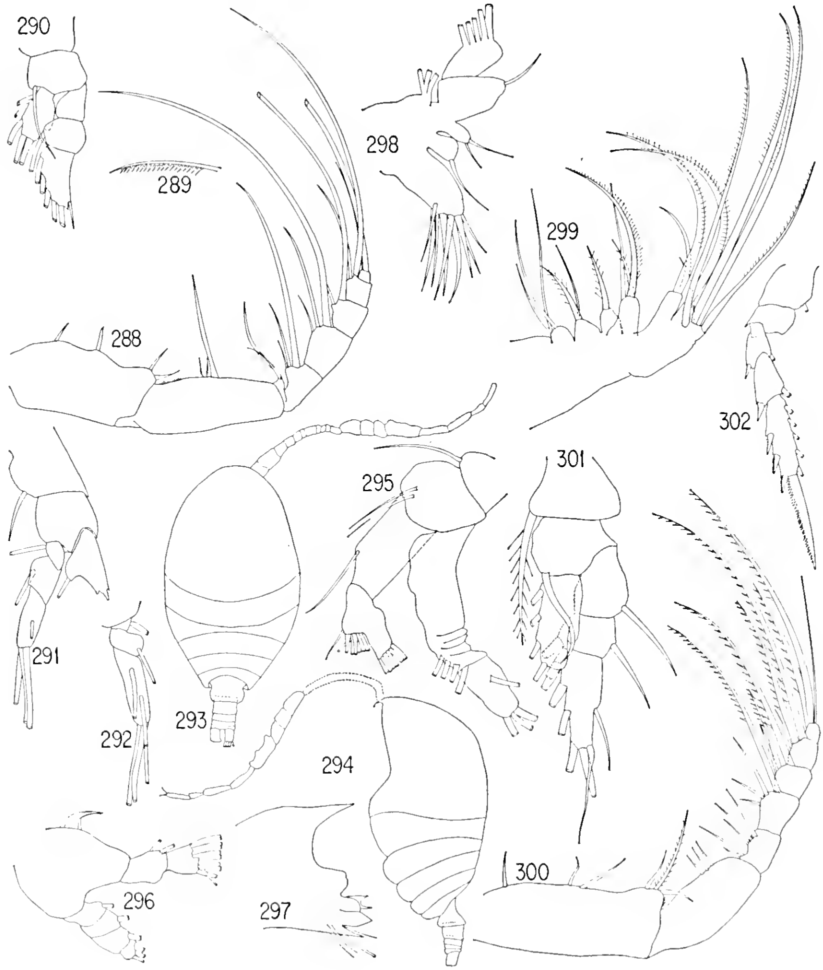
FIGURES 251–260.—*Pontoptilus robustus*, female: 251, second antenna; 252, mandible palpus; 253, mandible blade; 254, first maxilla; 255, second maxilla; 256, maxilliped; 257, first foot; 258, fifth foot. *Pontoptilus lacertosus*, new species, female: 259, dorsal view; 260, lateral view.



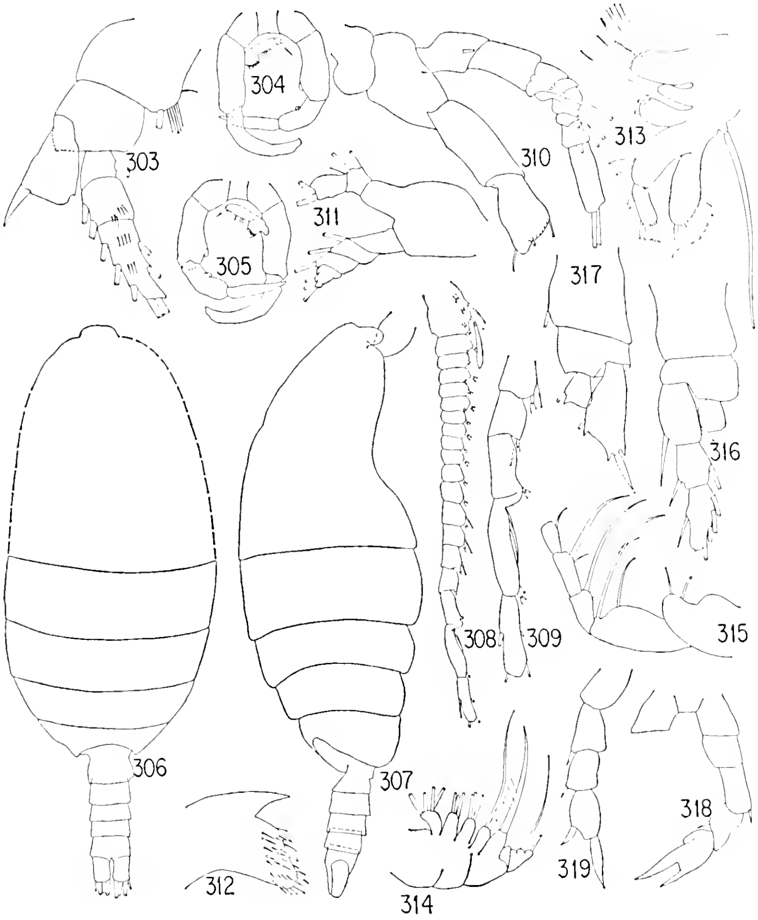
Figures 261–269.—*Pontoptilus lacertosus*, new species, female: 261, second antenna; 262, mandible palpus; 263, first maxilla; 264, second maxilla; 265, maxilliped. *Phyllopus muticus*, female: 266, lateral view; 267, first maxilla; 268, second maxilla; 269, fifth foot.



FIGURES 270–287.—*Phyllopus muticus*, female: 270, dorsal view. *Bathypontia elongata*, male: 271, fifth thoracic segment and abdomen, lateral view; 272, anterior portion of head, lateral view; 273, right fifth foot; 274, left fifth foot. *Bathypontia regalis*, new species, male: 275, anterior portion of head, lateral view; 276, fifth thoracic segment and abdomen, lateral view; 277, mandible blade; 278, first foot; 279, right fifth foot; 280, left fifth foot. *Rhinomaxillaris bathybia*, new genus and new species, female: 281, dorsal view; 282, lateral view; 283, second antenna; 284, mandible palpus; 285, mandible blade; 286, first maxilla; 287, second maxilla.



Figures 288–302.—*Rhinomaxillaris bathybia*, new genus and new species, female: 288, maxilliped; 289, distal portion of strong spine on maxilliped, enlarged; 290, first foot; 291, fourth foot (exopod incomplete); 292, endopod of fourth foot, another view. *Zenkevitchiella crassa*, new species, male: 293, dorsal view; 294, lateral view; 295, second antenna; 296, mandible palpus; 297, mandible blade; 298, first maxilla; 299, second maxilla; 300, maxilliped; 301, first foot; 302, third foot (endopod omitted).



FIGURES 303–319.—*Zenkevitchiella crassa*, new species, male: 303, second foot (exopod incomplete); 304, fifth feet, posterior side; 305, fifth feet; anterior side. Unidentified male: 306, dorsal view; 307, lateral view; 308, left first antenna; 309, distal segments of left first antenna (enlarged); 310, second antenna; 311, mandible palpus; 312, mandible blade; 313, first maxilla; 314, second maxilla; 315, maxilliped; 316, first foot (endopod incomplete); 317, third foot (exopod and endopod incomplete); 318, left fifth foot with first segment of right fifth foot; 319, right fifth foot without first segment.

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THE EXTINCT SEA MINK, WITH TAXONOMIC NOTES

By Richard H. Manville[1]

A century ago, along the coasts of New England, there appears to have lived a large, distinctive mustelid variously known as the sea or seashore mink, the giant or big mink, bull mink, salt-water mink, shell-heap mink, or ancient mink. It long since has slipped into oblivion, leaving such a fragmentary record that its true nature is largely a mystery. With the present concern for rare and endangered species similarly threatened with extinction, it seems appropriate to summarize our knowledge of this former member of the American fauna.

For the opportunity to examine the Clark specimen I am indebted to James C. Sullivan of East Winthrop, Maine. Sea mink materials from the Museum of Comparative Zoology were kindly made available by Barbara Lawrence. Arthur Stupka provided much useful, unpublished information. John L. Paradiso assisted with helpful suggestions and by checking my measurements of various specimens. Joseph P. E. Morrison and William C. Schroeder confirmed the identification of certain items reported in the sea mink's diet. To all these individuals, I am most grateful for their willing assistance.

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[1] Director, Bird and Mammal Laboratories, U.S. Fish and Wildlife Service, and Honorary Research Associate, Smithsonian Institution.

General Description

Along the Atlantic coast from Maine to New York are thousands of shell heaps or kitchen middens, from a few square yards to an acre or so in extent. These middens were produced by Indian encampments dating back to pre-Columbian times. They have long excited interest (Wyman, 1868) and many are still being explored (Waters and Mack, 1962). In one such shell heap at Brooklin, Hancock Co., Maine—on the western shore of Bluehill Bay—F. W. True and D. W. Prentiss unearthed, in 1897, the fragmentary skull of an unusually large mink. This specimen, no. 115178 in the U. S. National Museum, was described by Prentiss (1903) as a new species, *Lutreola macrodon.*

The type specimen consists of the maxillae, portions of the nasals, the right zygoma, and the palate to beyond the last molar. All teeth are present on the right side, but only the incisors and one premolar on the left. (The right upper canine of the holotype has come loose and has been firmly affixed, inadvertently, on the left side.) All teeth are in good condition except the canine, which is broken at the tip. Prentiss described the rostrum as very wide and the nasal aperture and the infraorbital foramina as large. He pointed out that the nasals ascend more abruptly in the type specimen than in *Mustela vison mink*, its nearest relative; the dentition is similar except for the larger size of the teeth and the more acute angle of the carnassial with the long axis of the skull in *macrodon*. Compared with *M. v. ingens* of Alaska, the largest mink extant, he found *macrodon* to be decidedly larger; e.g., the toothrow (anterior incisor to posterior molar) measured 28.0 vs. 30.0 mm.

Subsequently, many other skeletal remains of *macrodon* have been recovered from old Indian sites along the New England coast. Evidently the sea mink served as food for the Indians. Loomis (1911) reported that "every skull has the brain case broken and lost." Many mandibles were scored, as if by a scraping implement used to remove the flesh. Loomis characterized his mink as large and heavily built, with a low sagittal crest and short, wide postorbital processes. The frontal region was slightly arched between the orbits. Teeth were typical of the genus but stouter and heavier; the inner tubercle of the upper carnassial was single and rather small.

Norton (1930, p. 28) further described a specimen from Goose Island, in the collection of the Portland Society of Natural History, as showing "a well pronounced sagittal crest, a rugose parietal, an ample foramen magnum and massive occipital condyles. The basioccipital has a strong knob on each margin which extends forward as a distinct ridge. The audital bulla is low, with a spine 1.5 mm. long at the inner anterior point."

Distribution

Different authors have ascribed to the sea mink a probable range along the Atlantic seaboard from southwestern Nova Scotia to the coast of Connecticut. It probably is now impossible to document records from all of this area, but certainly the sea mink once occurred along most of the coasts of Maine and Massachusetts.

Near the type-locality, Moorehead (1922) reported remains of "the large mink" from Boynton's shell heap at Lamoine, near the head of Frenchman's Bay. His specimens were examined by G. M. Allen, who later (1942, pp. 181–183) reported remains of the "sea mink" from sites as distant as "Casco Bay in the south, and northeastward to Mount Desert and Frenchman's Bay, and Roques Island, Washington County, Maine." Loomis (1911), on the basis of fragments from no less than 45 individuals on Flagg Island, near South Harpswell on Casco Bay, described the mink as *Lutreola vison antiquus*. A year later, Loomis and Young (1912) reported remains of 53 individuals from Flagg Island, 3 from Sawyer's Island near Boothbay, 2 from Seward Island in Frenchman's Bay, and 1 from Winter Harbor. Hollister (1913, p. 478) examined the mandible of a specimen from Lower Babson Island, Maine. Summarizing the distributional data then available, Norton (1930, p. 27) listed the range as between "Great Diamond Island, Casco Bay, on the west, and Roque's Island in Washington County on the east," and probably also on the shores of New Brunswick. He noted that a skin, probably of this species, was handled at Campobello Island, near the mouth of the Bay of Fundy, in 1894. Norton also pointed out, with supporting evidence, that specimens from Crouch's Cove on Goose Island in Casco Bay, reported by Wyman (1868) as *Putorius vison*, probably represented the sea mink.

Long ago, Gilpin (1867, p. 12) reported from Nova Scotia large skins which may have come from the sea mink. Some measured as much as 32.5 inches in total length; this may have been due in part to stretching. Skins of *M. v. mink* from the Maine coast seldom exceed 23 inches in length.

More recently, Waters and Ray (1961) unearthed remains of *macrodon* from an archeological site at Assawampsett Pond in Middleboro, Plymouth Co., Mass. The bones were in excellent condition, although fire blackened. Radio-carbon dating indicated their age in the order of 4,300±300 years. This site is now 12 miles from the nearest salt water. The authors speculated that the animals may have reached there via the Taunton or Mattapoisett Rivers, or may have been transported by Indians from Narragansett or Buzzards Bay. The next year, Waters and Mack (1962) reported further remains from Conant's Hill on the Weweantic River. This is a tidal river about 2 miles inland from Buzzards Bay and 15 miles from the earlier site at Middleboro. In Connecticut, Goodwin (1935, p. 70) suggested that the sea mink "might well have been found in the salt marshes and rivers along the coast of the state." In Rhode Island, Cronan and Brooks (1962, p. 104) consider the former occurrence of the sea mink as possible but speculative. Anderson (1947, p. 192) reported that it was "traditionally said to have been commonly trapped along the coast of the Bay of Fundy in southern New Brunswick" and may have "formerly occurred on the southwestern coast of Nova Scotia."

Recent History

The formal description of *macrodon* as a distinct species prompted Manly Hardy (1903) of Brewer, Maine, to write a short account of the sea mink. From about 1835, Hardy's father had been a fur buyer and had handled most of the furs from Penobscot to Frenchman's Bays. Manly Hardy himself continued this trade, and over 50,000 mink skins passed through his hands. He recognized as distinct an unusually large mink, especially from Swan's and Marshall's Islands, whose skins he received from the Indians of the Penobscot and Jericho Bay regions until about 1860. The fur of this mink was much coarser and of a more reddish color than in the inland form. It was usually extremely fat and possessed a very strong, peculiar, fishlike odor. In the early days, because of its large size, it brought a higher price and was persistently sought. Few were trapped; instead they were hunted with dogs. Some men pursued them from island to island, investigating any small ledge where a mink might live.

> They carried their dogs with them, and, besides guns, shovels, pick-axes and crow-bars, took a good supply of pepper and brimstone. If they took refuge in holes or cracks of the ledges, they were usually dislodged by working with shovels and crow-bars, and the dogs caught them when they came out. If they were in crevices of the rocks where they could not be got at and their eyes could be seen to shine, they were shot and pulled out by means of an iron rod with a screw at the end. If they could not be seen, they were usually driven out by firing in charges of pepper. If this failed, then they were smoked with brimstone, in which case they either came out or were suffocated in their holes (Hardy, 1903).

In a short time these practices exterminated the sea mink.

Mansueti (1954) reports that Lawrie Holmes, well-known conservationist of Mount Desert Island, recalled seeing mink traps made of laths, as well as the deadfall variety, in use during the late 1890s along the shore of the outer island near Northeast Harbor.

To Arthur Stupka, Naturalist at Acadia National Park on Mount Desert Island from 1932 to 1935, I am indebted for unpublished notes and correspondence on the sea mink. They include material from Mrs. Fannie Hardy Eckstorm, the daughter of Manly Hardy, who was custodian of her grandfather's and father's business records from 1835 to 1890. She was well acquainted with the large "seashore" mink and recalled seeing it when she was a child in the 1870s. The Abnaki Indians called it "mousebeysoo," meaning "wet thing." Mink skins commanded their highest price—about $10.00 for the top quality—at the close of the Civil War, and this, Mrs. Eckstorm believed, led to the animal's extermination.

Mrs. Eckstorm wrote further, in 1935, as follows:

> There is the question whether all mink that lived along the shore were the big sea mink. Were there two kinds there? I do not remember it, if there were. . . . I had a very practical acquaintance with birds for many years, while my father was collecting his series, and I often observed the tendency of restricted island forms, or those peculiar to the sea-coast, to run larger and *darker* than the inshore sub-species. . . . Why should these mink *all* be redder and larger, if there were two species on the same territory? The variation was constant. . . . My own opinion is that there were not two *species* of mink on our coast, but an extra-large *sub-species* most highly developed on Swan's and Marshall's Islands. . . . My father laughed at the inferences drawn from a single skull. . . . As to their being styled "species *macrodon*," "big-toothed," of course an animal twice as large as another of the same sort would have a bigger skull and bigger teeth! This is only an individual difference. I see no reason for making a species out of this mink, though it was a stable variety. Father could tell some eight or ten different local forms of mink and he thought several entitled to as good specific standing as the seashore mink.

Other material provided by Stupka relates to an interview in 1934 with Captain Rodney Sadler of Bar Harbor. He recalled seeing the "bull mink" as late as perhaps 1920, swimming from one island to another in the Sorrento region. It made its home on the ocean front, among the rocks of the seawall piled up by the surf. Its den always had two entrances. An adult and four young, which Sadler estimated to be 3 or 4 weeks old (8–10 inches long), were seen along the beach of Sister's Island in August. This was "40 odd years ago." The young were very attractive, lighter in color than the dark brown adult. The bull mink were said to feed almost entirely on fish; the most common remains about their dens were of toad sculpin (probably *Myoxocephalus octodecemspinosus*) and horned pout (probably *Macrozoarces americanus*). Mansueti (1954) stated they had been reported in association with the banded snail, *Cepaea* (*Helix*) *hortensis*, on the outer islands. Probably mussels and other shellfish also contributed to their diet.

Allen (1942, p. 181) subscribes to the view that, in earlier times, only the large sea mink occurred in the eastern part of the Gulf of Maine, probably ranging as far as southern Nova Scotia. Evidently it was supplanted, within the last century, by the smaller southern race, *M. v. mink*, which also has a propensity for seacoasts.

The various early accounts of the sea mink prompted Seton (1921) to call attention to the possibility of still obtaining a specimen. "It was the custom in the small hotels of the region," he wrote, "to have mounted any local animal of unusual interest in point of size, etc. These rarities were kept in glass cases as parlor ornaments or as barroom accessories." As a result of Seton's plea, an unusually large mounted mink specimen was located at Lubec, in extreme eastern Maine near the Bay of Fundy, in the possession of Clarence H. Clark.

A Supposed Sea Mink Specimen

Clarence H. Clark—businessman, politician, historian, and county commissioner of Washington County—had over the years built up a considerable private collection of the fauna and flora of eastern Maine, housed in the upper part of his residence at Lubec. Included was a very large, light brown (and much faded) mounted specimen alleged to be the sea mink. Norton (1930, p. 27) first brought it to the attention of the scientific public. He saw the specimen in 1924 and was told by Clark that it was taken at Campobello Island, New Brunswick, in 1894.[2] This mink, mounted on a wooden base, was prepared in the old-fashioned way, with the skull and leg bones in place. The mouth is slightly open, permitting examination of the forward teeth. This and other items in the Clark collection were described in glowing terms by Keene (1929), who published a picture of the mink and was at pains to point out that it was "beyond price" and was sought by many of the nation's museums; however, Clark did not wish to part with it.

In 1935, Goodwin published a photograph (his plate IV, b) of the specimen, from Clarence Clark, depicting it as the sea-mink. Stupka, in the early 1930s, examined and photographed the same mount, and his picture was subsequently published by Leopold (1936). Mairs and Parks (1964) offered still another photograph, by the Portland Society of Natural History.[3] Mansueti (1954) presented his own drawing of the sea mink, posed beside the smaller northeastern mink of today.

By 1964, the Clark collection had come into the possession of James C. Sullivan, then of Dennysville, Maine. He was anxious to

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[2] Goodwin (1935, p. 70), in discussing the same specimen, says that Clark reported it taken "by a neighbor of his near the Bay of Fundy about 1874." This may have referred to the Jonesport specimen of "about 1880" mentioned by Norton (1930, p. 31).

[3] It should be pointed out that the measurements given by Mairs and Parks are *not* those of the Clark specimen under discussion but rather are the "probable dimensions" of *M. macrodon* as computed by Seton (1929, vol. 2, p. 562).

dispose of the whole lot and felt that he could sell the mink specimen for a sizeable sum. When we were approached at the National Museum on this matter, we agreed to examine the specimen to verify its identification before negotiating further regarding its acquisition. The lengendary specimen, which for safekeeping had been in storage at Waltham, Mass., reached us early in May 1965. Unfortunately, no data whatsoever accompanied it. It was examined with much interest and closely scrutinized by our staff and later by other, visiting scientists. In all, no less than 20 mammalogists expressed their opinions on it. The mink was subsequently returned to Mr. Sullivan, now residing at East Winthrop, Maine.

The Clark specimen (pl. 1) is indeed a large mink and in all probability was an adult male. The fur is coarse in texture and light reddish tan in color. The tail and hind feet are darkest, and the rest (particularly the right side and head) are much faded. Between the forelegs is a whitish patch about 50 x 15 mm in area; smaller white spots are present on the left forearm and medially in the inguinal region. Measurements of the mounted specimen are approximately as follows: total length 720, tail 210, hind foot 70 mm. In table 1, these measurements are compared with those of *M. macrodon*, as computed by Seton (1929, vol. 2, p. 562), as well as with examples, from the national collection, of specimens of *M. v. vison* and *M. v. mink*, from immediately north and south of the range in New England, and of *M. v. ingens*, the largest subspecies of mink extant, from Alaska. The Clark specimen, although larger in total length (possibly due to stretching), falls clearly within the limits of *Mustela vison* and well below those of *Mustela macrodon*.

TABLE 1.—*Skin measurements (mm) of various minks*

	Total length	Tail length	Hind foot
M. v. vison	580	150	68
1 ad. ♂, Quebec			
M. v. ingens	663	192	80
2 ad. ♂♂, Alaska	(630–695)	(174–210)	(75–85)
M. v. mink	644	231	74
3 ad. ♂♂, Maryland	(640–650)	(225–238)	(70–81)
Clark specimen	720	210	70
M. macrodon	914	254	88
Seton (1929) estimates			

Mustela macrodon was described from skull fragments only, and its distinguishing traits relate to the large teeth, particularly the upper canines. In table 2, tooth measurements of the Clark specimen are similarly compared with those of other minks in the national collection. These relationships are further illustrated in figure 1. Again, this controversial specimen falls clearly within the limits of *Mustela vison*.

TABLE 2.—*Tooth measurements (mm) of various minks*

	Greatest width across upper incisors	Greatest width across upper canines	Antero-posterior diameter of upper canine at alveolus
M. v. vison	5.6	12.1	3.2
3 ad. ♂♂, Quebec	(5.3–6.0)	(11.5–12.4)	(3.2)
M. v. ingens	7.2	15.7	4.3
3 ad. ♂♂, Alaska	(7.0–7.4)	(14.5–16.6)	(4.0–4.5)
M. v. mink	6.3	14.1	3.8
3 ad. ♂♂, Maryland	(6.1–6.5)	(13.6–14.7)	(3.7–3.9)
Clark specimen	6.0	13.9	3.6
M. macrodon	7.9	18.5	5.0
3 specimens, incl. holotype, Maine	(7.8–8.0)	(18.2–19.2)	(5.0)

One is forced to conclude that the Clark specimen, rather than representing the sea mink, *M. macrodon*, is actually an unusually large (probably adult male) specimen of the present mink, *M. vison*. The indications are that its affinity is closest to *M. v. mink*. There is even the possibility that the large Clark specimen was an intergrade between the sea mink and *M. vison*.

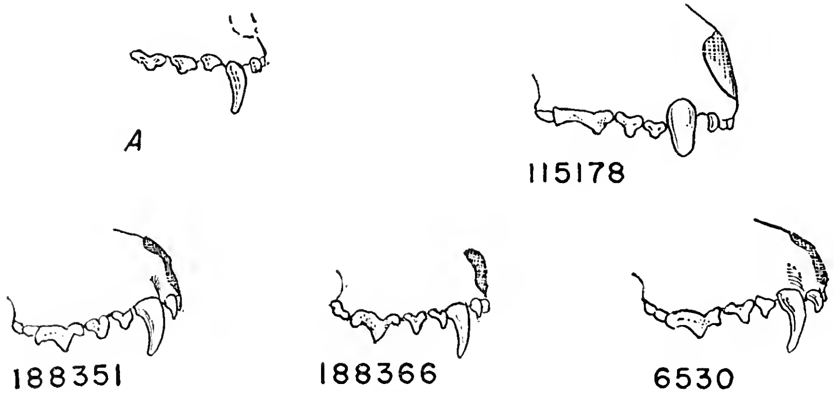

FIGURE 1.—Lateral views of the right upper teeth in various minks: *A*, the Clark specimen; 115178, holotype of *M. macrodon;* 188351, *M. v. mink*, Connecticut; 188366, *M. v. vison*, Quebec; 6530, holotype of *M. v. ingens*, Alaska.

Taxonomic Status

The status of the extinct sea mink, *Mustela macrodon,* itself seems in need of reappraisal. Known only from fragmentary skeletal remains, its supposed external measurements are largely a matter of conjecture. Certainly it must have been a large mink, but figures on its "probable dimensions" (Seton, 1929, vol. 2, p. 562) would appear to have been exaggerated. I feel it more reasonable to consider it as perhaps 25 per cent larger than *M. v. mink* of today and 15 per cent larger than the present *M. v. ingens.* In this I concur with Loomis (1911), who considered *antiquus* (=*macrodon*) as "all of 25 per cent larger" than *lutreocephalus* (=*mink*), with due allowance for adult females being normally about 20 per cent smaller than adult males in each species.

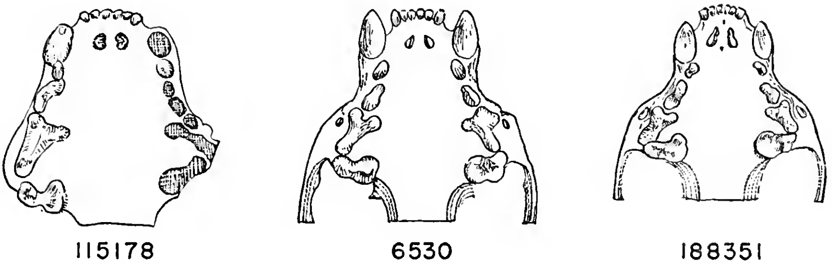

Figure 2.—Palatal views of teeth in three minks, drawn to approximately the same scale: 115178, holotype of *M. macrodon;* 6530, holotype of *M. v. ingens*, Alaska; 188351, *M. v. mink*, Connecticut.

In figure 2 are sketches of the upper dentition of *M. macrodon* and of two subspecies of present minks. The *macrodon* specimen is fragmentary and considerably worn; yet, aside from its size and generally massive character, I perceive in it no highly significant differences when compared with the other two specimens. The traits mentioned by Prentiss (1903), Hollister (1913), and Norton (1930)—wide rostrum, large infraorbital foramen, low audital bullae, rugose parietal, basioccipital with strong knob—appear to me to be relatively minor in nature, and not of the magnitude generally considered as distinguishing species. This was the opinion of Loomis (1911), whose materials, in all probability, represented *macrodon.* Loomis and Norton were not altogether in agreement as to the nature of the sagittal crest, which probably varied with the age of their specimens.

As attested by Hardy (1903), a number of recognizably different forms of mink occurred along the New England coast a century ago.

Many of the differences were probably attributable to individual or sexual variation. One of these forms, more distinct than others because of its large size, was pursued avidly for its pelt. Its seashore habitat rendered it relatively easy to capture. Overly zealous hunting, and possibly other factors of which we are unaware, led to its diminution and, ultimately, to its complete replacement by other, smaller forms of mink.

All the evidence indicates to me that the sea mink is most realistically considered as a subspecies, now extinct, of the prevalent mink, *Mustela vison*, of today. This view is strengthened if, as seems possible, the Clark specimen was indeed an intergrade between two other forms of mink. Accordingly, the sea mink should properly be known as follows.

Mustela vison macrodon (Prentiss)

Putorius vison Wyman, 1868, Amer. Nat., vol. 1, p. 574, January.
Lutreola macrodon Prentiss, 1903, Proc. U.S. Nat. Mus., vol. 26, p. 887, July 6.
Putorius macrodon Trouessart, 1904, Catalogus mammalium, Suppl., vol. 1, p. 206.
Lutreola vison antiquus Loomis, 1911, Amer. Journ. Sci., vol. 31, p. 228, March.
Mustela macrodon Miller, 1912, U.S. Nat. Mus. Bull. 79, p. 101, Dec. 31.

Type-locality: Shell heaps at Brooklin, Bluehill Bay, Hancock Co., Maine.

Range: Known only from skeletal remains; coast of New England from Penobscot and Casco Bays south to Middleboro, Plymouth Co., Mass.; possibly north to Campobello Island, New Brunswick, and south to the salt marshes and rivers of coastal Connecticut. Presumably extinct since about 1860 or somewhat later.

Specimens examined: 57 fragmentary crania and mandibles of *Mustela macrodon*, all from MAINE. HANCOCK COUNTY: Babson's Landing, 1 (USNM); Black Island, 4 (USNM); Brooklin, 2 (including the holotype, USNM); Campbell's Island, 5 (USNM); Conary's Cove, 8 (USNM); Eggemoggin Reach, 1 (USNM); Freethy's Bluff, 2 (USNM); Frenchman's Bay, 1 (MCZ); Harbor Island, 5 (MCZ); Kane's Point, 1 (USNM); Lower Babson Island, 3 (USNM); Naskeag Point, 6 (USNM); Penobscot, 2 (MCZ); Stonington, Deer Isle, 6 (USNM); Tibbitt's Cove, 1 (USNM). KNOX COUNTY: Great Spruce Head Island, 1 (MCZ); Port Clyde, 8 (MCZ). Also, numerous specimens of *Mustela vison*.

Summary

Reviewed is what we know of the natural history of the sea mink, *Mustela macrodon*, which inhabited the New England coasts until about 1880. Its probable earlier distribution is sketched, and reasons for its extinction are discussed. The only alleged skin extant, a

mounted specimen, is shown to be that of a large *Mustela vison*, possibly *M. v. mink*, or even an intergrade between *M. v. mink* and *M. macrodon*. The sea mink itself is reduced to subspecific rank, as *Mustela vison macrodon* (Prentiss).

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NEOTROPICAL MICROLEPIDOPTERA, XII[1]

FURTHER STUDIES ON GENUS LETHATA (LEPIDOPTERA: STENOMIDAE)

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After completion of my paper on the genus *Lethata* (1964), sufficient additional information has accumulated to warrant a supplement. This additional information has been derived from a number of sources including fieldwork, specimens borrowed from various institutions, and examination of heretofore unstudied type material.

As first defined, the genus *Lethata* consisted of 13 species of which 9 were removed from other genera and 4 were described as new. As a result of the current study, the genus has been enlarged to 31 species, 13 of which are herein described as new. Examination of type ma-

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[1] Prepared with the aid of a National Science Foundation Grant. Previous parts of this same series are: I and II, Clarke, 1962, Proc. U.S. Nat. Mus., vol. 113, no. 3457, pp. 373–388; III, Clarke, 1964, ibid., vol. 115, no. 3480, pp. 61–84; IV, Duckworth, 1964, ibid., vol. 116, no. 3497, pp. 97–114; V, Obraztsov, 1964, ibid., vol. 116, no. 3501, pp. 183–196; VI, Clarke, 1964, ibid., vol. 116, no. 3502, pp. 197–204; VII, Obraztsov, 1966, ibid., vol. 118, no. 3727, pp. 221–232; VIII, Duckworth, 1966, ibid., vol. 118, no. 3531, pp. 391–404; IX, Obraztsov, 1966, ibid., vol. 118, no. 3535, pp. 577–622; X, Duckworth, 1966, ibid., vol. 119, no. 3540, pp. 1–6; XI, Obraztsov, 1966, ibid., vol. 119, no. 3543, pp. 1–12.

terial has disclosed that five species formerly placed in other genera required transfer. In addition, the females of four previously described species are described and figured for the first time, and the first host plant information is recorded. The key to the species of *Lethata* has been completely revised and includes all species currently assigned to the genus, thus superseding all previous keys. Color characters were not utilized in the key due to the variability observed in several species where sufficient specimens were available to reflect inconsistences. It is becoming more and more apparent that examination of the genitalia is required for reliable species recognition in the Stenomidae.

Although distributional data are sorely lacking for most species, distribution maps have been prepared for all of the species (except *myopina* and *glaucopa*) in order to demonstrate the available information in the most graphic fashion. In addition, many of the localities are difficult to locate on the most commonly available maps; thus, the included maps will provide a useful guide to the geographic location.

One of the most perplexing problems encountered during the course of this study is the paucity of specimens and biological data. This situation was mentioned in my earlier paper with an expressed hope that planned fieldwork would provide additional information. Although progress has been made during the intervening two years, it has become apparent that the rate of accumulation will be much slower than originally anticipated. The numbers of individual specimens encountered through conventional collecting techniques, e.g., attraction to light, have been very sparse; and since very little rearing is being done in Central and South America, except for economic plants, the outlook is rather dim. The one bright spot to date is the receipt from Venezuela of a large series of *Lethata anophthalma* (Meyrick) reared from Guava, *Psidium guajava* L., which represents the first host plant record for the genus. Although it would be rash to attempt to generalize on this small piece of information, several possibilities seem worthy of mention here. First, the acquisition of a large series (30 specimens) through rearing would seem to indicate that the failure to obtain larger samples through light attraction is possibly due to only a slight attraction to light and/or not having the light in the right place at the right time. Second, should there prove to be host specificity between *Lethata* and either the family Myrtaceae or the genus *Psidium*, it would seem reasonable to suspect that there will prove to be a large number of as yet undescribed species of *Lethata* to be discovered. Certainly the increase in size of the genus from 13 to 31 recognized species in two years time would suggest that the ultimate size in terms of species will be much greater. A great deal more rearing will be necessary before answers to the many questions posed by this genus are answered. It is hoped that the recording of the first host plant association will provide a starting point for additional activity in this area.

The author wishes to acknowledge with thanks the cooperation and aid of the following individuals and institutions who, through their support and encouragement, have materially aided the present study: Dr. F. Fernandez Yepez, Falcultad de Agronomia, Universidad Central de Venezuela; Dr. Robert L. Dressler, Smithsonian Tropical Research Institute, Canal Zone, Panama; Mr. Karel A. Hallebeek, Dr. Léonce Bonnefil, Dr. J. K. Knoke, Instituto Interamericano de Ciencias Agricolas de la O.E.A., Turrialba, Costa Rica, for support and assistance in various field studies; Dr. J. J. Hanneman, Institut für Spezielle Zoologie und Zoologisches Museum der Humbolt-Universität zu Berlin; Dr. Fritz Kasy, Naturhistorisches Museum, Vienna; Mr. P. E. S. Whalley, Mr. Alan Watson, British Museum (Natural History); Dr. J. G. Franclemont, Cornell University; Dr. Klaus Sattler, Zoologische Sammlung des Bayerischen Staates, Munich, for lending types and other specimens in their charge for study.

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Genus *Lethata* Duckworth

Lethata Duckworth, 1964, Proc. U.S. Nat. Mus., vol. 116, p. 98.

Type-species: *Stenoma trochalosticta* Walsingham, by original designation.

The additional information contained herein has not materially affected the original concept of the genus and the original description requires only the following emendation.

Female genitalia: Ovipositor lobes lightly or heavily sclerotized; intersegmental membrane between ovipositor lobes and eight segment sclerotized or membranous; ostium bursae sclerotized or membranous; ductus bursae sclerotized or membranous; corpus bursae membranous, with two dentate signa connected by narrow, weakly sclerotized band.

Key to Species of *Lethata* Based on Genitalia

1.	Male	2
	Female	29
2.	Anellar lobes symmetrical	3
	Anellar lobes asymmetrical	27

3. Vesica armed with cornuti 4

Vesica without cornuti 25

4. Vesica armed with small spiculate cornuti 5

Vesica armed with one or more large, heavily sclerotized cornuti . . . 10

5. Harpe with saccular lobe bearing two long, heavily sclerotized setae. **trochalosticta** (Walsingham)

Harpe not as above 6

6. Aedeagus with a strong, laterally curved dorsal process at apical two-thirds, ventrally hooked process at apex . . . . . **myopina** (Zeller)

Aedeagus not as above 7

7. Gnathos cylindrical, finger-like 8

Gnathos dorsoventrally flattened 9

8. Anellar lobes approximately triangular with single, short spine at apex; aedeagus without spine, apex blunt . . . . . **fusca** Duckworth

Anellar lobes narrow with large, strongly recurved, hooklike spine at apex; aedeagus with posterior spine, apex sharply pointed . . **satyropa** (Meyrick)

9. Anellar lobes heavily sclerotized, spinelike at apex; apical process of aedeagus with large lateral spine . . . . . **dispersa,** new species

Anellar lobes not heavily sclerotized, evenly tapered at apex; apical process of aedeagus with small lateral spine . . . . **angusta,** new species

10. Aedeagus with one cornutus 11

Aedeagus with more than one cornutus 15

11. Aedeagus with one or more lateral spines 12

Aedeagus without lateral spines 14

12. Aedeagus with one lateral spine 13

Aedeagus with two lateral spines . . . . . **obscura,** new species

13. Anellar lobes divided into two acute apical processes; lateral spine of aedeagus at approximately apical two-thirds . . . . . . **irresoluta,** new species

Anellar lobes not divided, apex truncate with dentate spines; lateral spine of aedeagus at apex . . . . . **aletha,** new species

14. Aedeagus with slightly recurved process at apex; cornutus long, slender. **gypsolitha** (Meyrick)

Aedeagus without process at apex; cornutus short, stout. **fernandezyepezi,** new species

15. Aedeagus with large apical process; anellar lobes narrowing sharply at middle forming narrow, apically acute projections 16

Aedeagus without large apical process; anellar lobes not as above . . . 17

16. Aedeagus with apical process hooklike . . . . . **buscki** Duckworth

Aedeagus with apical process straight . . . . . **asthenopa** (Meyrick)

17. Aedeagus with vesica armed with more than six cornuti 18

Aedeagus with vesica armed with less than six cornuti 22

18. Harpe with saccular lobe bearing one short, heavy seta at apex; apex of gnathos heart shaped . . . . . **striolata** (Meyrick)

Harpe without saccular lobe; apex of gnathos not as above 19

19. Gnathos cylindrical, finger-like 20

Gnathos dorsoventrally flattened 21

20. Aedeagus large, broad basally, vesica armed with ladder-like series of large to small cornuti extending from base to apex; anellar lobes of near uniform width throughout . . . . . **invigilans** (Meyrick)

Aedeagus small, narrow, vesica armed with two clusters of small cornuti at apex and single, large cornutus basally; anellar lobes approximately triangular in shape, pointed at apex . . . . . **anophthalma** (Meyrick)

21. Anellar lobes long, narrow; aedeagus with a small posteriorly directed spine at apex . . . . **herbacea** (Meyrick)

Anellar lobes short, broad; aedeagus without posteriorly directed spine. **monopa,** new species

22. Aedeagus with one or more lateral spines 23

Aedeagus without lateral spines 24

23. Aedeagus with two lateral spines, one at apex, one at apical two-thirds. **mucida,** new species

Aedeagus with one lateral spine at apical four-fifths . . **optima,** new species

24. Anellar lobes serrate beyond apical third; harpe broader basally. **bovinella** (Busck)

Anellar lobes not serrate; harpe of approximately equal width throughout. **leucothea** (Busck)

25. Gnathos with dorsal lobe at apex; harpe with dense cluster of long setae at midpoint; apex of anellar lobes produced into large hooklike process. **lanosa,** new species

Gnathos without dorsal lobe; harpe without dense cluster of long setae on harpe; apex of anellar lobes simple 26

26. Aedeagus with two laterally directed processes at apex, one extending from each side, the larger one slightly recurved . . . . . **glaucopa** (Meyrick)

Aedeagus with large, heavily sclerotized process posteriorly. **pyrenodes** (Meyrick)

27. Aedeagus with large lateral spine at apical three-fourths, vesica armed with one large cornutus . . . . **illustra,** new species

Aedeagus without lateral spine, vesica without cornuti 28

28. One anellar lobe long, narrow, curved 90° laterad at middle and extending to base of opposite harpe; the other shorter, broader, sharply recurved; aedeagus with large, recurved spine at apex . . . . **aromatica** (Meyrick)

One anellar lobe narrow, pointed at apex; the other broad with three large spines apically; aedeagus with apex on one side produced into long bladelike process . . . . **ruba** Duckworth

29. Inception of ductus seminalis near ostium 30

Inception of ductus seminalis near midpoint or corpus bursae 35

30. Ductus bursae with corrugated sclerotization 31

Ductus bursae not as above 32

31. Lateral margins of ostium bursae straight, parallel; ductus bursae adjacent to ostium bursae enlarged, pouchlike, with heavy, corrugated sclerotization . . . . **anophthalma** (Meyrick)

Lateral margins of ostium bursae concave; ductus bursae adjacent to ostium bursae not enlarged . . . . **aromatica** (Meyrick)

32. Ostium bursae membranous; lobes of ovipositor heavily sclerotized; intersegmental membrane between ovipositor lobes and eighth segment sclerotized . . . . **amazona,** new species

Ostium bursae sclerotized, lobes of ovipositor lightly sclerotized; intersegmental membrane not as above 33

33. Ostium bursae reniform, width greater than length . . **pyrenodes** (Meyrick)

Ostium bursae not reniform, length equal to or greater than width . . . 34

34. Ostium bursae with a large lateral indentations; ductus bursae membranous, emerging laterally from ostium bursae. . . . . **sciophthalma** (Meyrick)

Ostium bursae without lateral indentation; ductus bursae sclerotized at junction with ostium bursae, not emerging laterally. **oculosa,** new species

35. Ductus bursae membranous; ostium bursae sclerotized, with two lateral pouches; ostium V-shaped . . . . **trochalosticta** (Walsingham)
Ductus bursae partially sclerotized or with patch of spines; ostium bursae without lateral pouches; ostium not as above 36
36. Ductus bursae with small patch of spines near inception of ductus seminalis. **bovinella** (Busck)
Ductus bursae without spines. 37
37. Ductus bursae with sinuous, ribbon-like sclerotization from ostium bursae to inception of ductus seminalis . . . . **invigilans** (Meyrick)
Ductus bursae not as above. 38
38. Ostium a heavily sclerotized ring; ostium bursae with heavily sclerotized corrugations . . . . **buscki** Duckworth
Ostium not a heavily sclerotized ring; ostium bursae sclerotized, partially divided at middle by incomplete, internal partition from lateral wall. **illustra**, new species

Lethata trochalosticta (Walsingham)

FIGURE 31; MAP 1

Stenoma trochalosticta Walsingham, 1913, *in* Godman and Salvin, Biologia Centrali-Americana, vol. 42 (Lepidoptera-Heterocera, vol. 4), p. 177.

Female genitalia (slide WDD 3597): Ductus bursae membranous; ostium bursae sclerotized, with two lateral pouches extending from ostium to midpoint of ostium bursae; ostium irregular, V-shaped; inception of ductus seminalis near midpoint of ductus bursae.

Type: In the U.S. National Museum.

Type-locality: Chiriquí, Panama.

Distribution: PANAMA: Chiriquí (no date). COSTA RICA: Sixaola Río (no date); Turrialba (February, March). ECUADOR: Balzapamba, Pr. Bolívar (no date).

Two female specimens collected by the author in Costa Rica provided the basis for the above description and are the first representatives of this sex obtained thus far.

The specimen from Ecuador has considerably more reddish-brown shading on the forewing, causing the general appearance to be much darker; however, the maculation is unchanged.

The two lateral pouches in the ostium bursae readily separate the females of *L. trochalosticta* from all other species.

Lethata anophthalma (Meyrick)

MAP 2

Stenoma anophthalma Meyrick, 1931, Exotic Microlepidoptera, vol. 4, p. 36.
Stenoma badiella Amsel, 1956, Bol. Ent. Venezolana, vol. 10, p. 298.
Lethata maculata Duckworth, 1964, Proc. U.S. Nat. Mus., vol. 116, p. 106.

Type: In the Naturhistorisches Museum, Vienna.

Type-localities: Fiebrig, Paraguay (*anophthalma*); Caracas, Los

Venados, Venezuela (*badiella*); Nova Teutônia, Brazil, 300–500 m (*maculata*).

Food plant: *Psidium guajava* L.

Distribution: PARAGUAY: San Bernadino (no date); Central Paraguay (no date); Sapucay (September). BOLIVIA: Río Yacuma, Espíritu (July). ARGENTINA: Paraná, San Ignacio Mission (August). BRAZIL: Nova Teutônia, 300–500 m (October); Teffé (December, January); Santarém (no date). FRENCH GUIANA: St. Laurent (October). SURINAM: Moengo, Boven, Cottica River (May). BRITISH GUIANA: Christianburg, R. Demerara (no date). VENEZUELA: Caracas, Los Venados (no date); Maracay (August); Macapo (June). COLOMBIA: Bogotá (no date).

Through the courtesy of Dr. F. Fernandez Yepez, Facultad de Agronomia, Universidad Central de Venezuela, I have had the opportunity to study a large series of specimens of this species reared from guava, *Psidium guajava* L., in Venezuela. This represents the first host-plant record in the genus *Lethata* and suggests some interesting possibilities should additional information indicate a close relationship between this genus and either the family Myrtaceae in general or the genus *Psidium* in particular. In any event, the knowledge at hand permits a clearer understanding of the widespread distribution of this species (see map 2) that has undoubtedly contributed to its description as new on three separate occasions as established in my recent paper (1966) and listed in the above synonymy.

Lethata aromatica **(Meyrick)**

FIGURE 32; MAP 1

Stenoma aromatica Meyrick, 1915, Exotic Microlepidoptera, vol. 1, p. 449.

Female genitalia (slide WDD 3608): Ductus bursae with corrugated sclerotization from ostium bursae to beyond inception of ductus seminalis, with accessory pouch originating from near corpus bursae; ostium bursae sclerotized, flaring laterally at inception of ductus bursae; inception of ductus seminalis near ostium bursae.

Type: In the British Museum (Natural History).

Type-locality: São Paulo, Brazil.

Distribution: BRAZIL: São Paulo (no date); Paraná (no date); Castro, Paraná (no date); Espírito Santo (June); Santa Catherina (no date); Taperinha (June, August, September).

Additional material obtained primarily from the British Museum has increased the range of this species; however, it still appears to be restricted to Brazil. This same material provided the first female specimens of this species from which the above description was derived.

Lethata buscki **Duckworth**

Figure 33; Map 3

Lethata buscki Duckworth, 1964, Proc. U.S. Nat. Mus., vol. 116, p. 102.

Female genitalia (slide WDD 3055): Ductus bursae with irregular sclerotized corrugations from ostium bursae to inception of ductus seminalis, membranous beyond; ostium a heavily sclerotized ring; ostium bursae with heavy sclerotized corrugations; inception of ductus seminalis near midpoint of ductus bursae.

Type: In the U.S. National Museum.

Type-locality: Punta Gorda, British Honduras.

Distribution: British Honduras: Punta Gorda (June, July, August, October, November). Honduras: Río Temas (April). Mexico: Santo Domingo, 15 miles southeast of Simojovel, Chiapas (July); El Zapotal, 2 miles south of Tuxtla, Chiapas (August); Córdoba, Veracruz (August).

Additional material from the British Museum and the University of California collection has increased the known distribution of this species and provided the first examples of the female.

Lethata pyrenodes **(Meyrick)**

Figure 34; Map 4

Stenoma pyrenodes Meyrick, 1915, Exotic Microlepidoptera, vol. 1, p. 448.

Female genitalia (slide WDD 3603): Ductus bursae membranous; ostium bursae sclerotized, short, reniform; ostium broad; inception of ductus seminalis near ostium.

Type: In the British Museum (Natural History).

Type-locality: Paraná, Argentina.

Distribution: Argentina: Paraná (no date). Brazil: Castro, Paraná (no date).

Additional female specimens from the British Museum have enabled the author to describe and illustrate the female genitalia of this species.

Lethata striolata **(Meyrick), new combination**

Plate 1 (fig. 1); Figures 1, 2; Map 5

Stenoma striolata Meyrick, 1932, Exotic Microlepidoptera, vol. 4, p. 302.

Alar expanse 25 mm.

Antenna brownish. Head ochreous shaded with brown; second segment of labial palpus ochreous, heavily shaded with brown on outer surface, apical segment ochreous. Legs ochreous, fore- and midlegs shaded with brown. Thorax and tegula ochreous. Forewing ochreous, irregularly covered with light gray transverse striae and occasional fuscous scales; costal edge pale yellow, terminal edge yellow, a gray streak on dorsum from basal fourth to apical three-fourths; cilia whitish gray. Hindwings pale gray, costal third and cilia suffused ochreous white.

Male genitalia (slide WDD 3353, type): Uncus short, recurved; gnathos heart-shaped at apex; harpe narrow, rounded at apex, with two or more heavy setae on saccular margin, the innermost one borne apically on distinct lobe; aedeagus pointed at apex, vesica armed with numerous cornuti.

Female genitalia: Unknown.

Type: In the Naturhistorisches Museum, Vienna, Austria.

Type-locality: Neu Bremen, Santa Catharina, Brazil.

Distribution: Known only from the type-locality.

The presence of a saccular lobe bearing a short, heavy, apical seta on the harpe in the male genitalia readily distinguishes this species.

The transverse striae on the forewing are unique in the genus *Lethata* and are very similar to the maculation found in the oecophorid genus *Psilocorsis* Clemens.

***Lethata monopa*, new species**

PLATE 1 (FIG. 2); FIGURES 3, 4; MAP 8

Alar expanse 33 mm.

Antenna brown. Head fuscous; second segment of labial palpus fuscous on outer side, light brown on inner side, apical segment light brown. Legs brown. Thorax and tegula brown. Forewing brown with costa and termen faintly ochreous; from anal angle an area of fuscous shading extends upward and outward to near costa and spot at end of cell; spot at end of cell consisting of a ring of light brown enclosing a spot of slightly darker brown; at apical fourth a transverse, outwardly curved faint fuscous line extending from costa to dorsum; cilia brown basally, faintly ochreous apically. Hindwing gray, cilia gray, lighter at anal angle.

Male genitalia (slide WDD 3600, type): Uncus short, recurved, pointed at apex; gnathos broad, dorsoventrally flattened; harpe long, rather narrow, broadly pointed at apex; anellar lobes symmetrical, short, broad with slight posterior projections; aedeagus with a ventrolateral lump, apex broadly pointed, vesica armed with two clusters of cornuti, one group with cornuti more than twice the length of the other.

Female genitalia: Unknown.

Type: In the collection of the British Museum (Natural History).

Type-locality: Río de Janeiro, Brazil.

Distribution: Known only from the type-locality.

Described from male holotype: "Río Jan., Felder Coll., Rothschild 1913–86"; and one male paratype: "Río de Janeiro, Nov., (H. H. Smith)."

The size and shape of the anellar lobes and the shape and armature of the aedeagus in the male genitalia readily distinguish this species.

Lethata oculosa, new species

Plate 1 (fig. 3); Figure 38; Map 10

Alar expanse 28 mm.

Antenna brownish. Head brown shading to whitish between eyes; second segment of labial palpus brown on outer side, whitish on inner side, apical segment whitish. Legs whitish, fore- and midlegs lightly shaded with brown. Thorax and tegula deep brown. Forewing grayish brown with costal edge light ochreous; deep brown suffusion from anal angle over basal third; spot at end of cell consisting of ring of deep brown enclosing whitish scales with dot of deep brown in center; an indistinct outwardly curving deep brown transverse line from costa to dorsum at apical two-thirds; cilia brown at base, whitish beyond. Hindwing gray; cilia gray.

Male genitalia: Unknown.

Female genitalia (slide WDD 3602, type): Ductus bursae sclerotized at junction with ostium bursae, membraneous beyond; ostium bursae sclerotized, length and width approximately equal; ostium slightly flaring at edge; inception of ductus seminalis near ostium bursae.

Type: In the collection of the British Museum (Natural History).

Type-locality: São Paulo, Brazil.

Distribution: Known only from the type-locality.

Described from the female holotype: "São Paulo, S. E. Brazil, 1892–5, (E. D. Jones), 1912–534."

The size and shape of the ostium bursae serves to distinguish *L. oculosa* from the other known females in the genus.

Lethata lanosa, new species

Plate 1 (fig. 4); Figures 5, 6; Map 8

Alar expanse 24 mm.

Antenna brownish. Head brown with pink shading, face whitish, second segment of labial palpus brown on outer side, pinkish white on inner side, apical segment brown. Legs whitish, fore- and midlegs shaded with fuscous. Thorax and tegula fuscous with postmedian ridge of raised scales. Forewing brown with costal edge narrowly deep ochreous; an indistinct fuscous line obliquely from anal angle to costa at midpoint; dorsal edge narrowly fuscous; spot at end of cell consisting of fuscous ring enclosing brown spot; outwardly curved transverse faint fuscous line at apical fourth; cilia brown. Hindwing fuscous, cilia gray.

Male genitalia (slide WDD 3626, type): Uncus short, recurved; gnathos with dorsal lobe producing teardrop shape to apex; harpe broadest at midpoint; anellar lobes symmetrical, broad basally, with large hooklike process at apex; aedeagus sinuate, pointed at apex, vesica without cornuti.

Female genitalia: Unknown.

Type: In the collection of the U.S. National Museum, no. 69085.

Type-locality: El Valle, Cocle Prov., Panama.

Distribution: Known only from the type-locality.

Described from the male holotype; "Panama: El Valle, Cocle Prov., 22.IV.65 (S. S. and W. D. Duckworth)."

The extraordinary development of the anellar lobes readily distinguishes this species.

Lethata gypsolitha (Meyrick), new combination

Plate 1 (fig. 5); Figures 7, 8; Map 7

Stenoma gypsolitha Meyrick, 1931, Exotic Microlepidoptera, vol. 4, p. 38.

Alar expanse 23 mm.

Antenna brownish. Head brownish gray shaded with rose; second segment of labial palpus brown, apical segment whitish. Legs whitish. Thorax and tegula brownish ochreous. Forewing brownish ochreous with faintly rose costa; few to many scattered dark scales irregularly scattered over entire wing; a faint, outwardly curved, transverse line at apical fourth extending from costa to dorsum; at end of cell a fuscous spot or a circle of fuscous scales enclosing a graywhitish spot. Hindwing ochreous overcast with gray scales; cilia ochreous.

Male genitalia (slide WDD 3341, type): Uncus truncate, slightly recurved; gnathos bluntly rounded; harpe bluntly pointed at apex; anellar lobes symmetrical, without processes, smoothly rounded at apex; aedeagus with slightly recurved process at apex, vesica armed with one long, slender cornutus.

Female genitalia: Unknown.

Type: In the Naturhistorisches Museum, Vienna, Austria.

Type-locality: San Bernardino, Paraguay.

Distribution: PARAGUAY; San Bernardino (no date). ARGENTINA: Territ des Missions (September).

This species is known only from the male type in the Naturhistorisches Museum, Vienna, and one male specimen from Argentina in the collection of the United States National Museum.

***Lethata herbacea* (Meyrick), new combination**

PLATE 1 (FIG. 6); FIGURES 9, 10; MAP 7

Stenoma herbacea Meyrick, 1931, Exotic Microlepidoptera, vol. 4, p. 38.

Alar expanse 25 mm.

Antenna brown. Head brownish fading to white on face; labial palpus broken. Legs broken. Thorax and tegula pale green. Forewing pale green with scattered fuscous scales; costal edge yellow ochreous, dorsal edge white at base, brown beyond; an oblique brown line from dorsum at basal angle extending half across wing; spot at end of cell composed of ring of dark green enclosing spot of pinkish green with dull greenish spot at its center, a faint brownish oblique line from lower extremity to near dorsum; an outwardly curved transverse line from costa at apical third to dorsum before tornus, upper half dark green, lower brown; a dark green terminal line; cilia light green basally, grayish beyond. Hindwing pale grayish; cilia yellow ochreous basally, whitish beyond.

Male genitalia (slide WDD 3339, type): Uncus short, slightly recurved; gnathos short, dorsoventrally flattened; harpe broad at base tapering to bluntly rounded apex; anellar lobes symmetrical, somewhat broader at base narrowing to elongate finger-like apex; aedeagus with a small, posteriorly directed spine at apex, vesica armed with numerous heavy cornuti.

Female genitalia: Unknown.

Type: In the Naturhistorisches Museum, Vienna, Austria.

Type-locality: Ypiranga, São Paulo, Brazil.

Distribution: Known only from the type-locality.

This species is easily recognized by the shape and armature of the aedeagus in the male genitalia.

***Lethata myopina* (Zeller), new combination**

PLATE 2 (FIG. 1); FIGURES 11, 12

Cryptolechia myopina Zeller, 1877, Horae Soc. Ent. Rossicae, vol. 13, p. 271.

Alar expanse 24 mm.

Antenna broken. Head rosy white; labial palpus broken. Legs whitish, fore- and midlegs shaded with brown. Thorax and tegula yellow. Forewing yellow; costal edge faintly shaded with rose; dorsal edge rosy ochreous from basal angle to apical three-fourths; spot at end of cell composed of ring of rosy ochreous enclosing white spot; cilia yellow at base, white beyond. Hindwing whitish; cilia whitish at anal angle, ochreous at wing apex.

Male genitalia (slide WDD 3574, type): Uncus short, slightly recurved, pointed at apex; gnathos short, broad; harpe broad to midpoint, narrowing to blunt apex; anellar lobes symmetrical, broad at base with two pointed apical lobes, anterior lobe much longer than posterior; aedeagus with a strong laterally curved, dorsal process at apical two-thirds, ventrally hooked process at apex, vesica without cornuti.

Female genitalia: Unknown.

Type: In the Zoologisches Museum der Humboldt-Universität zu Berlin.

Type-locality: Brazil.

Distribution: Known only from the type-locality.

This is one of the two species for which a distribution map was not prepared. The species is known only from the type specimen, for which the only locality given is Brazil. This obviously is insufficient for mapping purposes and further information must be acquired before a map is prepared.

The strong, ventrally hooked apical process and laterally curved dorsal process at apical two-thirds on the aedeagus in the male genitalia readily separates *L. myopina* from other species in the genus.

***Lethata dispersa*, new species**

PLATE 2 (FIG. 2); FIGURES 13, 14; MAP 6

Alar expanse 23 mm.

Antenna, head, labial palpus stramineous. Legs stramineous lightly shaded with brown. Thorax and tegula yellow. Forewing yellow with costa rosy; dorsum narrowly edged brown; faint spot in fold brown; spot at end of cell consisting of ring of brown enclosing whitish spot; oblique brown line extending from costa at near midpoint through spot at end of cell to tornus; terminal line brown; cilia brown basally, whitish beyond. Hindwing gray; cilia whitish.

Male genitalia (slide WDD 3308, type): Uncus short, recurved; gnathos short, broad; harpe short, broad, articulating with upper edge of anellar lobe; anellar lobes symmetrical, broad at base narrowing sharply at midpoint, apical half falciform; aedeagus broad, with acute apical projection bearing one laterally directed spine, vesica armed with numerous spiculate cornuti.

Female genitalia: Unknown.

Type: In the collection of the U.S. National Museum, no. 69086.

Type-locality: Chapada, Matto Grosso, Brazil.

Distribution: Known only from the type-locality.

Described from the male holotype: "Chapada, near Cuyabá, Matto Grosso, Brazil (H. H. Smith)."

This species is very closely related to *L. angusta*; however, the form of the anellar lobes and the large, laterally directed spine on the apical process of the aedeagus in the male genitalia serve to distinguish *L. dispersa*.

***Lethata angusta*, new species**

PLATE 2 (FIG. 3); FIGURES 15, 16; MAP 9

Alar expanse 28 mm.

Antenna missing. Head whitish, labial palpus missing. Legs whitish shaded with brown. Thorax and tegula brown. Forewing ochreous overcast with brown; costa narrowly brick red; a faint brownish spot on costa at midpoint; spot at end of cell consisting of irregular patch of purplish scales; terminal line brown; cilia brown basally, lighter beyond. Hindwing whitish overcast with gray; cilia whitish, irregularly brownish basally.

Male genitalia (slide WDD 3606, type): Uncus sharply recurved; gnathos as in *dispersa*; harpe as in *dispersa*; anellar lobes symmetrical, similar to those in *dispersa* except slimmer and not as heavily sclerotized and recurved at apex; aedeagus as in *dispersa* except apical process narrower and laterally directed spine much smaller.

Female genitalia: Unknown.

Type: In the collection of the British Museum (Natural History).

Type-locality: Castro, Paraná, southern Brazil.

Distribution: Known only from the type-locality.

Described from the male holotype: "Castro, Paraná, S. Brazil, 1898 (Jones), Walsingham Collection, B. M. 1910–427."

This species is very close to *L. dispersa* and the distinguishing characteristics have been discussed in the remarks concerning that species.

***Lethata fernandezyepezi*, new species**

PLATE 2 (FIG. 4); FIGURES 17, 18; MAP 6

Alar expanse 27 mm.

Antenna brownish. Head whitish shaded with rose; second segment of labial palpus brown on outer side, whitish on inner side, apical segment whitish. Legs whitish, forelegs heavily shaded with brown. Thorax and tegula reddish brown anteriorly, gray scales with white tips posteriorly. Forewing yellow shaded with brown, costal edge deep ochreous underlined with reddish brown; dorsum reddish brown; a reddish-brown area extending from anal angle to basal third; spot in fold at basal third fuscous; spot at end of cell indistinct, consisting of irregular ring of reddish-brown scales enclosing white spot; an outwardly curving transverse line of reddish-brown spots from costa to dorsum; cilia rosy gray. Hindwing gray in anal area, yellow at apex; cilia yellow shaded with gray at anal angle.

Male genitalia (slide WDD 3625, type): Uncus short, recurved; gnathos long with finger-like projection at apex; harpe with soft, fleshy area on sacculus; anellar lobes symmetrical, only slightly narrowing to rounded apex; aedeagus long, curved, blunt at apex; vesica armed with one short, stout cornutus.

Female genitalia: Unknown.

Type: In the collection of the U.S. National Museum, no. 69087.

Type-locality: Rancho Grande, Aragua, Venezuela.

Distribution: Known only from the type-locality.

Described from the male holotype: "Venezuela, Ar., Rancho Grande, 1100 m., 16–19.I.66, (S. S. and W. D. Duckworth)"; and one male paratype with the same data.

This species is named in honor of Dr. F. Fernandez Yepez, distinguished entomologist at the Universidad Central de Venezuela, Maracay, who has been of invaluable aid in my study of the family Stenomidae.

The long finger-like projection at the apex of the gnathos, fleshy area on the sacculus, and shape and armature of the aedeagus in the male genitalia readily separate this species from all others.

Lethata irresoluta, new species

Plate 2 (fig. 5); Figures 19, 20; Map 8

Alar expanse 30 mm.

Antenna whitish. Head brownish, lighter between eyes; second segment of labial palpus light brown on outer side, whitish on inner side, apical segment white. Legs whitish, fore- and midlegs shaded with brown. Thorax and tegula fulvous. Forewing fulvous with costa narrowly deep ochreous underlined with purplish from base to apical three-fourths; from apical three-fourths to tornus deep yellow; dorsum irregularly edged with gray; spot at end of cell purplish; cilia brown with white tips. Hindwing whitish; cilia with tinge of brown basally, whitish beyond.

Male genitalia (slide WDD 3615, type): Uncus short, recurved; gnathos short, thick, flattened dorsally; harpe broad, bluntly rounded; anellar lobes symmetrical, consisting of broad base with two apical processes, one long, digitate, the other short, recurved; aedeagus with large lateral spine near apex from base of which a small sclerotized flange extends posteriorly, vesica armed with one large cornutus.

Female genitalia: Unknown.

Type: In the collection of the British Museum (Natural History).

Type-locality: Agualani, Carabaya, 900 ft., Peru.

Distribution: Known only from the type-locality.

Described from the male holotype: "Agualani, Carabaya, 900 ft., Oct. 05. wet season (G. R. Ockenden)."

The shape of the anellar lobes and armature of the aedeagus readily separates *irresoluta* from the other species of *Lethata*.

This species, along with *illustra, aletha, mucida, obscura,* and *optima,* appear to form a closely related group within the genus. The maculation is very similar and the genitalia have certain general characteristics in common. There are sufficient distinguishing characters to separate the species; however, additional remarks concerning relationships must await further information.

***Lethata illustra*, new species**

Plate 2 (fig. 6); Figures 21, 22, 37; Map 6

Alar expanse 27–32 mm.

Antenna brownish. Head whitish, second segment of labial palpus brown on outer side, whitish on inner side, apical segment brownish. Legs whitish shaded with brown. Thorax and tegula purplish brown. Forewing brown shaded with darker brown on basal two-thirds; costa narrowly ochreous; spot at end of cell consisting of ring of purplish scales enclosing white spot; a faint, outwardly curving transverse line from costa above spot to near tornus; entire wing sprinkled with fuscous scales; cilia brown. Hindwing whitish overcast with gray; cilia whitish at anal angle, grayish at apex.

Male genitalia (slide WDD 3618): Uncus short, recurved; gnathos short, broad, dorsally concave; harpe short, of approximately uniform width to midpoint, then tapering to bluntly pointed apex; anellar lobes asymmetrical, one consisting of a lightly sclerotized, setiferous, digitate process anteriorly and a long, heavily sclerotized, falciform process posteriorly, other consisting of large basal area with two apical processes similar in position and shape to opposite lobe but shorter; aedeagus with large lateral spine near apex, vesica armed with one large cornutus.

Female genitalia (slide WDD 3616, type): Ductus bursae sclerotized and corregated from ostium bursae to inception of ductus seminalis; ostium bursae sclerotized, partially divided at middle by incomplete internal partition from lateral wall; ostium broad, somewhat flared laterally; inception of ductus seminalis near corpus bursae.

Type: In the collection of the British Museum (Natural History).

Type-locality: La Oroya, Río Inambari, 3100 ft., Peru.

Distribution: Peru: La Oroya, Río Inambari, 3100 ft. (October); Santo Domingo, Carabaya, 6000–6500 ft. (December).

Described from the female holotype: "La Oroya, R. Inambari, S. E. Perú, 3100 ft., wet s., Oct. 1904 (G. Ockenden)"; one female paratype: "Diff. local in Carabaya, dry s., 2500–6000 ft., VI 04 (G. Ockenden)"; one female paratype: "S. Domingo, Carabaya, 6500 ft., Dec. 02, wet s., (G. Ockenden)"; and one male paratype: "S. Domingo, Carabaya, 6000 ft., XII 01, wet seas. (Ockenden)."

The asymmetrical anellar lobes readily distinguish this species.

Lethata aletha, new species

PLATE 3 (FIG. 1); FIGURES 23, 24; MAP 9

Alar expanse 33 mm.

Antenna brownish. Head brownish, lighter between eyes; second segment of labial palpus brown on outer side, whitish on inner side, apical segment whitish. Legs whitish, fore- and midlegs heavily shaded with brown. Thorax and tegula brown. Forewing brown shaded with deep ochreous scales; costa narrowly deep ochreous; dorsum purplish to apical two-thirds; spot at end of cell consisting of purplish scales overcast with whitish scales; termen shaded with deep ochreous; cilia whitish basally, brown beyond. Hindwing whitish, heavily shaded with gray scales in anal area; cilia brownish.

Male genitalia (slide WDD 3612, type): Uncus short, recurved; gnathos dorsoventrally flattened; harpe broad, bluntly rounded; anellar lobes symmetrical, approximately uniform in width, truncate apex bearing dentate spines; aedeagus with one prominent lateral spine at apex, vesica armed with one large cornutus.

Female genitalia: Unknown.

Type: In the collection of the British Museum (Natural History).

Type-locality: Santo Domingo, 6000 ft., southeast Peru.

Distribution: Known only from the type-locality.

Described from the male holotype: "Santo Domingo, S.E. Peru, 6000 ft., xi. 1904 (G. Ockenden)."

The single lateral spine at the apex of the aedeagus in the male genitalia separates this species from all others.

Lethata mucida, new species

PLATE 3 (FIG. 2); FIGURES 25, 26; MAP 8

Alar expanse 28 mm.

Antenna brownish. Head brownish, lighter between eyes, labial palpus brownish. Legs whitish shaded with brown. Thorax and tegula purplish brown. Forewing as in *obscura* except with heavy suffusion of purplish in anal area. Hindwing whitish heavily overcast with gray scales; cilia gray.

Male genitalia (slide WDD 3610, type): Uncus, gnathos, harpe as in *obscura;* anellar lobes symmetrical, tapering to rounded apex; one large, posteriorly directed spine at apical two-thirds; aedeagus as in *obscura* except laterally directed spines wider apart and vesica armed with two large cornuti.

Female genitalia: Unknown.

Type: In the collection of the U.S. National Museum, no. 69088.

Type-locality: San Jaoquín, Dept. Santander, Colombia.

Distribution: Known only from the type-locality.

Described from the male holotype: "Colombia: San Jaoquín, Dept. Santander, 30.VIII.65 (W. D. Duckworth)."

This species is very closely related to the following one, *obscura;* however, the differences in shape and armament of the anellar lobes plus the number of cornuti and placement of lateral spines in the aedeagus readily distinguish between the two.

Lethata obscura, new species

Plate 3 (fig. 3); Figures 27, 28; Map 10

Alar expanse 29 mm.

Antenna brownish. Head whitish, second segment of labial palpus brown on outer side, whitish on inner side, apical segment whitish. Legs whitish, shaded with brown. Thorax and tegula whitish ochreous. Forewing whitish varyingly overcast with brownish ochreous; costa, apex termen narrowly deep ochreous; spot in fold small, purplish; spot at end of cell purplish with scattered whitish scales; faint, outwardly curving, transverse line from costa at apical third to near tornus; a few fuscous scales scattered irregularly over entire wing; cilia brownish basally, whitish beyond. Hindwing whitish, overcast with gray scales in anal area; cilia whitish becoming darker near wing apex.

Male genitalia (slide WDD 3611, type): Uncus short, recurved; gnathos short, broad, dorsoventrally flattened; harpe short, regularly tapering to rounded apex; anellar lobes symmetrical, slightly broader apically, with a group of posteriorly directed spines at posterior apex; aedeagus with two laterally directed spines near apex, vesica armed with one large cornutus.

Female genitalia: Unknown.

Type: In the collection of the British Museum (Natural History).

Type-locality: La Oroya, Río Inambari, 3100 ft., Peru.

Distribution: Known only from the type-locality.

Described from the male holotype: "La Oroya, R. Inambari, S. E. Perú, 3100 ft., wet s., Oct. 1904 (G. Ockenden)."

This species is very similar to the preceding one, *mucida,* and the distinguishing characteristics are discussed in the remarks concerning that species.

Lethata optima, new species

Plate 3 (fig. 4); Figures 29, 30; Map 10

Alar expanse 34 mm.

Antenna brown. Head brown dorsally, lighter between eyes; second segment of labial palpus brown on outer side, lighter on inner side, apical segment brown. Fore- and midlegs brown, hindlegs whitish. Thorax and tegula reddish brown. Forewing grayish overcast with reddish brown especially in anal area; costa narrowly ochreous; termen ochreous; spot at end of cell purplish with scattered white scales; entire wing with scattered fuscous scales; cilia white basally, gray beyond. Hindwing whitish overcast with gray; cilia white basally, gray beyond.

Male genitalia (slide WDD 3614, type): Uncus short, recurved; gnathos short, dorsally flattened; harpe short, somewhat excavated in saccular area, rounded at apex; anellar lobes symmetrical, median edge approximately straight to apex, lateral edge sinuate and tapering to acute apex, bladelike; aedeagus with one lateral spine near apex, vesica armed with three cornuti, one large, one medium, one small.

Female genitalia: Unknown.

Type: In the collection of the British Museum (Natural History).

Type-locality: Huancabamba, Cerro de Pasco, 6000–10,000 ft., Peru.

Distribution: Known only from the type locality.

Described from the male holotype: "Huancabamba, Cerro de Pasco, 6–10,000 ft., (Böttger)."

The shape of the anellar lobes and shape and armature of the aedeagus in the male genitalia distinguishes this species from all others.

Lethata amazona, new species

Plate 3 (fig. 5); Figure 36; Map 9

Alar expanse 38 mm.

Antenna brownish. Head white; labial palpus white shaded with brown on outer side. Legs whitish, forelegs heavily shaded with brown. Thorax and tegula white. Forewing rosy tan with costa narrowly deep ochreous; dorsal edge brown; from middle of base a white suffusion blends outward and upward with ground color; spot at end of cell composed of ring of white enclosing brown transverse line; spot in fold at basal one-third composed of ring of white enclosing brown spot; median spot at basal one-third white with faint brown scaling in center; entire wing sprinkled with occasional brown scales; cilia brown. Hindwing yellow ochreous deepening toward apex; cilia whitish in anal area, brownish at apex.

Male genitalia: Unknown.

Female genitalia (slide WDD 3601, type): Ductus bursae membranous; ostium bursae membranous; ostium broad; inception of ductus seminalis very near ostium bursae; lobes of ovipositor heavily sclerotized, intersegmental membrane between ovipositor lobes and eighth segment sclerotized holding lobes in close association with eighth segment.

Type: In the collection of the British Museum (Natural History).

Type-locality: Santo Antônio do Javary, Upper Amazon, Brazil.

Distribution: Known only from the type-locality.

Described from the female holotype: "Santo Antônio do Javary, Upper Amazon, June 07 (S. M. Klages), Rothschild Bequest, B. M. 1939–1."

This species is one of the largest and most striking of the entire genus. It is indeed unfortunate that it is known only from the holotype.

The heavily sclerotized ovipositor lobes and sclerotized intersegmental membrane between the ovipositor lobes and eighth segment readily spearate *L. amazona* from all other females in this genus.

Lethata sciophthalma **(Meyrick), new combination**

Plate 3 (fig. 6); Figure 35; Map 5

Stenoma sciophthalma Meyrick, 1931, Exotic Microlepidoptera, vol. 4, p. 34.

Alar expanse 22 mm.

Antenna brown. Head rosy gray; labial palpus pale grayish pink. Legs whitish, fore- and midlegs overcast with brown. Thorax and tegula rosy gray. Forewing rosy ochreous, costal edge pink; spot at end of cell purple suffused with whitish scales in center; cilia rosy white, darker at apex. Hindwing ochreous, overcast with gray; cilia rosy white.

Male genitalia: Unknown.

Female genitalia (slide WDD 3342, type): Ductus bursae membranous, emerging laterally from ostium bursae; ostium bursae sclerotized with a large lateral indentation; ostium broad; inception of ductus seminalis near ostium.

Type: In the Naturhistorisches Museum, Vienna, Austria.

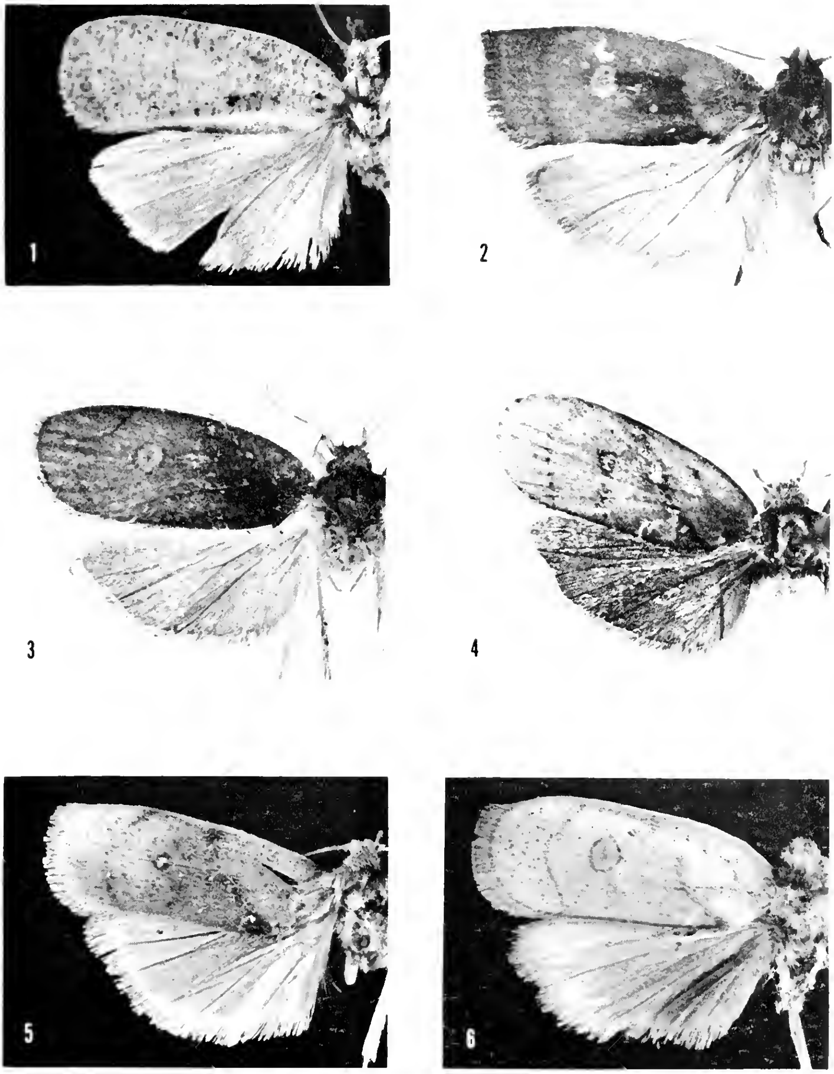
Type-locality: Rio Prêto, zw. Boquerão u. Sta. Rita, Brazil.

Distribution: Known only from the type-locality.

The large lateral indentation in the ostium bursae serves to separate this species from the others included in the genus *Lethata*.

Checklist of *Lethata*

1. *trochalosticta* (Walsingham)
2. *aromatica* (Meyrick)
3. *asthenopa* (Meyrick)
4. *bovinella* (Busck)
    - *curiata* Meyrick
    - *indistincta* Amsel
5. *buscki* Duckworth
6. *fusca* Duckworth
7. *glaucopa* (Meyrick)
8. *invigilans* (Meyrick)
9. *leucothea* (Busch)
10. *anophthalma* (Meyrick)
    - *badiella* Amsel
    - *maculata* Duckworth
11. *pyrenodes* (Meyrick)
12. *ruba* Duckworth
13. *satyropa* (Meyrick)
14. *gypsolitha* (Meyrick)



Left wings: 1, *Lethata striolata* (Meyrick); 2, *L. monopa*, new species; 3, *L. oculosa*, new species; 4, *L. lanosa*, new species; 5, *L. gypsolitha* (Meyrick); 6, *L. herbacea* (Meyrick).

15. *herbacea* (Meyrick)
16. *myopina* (Zeller)
17. *sciophthalma* (Meyrick)
18. *striolata* (Meyrick)
19. *amazona* Duckworth
20. *fernandezyepezi* Duckworth
21. *lanosa* Duckworth
22. *monopa* Duckworth
23. *oculosa* Duckworth
24. *dispersa* Duckworth
25. *angusta* Duckworth
26. *mucida* Duckworth
27. *optima* Duckworth
28. *obscura* Duckworth
29. *illustra* Duckworth
30. *irresoluta* Duckworth
31. *aletha* Duckworth

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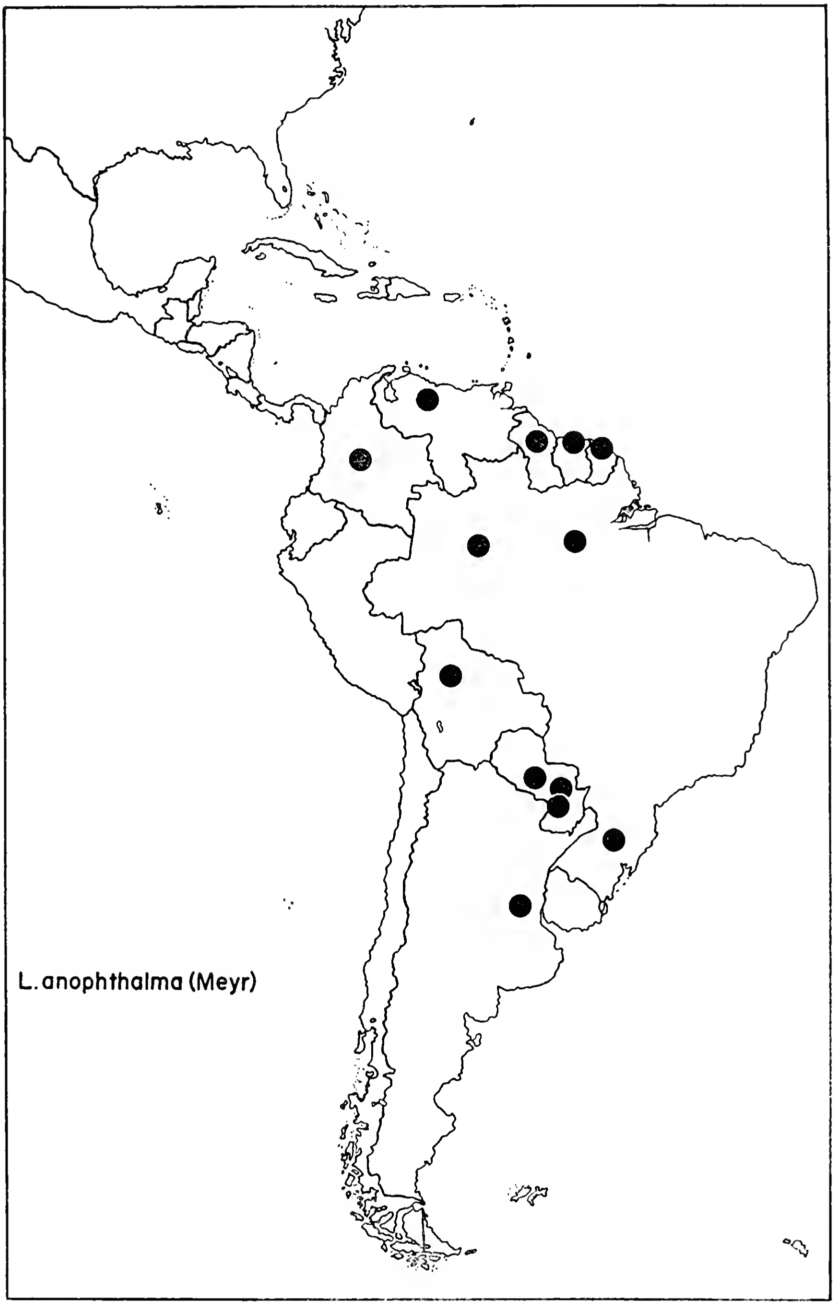
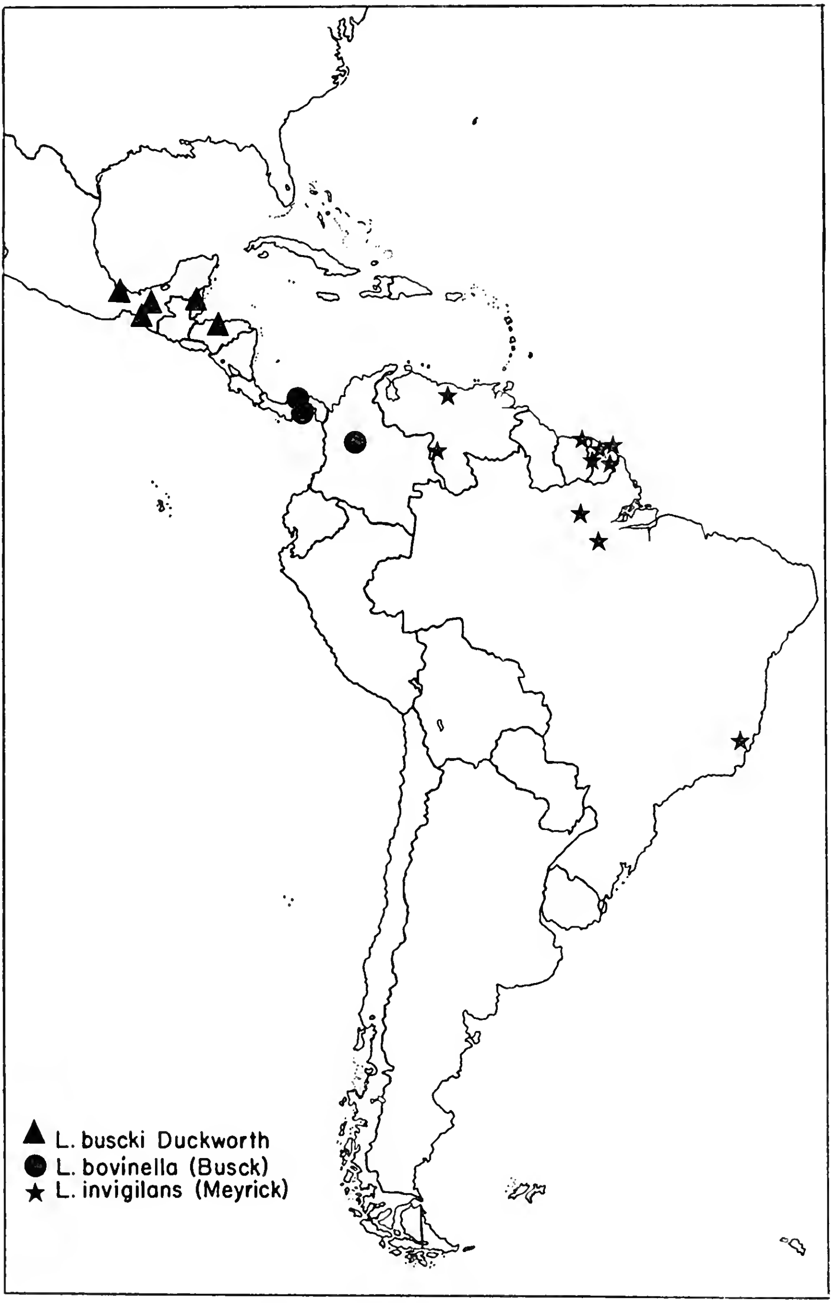
1966. New synonymy and new assignments in Western Hemisphere Stenomidae (Lepidoptera: Gelechioidea). Proc. Ent. Soc. Washington, vol. 68, pp. 195–198.

Map 1.—Distribution of species.



Map 2.—Distribution of species.



Map 3.—Distribution of species.

MAP 4.—Distribution of species.

Map 5.—Distribution of species.

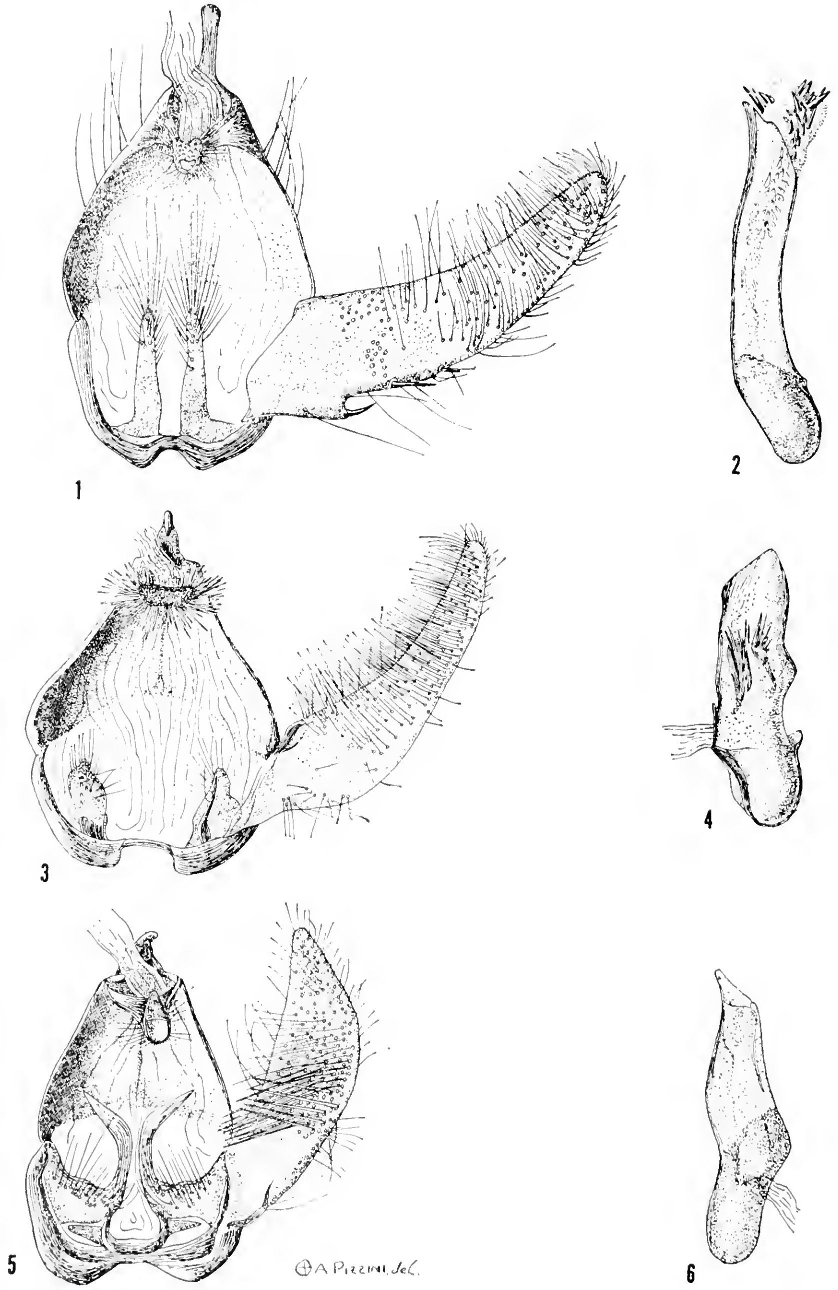
Map 6.—Distribution of species.

Map 7.—Distribution of species.

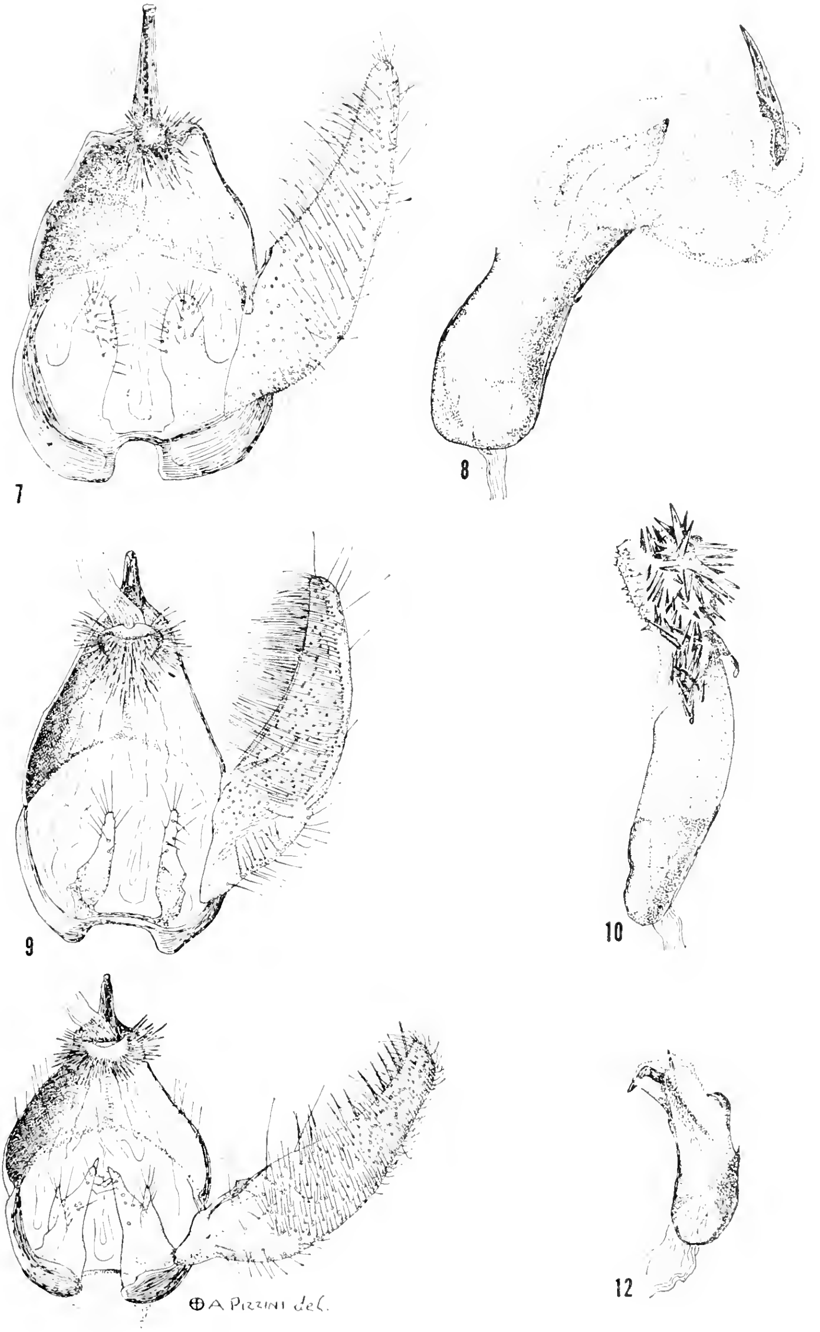
Map 8.—Distribution of species.

Map 9.—Distribution of species.

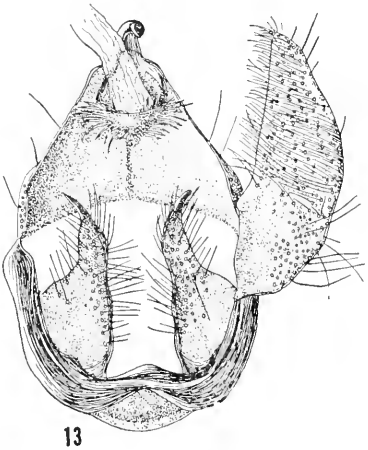
MAP 10.—Distribution of species.



FIGURES 1-6.—Ventral view of male genitalia (aedeagus removed): 1, *Lethata striolata* (Meyrick); 3, *L. monopa*, new species; 5, *L. lanosa*, new species. Aedeagus: 2, *L. striolata* (Meyrick); 4, *L. monopa*, new species; 6, *L. lanosa*, new species.



FIGURES 7–12.—Ventral view of male genitalia (aedeagus removed): 7, *Lethata gypsolitha* (Meyrick); 9, *L. herbacea* (Meyrick); 11, *L. myopina* (Zeller). Aedeagus: 8, *L. gypsolitha* (Meyrick); 10, *L. herbacea* (Meyrick); 12, *L. myopina* (Zeller).



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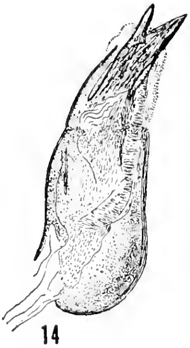

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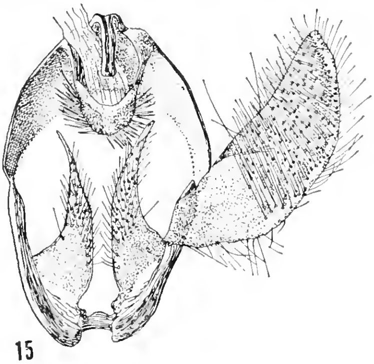

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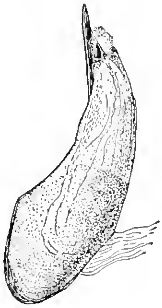

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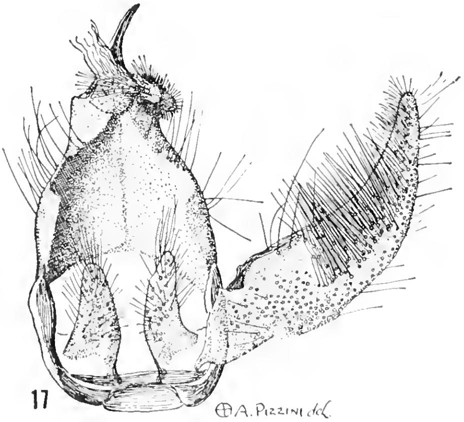

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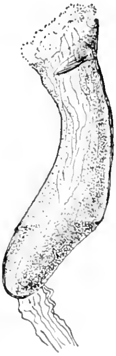

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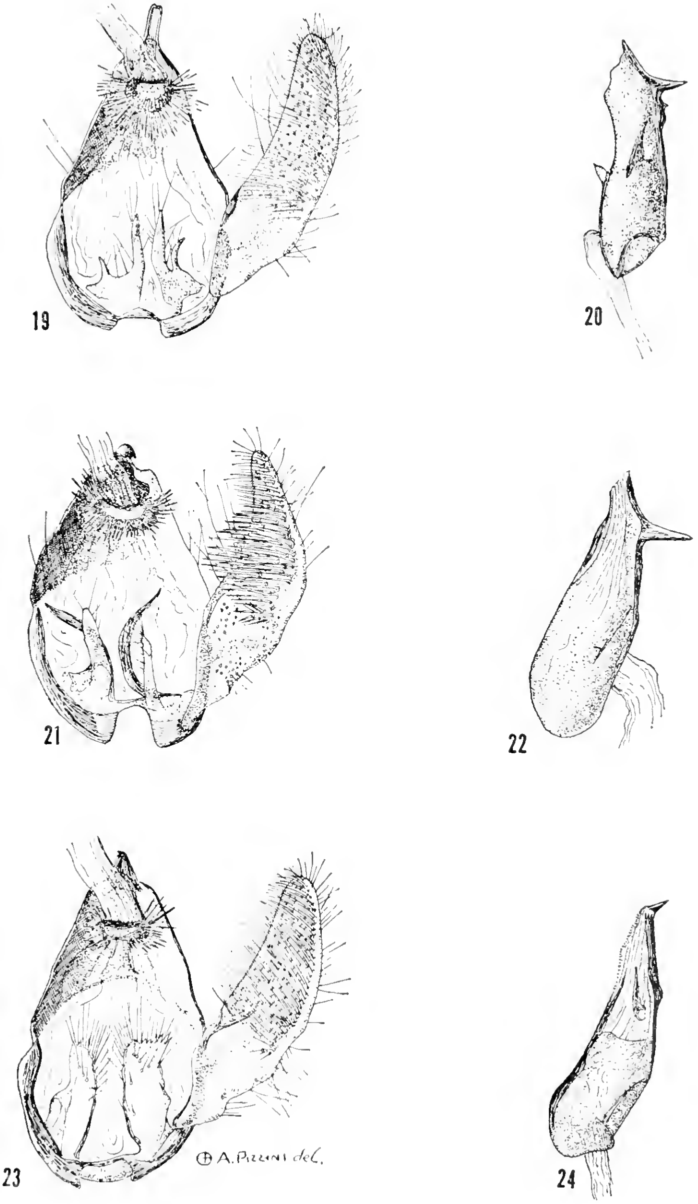
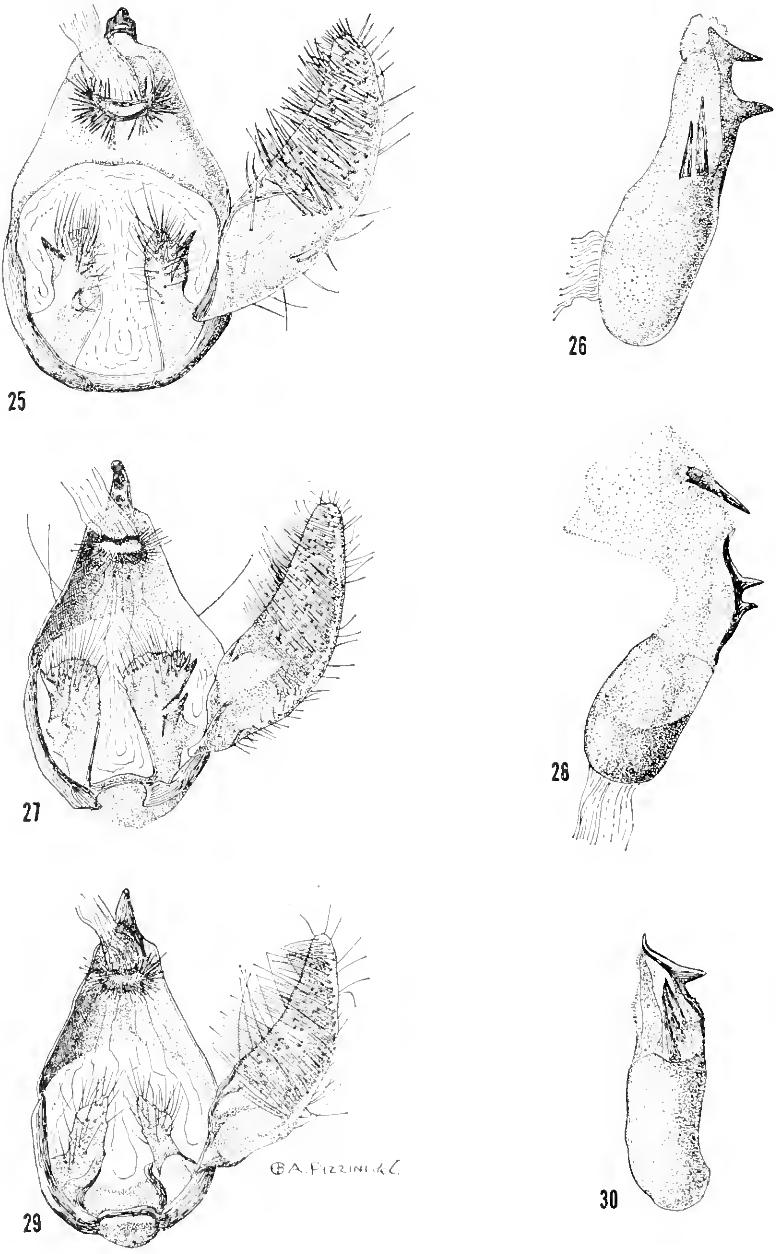
FIGURES 13–18.—Ventral view of male genitalia (aedeagus removed): 13, *Lethata dispersa*, new species; 15, *L. angusta*, new species; 17, *L. fernandezyepezi*, new species. Aedeagus: 14, *L. dispersa*, new species; 16, *L. angusta*, new species; 18, *L. fernandezyepezi*, new species.

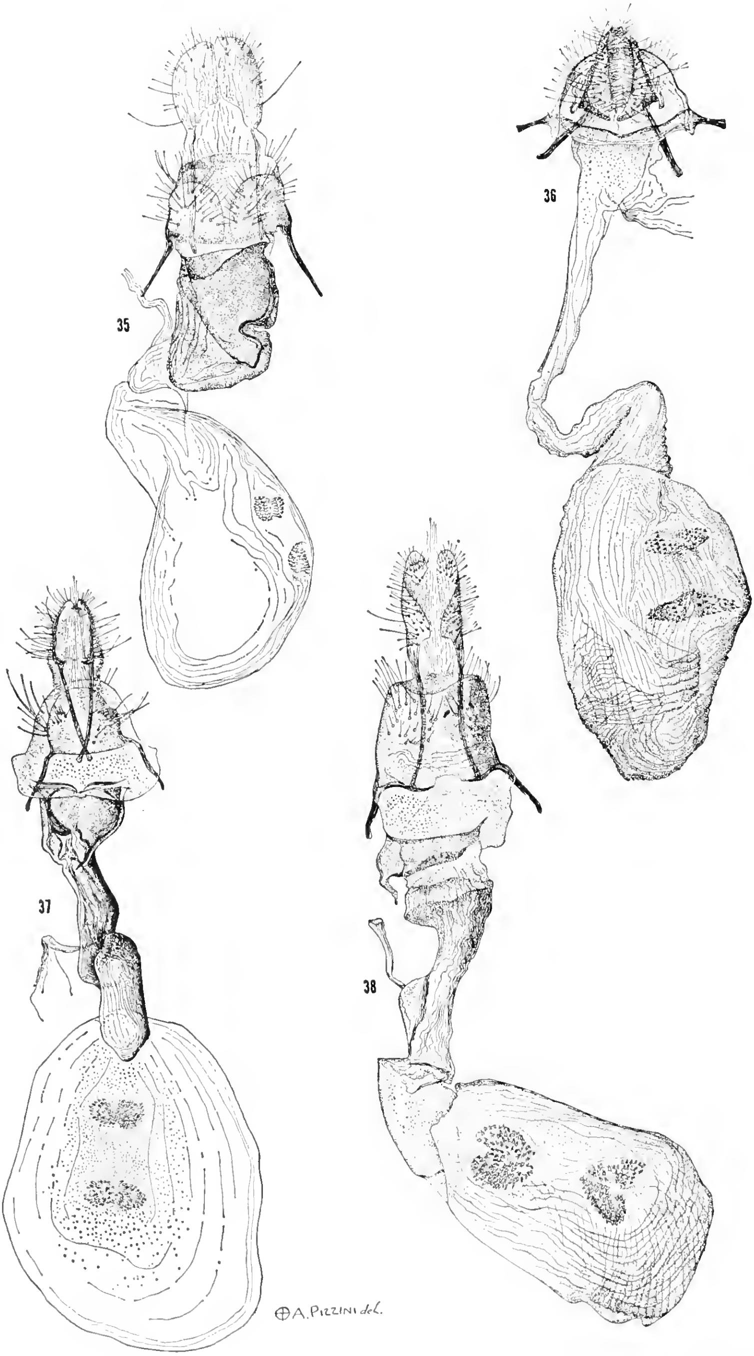


FIGURES 19–24.—Ventral view of male genitalia (aedeagus removed): 19, *Lethata irresoluta*, new species; 21, *L. illustra*, new species; 23, *L. aletha*, new species. Aedeagus: 20, *L. irresoluta*, new species; 22, *L. illustra*, new species; 24, *L. aletha*, new species.



Figures 25–30.—Ventral view of male genitalia (aedeagus removed): 25, *Lethata mucida*, new species; 27, *L. obscura*, new species; 29, *L. optima*, new species. Aedeagus: 26, *L. mucida*, new species; 28, *L. obscura*, new species; 30, *L. optima*, new species.

FIGURES 31-34.—Ventral view of female genitalia: 31, *Lethata trochalosticta* (Walsingham); 32, *L. aromatica* (Meyrick); 33, *L. buscki* Duckworth; 34, *L. pyrenodes* (Meyrick).



FIGURES 35–38.—Ventral view of female genitalia: 35, *Lethata sciophthalma* (Meyrick); 36, *L. amazona*, new species; 37, *L. illustra*, new species; 38, *L. oculosa*, new species.

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NEW CYCLOPOID COPEPODS ASSOCIATED WITH THE CORAL PSAMMOCORA CONTIGUA (ESPER) IN MADAGASCAR

By Arthur G. Humes and Ju-Shey Ho[1]

Several species of copepods are known to live in association with madreporarian corals in the region of Nosy Bé, in northwestern Madagascar (Humes, 1962a, 1962b; Humes and Frost, 1964). Only one of these, *Kombia angulata* Humes, 1962, has been recovered from the genus *Psammocora* (family Thamnasteriidae), that is to say, from *Psammocora* species.

An examination of *Psammocora contigua* (Esper) from Ambariobe, a small island situated nearly between Nosy Bé and Nosy Komba, has revealed the four new associated copepods described in this paper.

All collections were made by the senior author while participating in the activities of the U.S. Program in Biology of the International Indian Ocean Expedition at Nosy Bé in 1963–64.

The study of the material has been aided by a grant (GB-1809) from the National Science Foundation.

All figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn. Abbreviations used in figures: A_1=first antenna, A_2=second antenna, L=labrum, MD=mandible, P=paragnath,

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[1] Both authors: Department of Biology, Boston University, Boston, Massachusetts.

MX_1=first maxilla, MX_2=second maxilla, MXPD=maxilliped, P_1=first leg.

We wish to thank Dr. Michel Pichon for the identification of the coral and to express our appreciation for the many courtesies received from the staff of the Centre d'Océanographie et des Pêches at Nosy Bé.

Family Xarifiidae Humes, 1960

Genus *Xarifia* Humes, 1960

Xarifia diminuta, new species

FIGURES 1–24

TYPE MATERIAL.—148 ♀♀ and 262 ♂♂ washed from a colony of the coral *Psammocora contigua* (Esper) in a depth of 1 m, southeast of Ambariobe, near Nosy Bé, Madagascar. Collected Sept. 6, 1963. Holotype female, allotype, and 155 paratypes (50 ♀♀, 105 ♂♂) deposited in the United States National Museum, Washington; 80 paratypes (30 ♀♀, 50 ♂♂) in the Museum of Comparative Zoology, Cambridge, and in the Zoölogisch Museum, Amsterdam; and the remaining paratypes in the collection of A. G. Humes.

OTHER SPECIMENS (all from *Psammocora contigua* in 1–2 m at Ambariobe, collected during 1963).—10 ♀♀, 2 ♂♂, Sept. 6; 143 ♀♀, 87 ♂♂, Sept. 8; 173 ♀♀, 116 ♂♂, Sept. 17; and 65 ♀♀, 30 ♂♂, Oct. 6.

FEMALE.—Body (figs. 1, 2) moderately slender, about five times longer than wide. Length (not including setae on caudal rami) 0.98 mm (0.78–1.18 mm), greatest width 0.18 mm (0.14–0.21 mm), based on 10 specimens. Segmentation not defined externally. Region dorsal to fifth legs bearing three long, posteriorly directed processes, median one only slightly shorter than lateral ones. Genital and postgenital segments together (fig. 3) less than one-fifth total body length. Areas of attachment of egg sacs dorsal in position. Behind these areas a pair of minute ventrolateral setules. Caudal ramus (fig. 4) 45μ x 17μ (width taken at middle), about 2.65 times longer than wide; with four short naked setae (one outer and subterminal, others terminal) and a few minute setules. Egg sac (fig. 5), in one female 290μ x 198μ, containing usually five eggs in a flattened cluster (in some females six or seven), eggs about 97μ in average diameter.

Rostral area protuberant in lateral view (fig. 6) between bases of first antennae and bearing relatively long slender setules (fig. 7). First antenna (fig. 7) short (48μ in length without setae) and apparently 3-segmented, though middle segment showing partial division. With numerous naked setae, armature being 3, 20+1 aesthete, and 8+2 aesthetes. Second antenna (fig. 8) 4-segmented, formula being

1, 1, 2, and I,1 (the Roman numeral referring to the claw). Recurved claw on last segment 6μ in length, slender seta 17μ.

Labrum with posteroventral border having two widely separated lateral lobes (fig. 9). Mandible (fig. 10) with an attenuated blade concealed in ventral view under posterior part of labrum (see fig. 9). Paragnath absent. First maxilla (fig. 11) a small rounded lobe bearing two naked setae. Second maxilla (fig. 12) probably 2-segmented, though separation of segments not complete. Second segment bearing two inner elements (a slender setule and a stout hyaline seta) and terminating in a finger-like process with a hyaline lamellate inner margin. Maxilliped (fig. 13) 2-segmented, second segment bearing two small naked setae and terminating in 2 irregular lobate processes.

Legs 1–4 with general form and segmentation like that shown for leg 1 in figure 14; exopods 3-segmented (the articulation obscure), endopods 2-segmented. Spine and setal formula as follows (Roman numerals indicating spines, Arabic numerals setae):

P_1	protopod	0–0	1–0	exp	I–0	I–0	I,3
				end	0–0	2	
P_2	protopod	0–0	1–0	exp	I–0	I–0	I,3
				end	0–0	2	
P_3	protopod	0–0	1–0	exp	I–0	I–0	I,2
				end	0–0	0	
P_4	protopod	0–0	1–0	exp	I–0	I–0	I,2
				end	0–0	2	

In all four legs coxa with a slender setule on posterior outer surface; basis with an outer naked seta and an inner tuft of long hairs. Exopod with stout spines recurved posteriorly (fig. 15); three small slender setae at inner base of terminal spine in legs 1 and 2, two such setae in legs 3 and 4. Long hairs arising from inner margins of first and second segments of exopod. Endopod with long hairs on outer margins of both segments; last segments with two terminal setae in legs 1, 2, and 4, but unarmed in leg 3 (fig. 16).

Leg 5 (fig. 17) elongated and slender, with its free segment not clearly delimited from body. Segment about 120μ in length and somewhat irregular in width, tapered distally, bearing two unequal terminal naked setae 13μ and 26μ long. A slender seta arising from body wall dorsal to base of segment. Leg 6 absent.

Color in life in transmitted light slightly reddish brown, eye red, egg sacs orange red to reddish green.

Male.—Body (figs. 18, 19) rather slender, slightly longer than female. Length 1.15 mm (0.94–1.35 mm), greatest width 0.16 mm (0.13–0.19 mm), based on 10 specimens. Without external segmentation. Caudal ramus (fig. 20) shorter than in female and not distinctly delimited from anal segment.

Rostral area (fig. 21) as in female. First antenna like that of female but with four aesthetes, one being added on midanterior margin of middle segment. Second antenna, labrum (see fig. 21), mandible, first maxilla, and second maxilla resembling those in female. Paragnath absent. Maxilliped (fig. 22) 4-segmented. First segment short and unarmed. Second large and swollen with two inner setae (one sclerotized proximally, other entirely hyaline) and having its distal outer surface minutely punctate. Third segment very short and unarmed. Fourth segment forming a terminal claw 39μ along its axis, bifurcated at its tip, with an outer hyaline lamella and an inner triangular hyaline process; bearing two setae (one sclerotized proximally, other entirely hyaline).

Legs 1–4 as in female, with same spine and setal forumla. Leg 5 (fig. 23) without a distinct segment and consisting of three small setae, the two more ventral ones forming a pair and probably homologous to the two setae on the end of leg 5 in the female. Leg 6 (figs. 19, 23) represented by a ventrolateral flap bearing two small setae.

Spermatophore (fig. 24) elongated, 255μ x 62μ, not including neck.

Color as in female.

ETYMOLOGY.—The specific name *diminuta*, from Latin=diminished, refers to the relatively small size of this species.

METHOD OF COLLECTION AND RELATION TO HOST.—The number of specimens of *X. diminuta* collected from *Psammocora contigua* depended upon the technique employed. When the corals were washed in weakly alcoholized sea water (with about 5 per cent ethyl alcohol) within one or two hours after being brought to the laboratory, few if any *Xarifia* were obtained. After crushing the corals with a hammer, relatively few *Xarifia* were recovered from the debris and mucus. When, however, the corals were left overnight (12–14 hours) in pails of alcoholized sea water, abundant specimens of the copepods were found in the sediment. This is in accord with the observations of Humes (1962a) on the collection of other species of *Xarifia*. Gerlach, as quoted by Humes (1960), observed that living *Xarifia* in *Pocillopora* in the Maldive Islands crawl about on the surface of the coral but may at times enter the polyps where they seem to tear up the tissue of the coral.

COMPARISON WITH RELATED SPECIES.—There are 10 species presently known in the genus *Xarifia*. *X. diminuta* may be distinguished from eight of these which have the endopods of legs 1–4 composed of a single segment (*X. maldivensis* Humes, 1960; *X. fimbriata* Humes, 1960; *X. gerlachi* Humes, 1962; *X. longipes* Humes, 1962; *X. reducta* Humes, 1962; *X. serrata* Humes, 1962; *X. tenuis* Humes, 1962; and *X. infrequens* Humes, 1962). In the two remaining species, *X. dispar* Humes, 1962, and *X. comata* Humes, 1962, the endopods of legs 1–4 are

2-segmented. The new species differs from *X. dispar*, which is larger (both sexes about 1.4 mm in length), has slender spines on the first two segments of the exopods in legs 1–4, has shorter processes on the region dorsal to the fifth legs, and has a terminal seta on the endopod of leg 3. It seems to be close to *X. comata*, with its fifth legs and three processes dorsal to them being similar to those in that species. *X. diminuta* differs from *X. comata*, however, in the following features: the first segment of the exopods of legs 1–4 has a well-developed outer spine (this spine minute in *X. comata*), the second segment of the exopods of legs 1–4 has an outer spine (lacking in *X. comata*), the endopod of leg 3 lacks terminal elements (two setae in *X. comata*), the endopod of leg 4 has two terminal setae (only one in *X. comata*), the terminal spine and seta of the second antenna are very unequal in length (nearly equal in *X. comata*), the egg sac usually contains five eggs (sometimes six or seven) (in *X. comata* usually two, sometimes one, three, or four), and the maxilliped of the male has a form different from that of *X. comata*.

Family Lichomolgidae Kossmann, 1877

Genus *Lichomolgus* Thorell, 1860

Lichomolgus rhadinus, new species

FIGURES 25–51

TYPE MATERIAL.—199 ♀♀, 227 ♂♂, and 9 copepodids washed from the coral *Psammocora contigua* (Esper) in a depth of 2 m, south of Ambariobe, near Nosy Bé, Madagascar. Collected Sept. 8, 1963. Holotype female, allotype, and 160 paratypes (88 ♀♀, 72 ♂♂) deposited in the United States National Museum, Washington; 85 paratypes (35 ♀♀, 50 ♂♂) in the Museum of Comparative Zoology, Cambridge, and in the Zoölogisch Museum, Amsterdam; and the remaining paratypes in the collection of A. G. Humes.

OTHER SPECIMENS (all from *Psammocora contigua* in 1–2 m at Ambariobe, collected during 1963).—33 ♀♀, 18 ♂♂, Sept. 6; 83 ♀♀, 39 ♂♂, Sept. 8; 9 ♀♀, Sept. 17; and 3 ♀♀, 1 ♂, Oct. 6.

FEMALE.—Body (fig. 25) moderately slender. Length (not including setae on caudal rami) 1.00 mm (0.95–1.04 mm) and greatest width 0.35 mm (0.33–0.36 mm), based on 10 specimens. Ratio of length to width of prosome 1.70:1. Segment of leg 1 separated from head by a dorsal furrow. Epimeral areas of metasomal segments formed as illustrated in figure.

Segment of leg 5 (fig. 26) 47μ x 105μ. Between this segment and genital segment a short ventral intersegmental sclerite. Genital segment about as long as wide, 110μ x 108μ, rather abruptly constricted in its posterior fourth. Areas of attachment of egg sacs situated dorsally (only slightly laterally), each area (fig. 27) bearing two small setae 5μ and 8μ in length. Three postgenital segments 50μ x 55μ, 39μ x 48μ, and 50μ x 47μ from anterior to posterior. Anal segment with a row of minute spinules along its posteroventral margin on each side.

Caudal ramus (fig. 28) elongated, 73μ x 22μ, about 3.3 times longer than wide. Outer lateral seta 88μ and naked; outermost terminal seta 91μ and naked; innermost terminal seta 112μ with inner hairs proximally. Two long median terminal setae 255μ (inner) and 203μ (outer) with lateral spinules in their midregions; these two setae inserted between dorsal (smooth) and ventral (with a row of minute spinules) flaps. Dorsal pedicellate seta 57μ and naked. Dorsal surface of ramus with scattered hairs.

Dorsal surface of prosome and urosome with few hairs (as in figs. 25, 26); ventral surface of urosome almost devoid of ornamentation. Ratio of length of prosome to that of urosome 1.85:1.

Egg sac (fig. 25) about 278μ x 170μ, containing a relatively small number of large eggs (five–seven), each egg about 92μ in average diameter.

Rostral area (fig. 29) not well developed, without a definite posteroventral margin.

First antenna (fig. 30) slender (280μ in length) and 7-segmented, with sclerite on third segment suggesting an intercalary segment weakly developed. Lengths of segments (measured along their posterior nonsetiferous margins) 28μ (44μ along anterior margin), 99μ, 28μ, 52μ, 28μ, 23μ, and 11μ respectively. Formula for armature, as in other species of *Lichomolgus*, 4, 13 (5+8), 6, 3, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. All setae naked.

Second antenna (fig. 31) 4-segmented, slender, and elongated (208μ in length). Outer edge of penultimate segment 52μ in length, and that of last segment 21μ. Armature 1, 1, 3, and I, 1. All setae small and naked; terminal claw 28μ along its axis. Row of slender spinules on inner surface of second segment distal to seta.

Labrum (fig. 32) with two posteroventral lobes.

Mandible (fig. 33) with proximal region constricted, a narrow waist separating basal and distal parts. That part distal to waist having on its inner side a prominent elongated posteriorly directed process followed by a row of minute blunt hyaline spinules; and on its outer side a bilobed margin with setules. Flagellum moderately long with lateral spinules. Paragnath (fig. 37) a prominent well-sclerotized lobe without visible ornamentation but with its distal surface slightly wrinkled. First maxilla (fig. 34) with 3 terminal elements. Second maxilla (fig. 35) 2-segmented. First segment unornamented. Second segment having on its outer (ventral) margin a small proximal setule followed by a seta and on its inner (dorsal) margin a seta with hyaline lamellae; terminal lash with a row of slender spinules. Maxilliped (fig. 36) 3-segmented. First segment stout and unornamented. Second segment elongated and slender with two inner setae. Third segment with two small setae and a terminal spiniform process with lateral spinules.

Area between maxillipeds and first pair of legs (fig. 37) not protuberant; sclerotized line between bases of maxillipeds.

Legs 1–4 (figs. 38–41) with trimerous rami except for endopod of leg 4 which is 2-segmented. Armature as follows (Roman numerals indicating spines, Arabic numerals setae):

P_1	protopod	0–1	1–0	exp	I–0	I–1	III, I, 4
				end	0–1	0–1	I, 5
P_2	protopod	0–1	1–0	exp	I–0	I–1	III, I, 5
				end	0–1	0–2	I, II, 3
P_3	protopod	0–1	1–0	exp	I–0	I–1	III, I, 5
				end	0–1	0–2	I, II, 2
P_4	protopod	0–0	1–0	exp	I–0	I–1	II, I, 5
				end	0–1	2	

Inner seta on coxa of legs 1 and 2 long and plumose, in leg 3 somewhat reduced in size, and in leg 4 absent. Hairs present on inner margin of basis in legs 1–3 but absent in leg 4. Outer spines on exopod of leg 1 flagellated. Endopod of leg 4 with hairs along outer margins of both segments. First segment 17μ x 13μ with plumose inner seta 26μ long; second segment 29μ long, 9μ wide proximally, 7μ wide distally, and armed with two slightly barbed setae 22μ (outer) and 33μ (inner).

Leg 5 (fig. 42) with an elongated free segment having a proximal inner expansion. This segment 90μ in length, 22μ wide at the expansion, and 17μ wide in its midregion; with a few small spinules on outer dorsal surface of distal half and with two terminal naked setae, outer 44μ, inner 72μ in length. Seta on body near free segment 68μ and slightly haired distally. A few small outer spinules near insertion of free segment.

Leg 6 probably represented by 2 setae near attachment of each egg sac (see fig. 27).

Color in life in transmitted light translucent, eye red, ovary black.

Male.—Body (fig. 43) slender. Length (without setae on caudal rami) 0.73 mm (0.69–0.76 mm) and greatest width 0.23 (0.22–0.24 mm), based on 10 specimens. Ratio of length to width of prosome 1.72:1.

Segment of leg 5 (fig. 44) 32μ x 73μ. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment longer than wide, 169μ x 135μ. Four postgenital segments 24μ x 43μ, 26μ x 42μ, 21μ x 40μ, and 31μ x 42μ from anterior to posterior.

Caudal ramus (fig. 45) resembling that of female but much shorter, 28μ x 18μ, or 1.55 times longer than wide.

Dorsal surface of body with few hairs (as in figs. 43, 44); ventral surface of urosome almost completely lacking ornamentation. Ratio of length of prosome to that of urosome 1.43:1.

Rostral area like that of female.

First antenna similar to that of female but with 3 aesthetes added, so that formula is 4, 13+2 aesthetes, 6, 3+1 aesthete, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. Second antenna resembling that of female but inner margin of second segment with a row of dentiform spinules (fig. 46).

Labrum, mandible, paragnath, first maxilla, and second maxilla similar to those in female. Maxilliped (fig. 47) elongated and slender, 4-segmented, assuming that proximal part of claw represents a fourth segment. First segment unarmed, second with two setae and rows of spinules on inner surface, third short and unarmed. Claw slender and gently recurved, 127μ along its axis (including terminal lamella), with faint indication of division about midway; two unequal setae on proximal part of claw.

Legs 1–4 as in female except for endopod of leg 1 where formula for last segment (fig. 48) is I,I,4, instead of I,5 as in female.

Leg 5 (fig. 49) with elongated free segment, 18μ x 6μ, lacking a basal expansion. Two terminal setae 8μ (inner) and 24μ (outer).

Leg 6 (fig. 50) a posteroventral flap on genital segment bearing two naked setae 18μ and 22μ long.

Spermatophore (fig. 51) moderately elongated, 127μ x 56μ (without neck), often attached to female in pairs.

Color in life in transmitted light similar to that of female.

Etymology.—The specific name *rhadinus*, from the Greek word ῥαδινός=slender, refers to the slender form of the body, of the first and second antennae, and of the maxillipeds in this species.

Method of collection and relation to host.—*Lichomolgus rhadinus* was recovered after washing the coral in alcoholized sea water within a few hours after collection. In contrast to the recovery of *Xarifia diminuta* and *Rhynchomolgus corallophilus*, where the greatest numbers of specimens were found after allowing the coral to remain in alcoholized sea water overnight or after crushing the coral, all *L. rhadinus* were obtained in the first washings and none were found in the second washings after an overnight delay or after crushing. This suggests that *L. rhadinus* lives on the surface of the coral whence it is easily dislodged, rather than in the polyps.

Comparison with related species.—The distinctive form of the mandible in *L. rhadinus* sets it apart from almost all of the other 70 or more species already described in the genus. Only five species have a mandible somewhat resembling that of the new species. *L. actinophorus* Humes and Frost, 1964, has an elongated posteriorly directed process on the inner side of the basal region, but this process is more pointed and dentiform than in *L. rhadinus*. In addition, *L. actinophorus* differs from *L. rhadinus* in lacking a basal expansion on leg 5 in the female. Four species show on the inner basal region of the mandible a dentiform process much shorter than in *L. rhadinus*. These are *L. decorus* Humes and Frost, 1964 (in which the last segment of the exopod of leg 4 is III,I,4), ?*L.* (*Epimolgus*) *protulae* Stock, 1959 (with no basal expansion on leg 5 in the female and with the last segment of the second antenna bearing three strong claws, three setiform claws, and one seta), and *L. organicus* Humes and Ho, 1967, and *L. conjunctus* Humes and Ho, 1967, from the alcyonarian coral *Tubipora musica*. In both of these there is no basal expansion on leg 5 in the female and the last segment of the second antenna bears two claws and five setae. All other species of *Lichomolgus* in which the mandible has been described or figured lack prominent processes of this sort.

Eight species of *Lichomolgus* can not be compared with *L. rhadinus* in respect to the mandible since that appendage in them is unknown. They may be easily separated from the new species, however, on other grounds. *L. dentipes* Thompson and A. Scott, 1903, and *L. rigidus* (Ummerkutty, 1962) have the formula III,I,5 on the last segment of the exopod of leg 4. *L. elegans* Thompson and A. Scott, 1903, has in the female a much shorter caudal ramus and leg 5 without a basal expansion. *L. gigas* Thompson and A. Scott, 1903, is much larger (female 2 mm) and leg 5 lacks a basal expansion. *L. longipes* (Sewell, 1949), *L. rotundus* Sewell, 1949, *L. tenuicornis* Brady, 1910, and *L. vagans* Gurney, 1927, have two claws included in the armature of the last segment of the second antenna.

L. rhadinus appears to be most closely related to *L. actinophorus* Humes and Frost, 1964. It is of interest to note here the strong similarity between the mandible of *L. rhadinus* and that of *Rhynchomolgus corallophilus* (compare figs. 33 and 90). In many other features, however, these two copepods from *Psammocora* are very different.

Genus *Monomolgus* Humes and Frost, 1964

Monomolgus psammocorae, new species

FIGURES 52–79

TYPE MATERIAL.—17 ♀♀, 27 ♂♂, and 2 copepodids washed from the coral *Psammocora contigua* (Esper) in a depth of 2 m, southeast of Ambariobe, near Nosy Bé, Madagascar. Collected Sept. 8, 1963. Holotype female, allotype, and 32 paratypes (12 ♀♀, 20 ♂♂) deposited in the United States National Museum, Washington; 6 paratypes (2 ♀♀, 4 ♂♂) in the Zoölogisch Museum, Amsterdam; and the remaining paratypes in the collection of A. G. Humes.

Other specimens (all from *Psammocora contigua* in 1 m at Ambariobe, collected during 1963).—9 ♀♀, 8 ♂♂, Sept. 6; 2 ♀♀, 2 ♂♂, Sept. 17; and 10 ♀♀, 3 ♂♂, Oct. 6.

Female.—Body (fig. 52) with broadened prosome. Length (excluding setae on caudal rami) 1.25 mm (1.21–1.29 mm) and greatest width 0.65 mm (0.62–0.68 mm), based on 10 specimens. Ratio of length to width of prosome 1.22:1. Segment of leg 1 separated from head by a dorsal furrow. Epimeral areas of segments of legs 1–3 expanded as shown in figure. Segment of leg 4 without such expanded areas.

Segment of leg 5 (fig. 53) 86μ x 213μ. Between this segment and genital segment a short ventral intersegmental sclerite. Genital segment wider than long, 146μ x 172μ, broadest in its anterior half and tapered posteriorly. Areas of attachment of egg sacs situated laterally (only slightly dorsally), each area (fig. 54) bearing two setae 10μ and 6μ in length, with a short spinous process between them. Three postgenital segments 73μ x 99μ, 62μ x 96μ, and 68μ x 97μ from anterior to posterior. Anal segment posteriorly with row of small spinules laterally and ventrally on each side.

Caudal ramus (fig. 55) moderately elongated, 92μ x 35μ in greatest dimensions (77μ along inner edge, 90μ along outer edge). Ratio of length to width 2.63:1. Outer lateral seta 57μ long with minute barbules; outermost terminal seta 58μ and innermost terminal seta 75μ, both with proximal hairs and distal barbules as in figures. Two long median terminal setae 237μ (inner) and 146μ (outer) with proximal spinules and distal barbules; these two setae inserted between dorsal and ventral flaps (both with a row of slender spinules). Dorsal pedicellate seta 37μ and naked. Dorsal surface of ramus with a few hairs and two small hyaline spinules.

Dorsal surface of prosome and urosome with scattered hairs (as in figs. 52, 53); ventral surface of urosome sparsely ornamented. Ratio of length of prosome to that of urosome 1.72:1.

Egg sac (figs. 52, 56) attached in somewhat oblique position, with posterior end lying dorsally over postgenital segments. In lateral view egg sac in one female 400μ x 285μ, containing about 12 large eggs, with their diameters 117μ–130μ.

Rostral area (fig. 57) with broadly rounded posterior margin.

First antenna (fig. 58) 7-segmented, with a small sclerite on third segment suggesting an intercalary segment. Lengths of segments (measured along their posterior nonsetiferous margins) 55μ (71μ along anterior margin), 62μ, 28μ, 28μ, 32μ, 33μ, and 18μ, respectively.

Formula for armature: 4, 13 (5+2+6), 6, 3, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. All setae naked. Row of minute spinules on first segment.

Second antenna (fig. 59) 4-segmented, last segment 50μ x 20μ. Armature 1, 1, 3, I, with terminal claw 43μ along its axis. A few minute spinules near bases of setae on third segment; two small setules on opposite surfaces of last segment near insertion of claw.

Labrum (fig. 60) with two posteroventral lobes and bearing numerous hairs.

Mandible (fig. 61) with its inner basal margin smooth, its outer basal margin with a distal row of slender setules and a proximal auricular expansion encircled with setules; lash elongated, its proximal inner margin with blunt hyaline dentations, both margins distal to this with spinules. Paragnath (fig. 62) an elongated lobe with distal hairs. First maxilla (fig. 63) with four elements as in figure. Second maxilla (fig. 64) 2-segmented. First segment somewhat swollen distoventrally, with small spinules. Second segment with a seta (having hyaline lamellae) on its anterior surface, a hyaline element on its inner (dorsal) margin, and a very small setule proximally on its outer (ventral) margin; distal part of segment forming a lash with a marginal row of three large slender proximal teeth gradating rapidly to many slender setules; a crescent of minute spinules at base of lash. Maxilliped (fig. 65) 3-segmented, first segment unarmed, second segment with two naked setae and a short row of minute spinules, and small third segment terminally with a spine, two hyaline setae, and a spinelike process with lateral spinules.

Area between maxillipeds and first pair of legs (fig. 66) not protuberant; sclerotized line connecting bases of maxillipeds.

Legs 1–4 (figs. 67–70) with trimerous rami except for endopod of leg 4 which consists of two segments. Armature as follows (Roman numerals indicating spines, Arabic numerals setae):

P_1	protopod	0–1	1–0	exp	I–0	I–1	III,I,4
				end	0–1	0–1	I,5
P_2	protopod	0–1	1–0	exp	I–0	I–1	III,I,5
				end	0–1	0–2	II,I,3
P_3	protopod	0–1	1–0	exp	I–0	I–1	III,I,5
				end	0–1	0–2	I,I,2
P_4	protopod	0–1	1–0	exp	I–0	I–1	II,I,5
				end	0–0	I	

Inner seta on coxa of legs 1–3 long and plumose, but in leg 4 very small (3μ long) and naked. Lamellae on spines of leg 1 more conspicuously spinulose than in legs 2–4. Spinules in row across distal margin of second segment of endopod of legs 1–3 much larger than those on first segment of these endopods. Endopod of leg 4 with both segments having inner and outer hairs. First segment 23μ x 18.5μ;

second segment 29μ x 13μ, armed with a single terminal spine 50μ in length having minutely spinulose lamellae.

Leg 5 in flat view of anterior surface as shown in figure 71, but in undissected specimens appearing in dorsal view as in figure 72. Free segment elongated and moderately broad, 84μ x 28μ, or three times longer than wide; with a few small spinules on its distal anterior surface and armed with two terminal barbed setae 77μ (outer) and 94μ (inner) in length. Seta on body near free segment 70μ long, haired proximally and barbed distally.

Leg 6 probably represented by two setae near attachment of each egg sac (see fig. 54).

Color in life in transmitted light amber in metasomal region, eye red, ovary gray.

MALE.—Body (fig. 73) with prosome broadened, but a little more spherical in dorsal outline than in female. Length (not including setae on caudal rami) 0.91 mm (0.85–0.97 mm) and greatest width 0.37 mm (0.36–0.38 mm), based on 10 specimens. Ratio of length to width of prosome 1.40 : 1.

Segment of leg 5 (fig. 74) 34μ x 138μ. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment in dorsal view broadly expanded, wider than long, 146μ x 208μ. Four postgenital segments 32μ x 60μ, 33μ x 60μ, 34μ x 58μ, and 33μ x 62μ from anterior to posterior.

Caudal ramus resembling that of female but smaller, 68μ x 26μ.

Dorsal surface of prosome and urosome with scattered hairs (as in figs. 73, 74); ventral surface of urosome almost without ornamentation. Ratio of length of prosome to that of urosome 1.45:1.

Rostral area like that of female.

First antenna (fig. 75) resembling that of female but with three aesthetes added. Lengths of segments (measured as in female) 30μ (50μ along anterior margin), 46μ, 15μ, 14μ, 21μ, 14μ, and 13μ, respectively. Formula for armature: 4, 13+2 aesthetes, 6, 3+1 aesthete, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. All setae naked.

Second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (fig. 76) elongated and slender, 4-segmented, assuming that proximal part of claw represents a fourth segment. First segment unarmed, second with two naked setae and a row of small blunt spines, third very short and unarmed. Claw strongly recurved, 57μ along its axis (including the lamella), with suggestion of bipartite nature midway along its length; proximal part bearing two unequal setae.

Area between maxillipeds and first pair of legs resembling that of female. Legs 1–4 as in female, without sexual dimorphism in endopod of leg 1. Endopod of leg 4 with dimensions proportionally much like those in female; first segment 19μ x 17.5μ, second segment 24μ x 11μ, and terminal spine 40.5μ.

Leg 5 in flat anterior view as shown in figure 77, but in undissected specimens appearing in dorsal view as in figure 78. Free segment more rectangular than in female, 34μ x 14μ, or 2.43 times longer than wide; terminal setae 51μ and 69μ in length, respectively.

Leg 6 (fig. 79) a posteroventral flap on genital segment bearing two setae, one 50μ in length and naked, other 45μ with a few lateral hairs.

Spermatophore not observed.

Color in life in transmitted light similar to that of female.

Etymology.—The specific name *psammocorae* is based on the generic name of the host.

Method of collection and relation to host.—Like the preceding species, *M. psammocorae* was recovered in greatest numbers from the first washings of the coral, without allowing the coral to stand overnight in alcoholized sea water and without crushing. Presumably the copepod lives on the surface of the coral rather than in the polyps.

Systematic position.—The genus *Monomolgus* is at present founded on a single species, *M. unihastatus* Humes and Frost, 1964, associated with a coral, *Porites* cf. *P. andrewsi* Vaughan (family Poritidae), in Madagascar.

The new species from *Psammocora* may readily be distinguished without dissection from *M. unihastatus* by its shorter and more compact body form, its shorter caudal ramus (in *M. unihastatus* 3.9 times longer than wide in the female, 5.7 times in the male), and its narrower free segment of leg 5 in the female (in *M. unihastatus* 1.7 times longer than wide).

M. psammocorae is similar to *M. unihastatus* in several basic respects, particularly the segmentation and armature of the first antenna, second antenna, leg 1 in the female, leg 2, the exopod of leg 3, the endopod of leg 4, and leg 5. The differences seen in leg 1 of the male (lack of sexual dimorphism in *M. psammocorae*), in the endopod of leg 3 (last segment I,I,2, instead of I,II,2), and in the exopod of leg 4 (last segment II,I,5, instead of III,I,5) are probably only of a specific rather than generic nature.

The mouthparts of *M. psammocorae* exhibit certain detailed differences from those of *M. unihastatus*. The mandible in the species from *Psammocora* has an outer basal auricular expansion and a relatively long terminal lash. The paragnath is elongated. The first maxilla is armed with four elements.

These differences are probably not to be construed as evidence against the congeneric position of the two species; comparable differences in mouthparts exist among the species of the genus *Lichomolgus.* The points of similarity are so great that we think it preferable for the present to regard *M. unihastatus* and *M. psammocorae* as members of the same genus. The form of the endopod of leg 4, regarded as especially diagnostic in lichomolgid copepods, supports this point of view.

The inclusion of *M. psammocorae* in *Monomolgus* will necessitate a revision of the original generic diagnosis, especially in relation to the mandible. We are not attempting such a revision at present, however, in the expectation that further studies will clarify the generic concept of *Monomolgus.*

Rhynchomolgus, new genus

FEMALE.—Cephalosome expanded, urosome narrow. Segment of leg 1 fused with head. Urosome 5-segmented. Rostrum tumid and snoutlike. First antenna 5-segmented. Second antenna 4-segmented with a single terminal claw. Mouthparts lichomolgid. Legs 1 and 2 with 2-segmented rami. Leg 3 reduced to two setae. Leg 4 represented by a single seta. Leg 5 consisting of three setae, without a free segment.

MALE.—Body elongated and rather vermiform. Segment of leg 1 fused with head. Urosome 5-segmented in immature male, 6-segmented in mature male. Caudal ramus reduced and lobate. Rostrum as in female. First antenna 1-segmented. Second antenna indistinctly 3-segmented. Labrum bulbous. Mandibles, paragnaths, and first maxillae absent. Second maxilla a well-developed hook in immature male, a minute spinous process in mature male. Maxilliped 1-segmented with clawlike tip in immature male, absent in mature male. Legs 1 and 2 much reduced, with rami of one segment. Leg 3 represented by a single seta. Legs 4 and 5 absent. Leg 6 present.

Other features as in the species described below.

Living in madreporarian corals.

Type and only known species: *Rhynchomolgus corallophilus,* new species.

Gender masculine.

ETYMOLOGY.—The generic name is a combination of the Greek words ῥύγχος=snout, referring to the prominent rostrum, and μολγός = sack made of leather.

Rhynchomolgus corallophilus, new species

FIGURES 80–115

TYPE MATERIAL.—45 ♀♀, 32 small ♂♂, and 47 large ♂♂ from the coral *Psammocora contigua* (Esper) in a depth of 1 m, southeast of Ambariobe, near Nosy Bé, Madagascar. Collected Sept. 6, 1963. Holotype female, allotype large male, and 58 paratypes (20 ♀♀, 15 small ♂♂, and 23 large ♂♂) deposited in the United States National Museum, Washington; 21 paratypes (7 ♀♀, 7 small ♂♂, and 7 large ♂♂) in the Zoölogisch Museum, Amsterdam; and the remaining paratypes in the collection of A. G. Humes.

OTHER SPECIMENS (all from *Psammocora contigua* in 1–2 m at Ambariobe, collected during 1963).—16 ♀♀, 19 small ♂♂, and 25 large ♂♂, Sept. 8; 5 small ♂♂ and 9 large ♂♂, Sept. 17.

FEMALE.—Body (figs. 80, 81) with cephalosome greatly expanded laterally; segments of metasome and urosome relatively slender and somewhat contractile, the postgenital segments sometimes telescoped. Length (not including setae on caudal rami) 1.07 mm (0.89–1.24 mm) and greatest width 0.56 mm (0.49–0.63 mm), based on 10 specimens in average state of contraction. Two fully extended females 1.49 x 0.54 mm. Ratio of length to width of prosome (not including rostrum) 1.29:1. Segment of leg 1 fused with head, the only indication of separation being an indistinct transverse dorsal fold.

Segment of leg 5 (fig. 82) 91μ x 166μ. Genital segment wider than long, 130μ x 161μ, subrectangular in dorsal outline. Areas of attachment of egg sacs situated dorsolaterally, each area (fig. 83) bearing medially two spiniform setae, both about 19μ in length and directed posteriorly. Three postgenital segments 86μ x 109μ, 65μ x 86μ, and 60μ x 75μ from anterior to posterior. Last segment with a lobate dorsal flap over anal area; at either side of this flap on both dorsal and ventral surfaces a patch of denticles. (Entire urosome in telescoped specimen shown in figure 3 about 325μ in length, but if expanded the length would reach about 475μ.)

Caudal ramus (fig. 84) 44μ x 23μ, with ratio of length to width 1.91:1. Six short naked setae near distal end of ramus, the longest about 36μ. (Of these setae, one more dorsally placed than others, one on outer corner, and two median, shown partly retracted in figure, corresponding respectively to dorsal pedicellate seta, outer lateral seta, and two long median terminal setae seen in less modified lichomolgids such as *Lichomolgus*.) Ramus with a few minute spinules, small setules, and refractile points as shown in figure.

Dorsal surface of prosome with scattered refractile points and setules in metasomal region (as in figs. 80, 81); urosome with dorsal and ventral surfaces similarly ornamented (see fig. 82). Ratio of length of prosome to that of urosome (in specimen shown in fig. 80) about 2.39:1, but this ratio subject to state of contraction.

Egg sac unknown, since none of females collected was ovigerous.

Rostrum (figs. 80, 81, 85) a conspicuous tumid snoutlike lobe bluntly rounded distally.

First antenna (fig. 86) 5-segmented and relatively short (about 80μ in length). Lengths of segments (measured along their posterior nonsetiferous margins) 21μ (25μ along anterior margin), 15.5μ, 16μ, 11.5μ, and 9μ, respectively. Formula for armature: 3, 10, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. Setae with strong lateral spinules, except five naked setae (one on segment 3, one on segment 4, and four on last segment).

Second antenna (fig. 87) 4-segmented and much longer (about 180μ including claw) than first antenna. First and second segments rather large and each with an inner barbed seta. Third and fourth segments smaller, third with three inner barbed setae, fourth (fig. 88) ornamented with five rather hyaline spinules and a short row of minute spinules, and bearing a terminal claw 28μ in length and only slightly recurved. External to base of second antenna and behind base of first antenna a prominent lobe (see figs. 81, 94).

Labrum (fig. 89) with posteroventral margin forming two lobes.

Mandible (fig. 90) with inner margin of basal region having proximally a prominent finger-like extension (directed posteriorly) and distally a row of small dentations; disto-inner margin of basal region with a row of moderately long spinules. Lash relatively short and not finely attenuated, with serrated margins. Paragnath (fig. 89) a small lobe bearing hairs distally. First maxilla (fig. 91) a single small segment with two terminal barbed setae. Second maxilla (fig. 92) 2-segmented, first segment unarmed, second with two barbed elements and extended to form a gladiate blade with short stout teeth along one edge. Maxilliped (fig. 93) 3-segmented, first segment unarmed, second segment with two spinulose elements, and third with one spinulose element and terminating in a spinulose spiniform process.

Area between maxillipeds and first pair of legs (fig. 94) not protuberant.

Legs 1–4 much modified. Legs 1 and 2 (figs. 95, 96) with similar intercoxal plates, protopods, and 2-segmented rami. In leg 1 terminal spine on exopod with a few inner serrations, and anterior surface of basis near insertion of endopod having a row of small spinules; these features absent in leg 2. Spines on both legs obtuse.

Leg 3 (fig. 97) reduced to two unequal setae, inner 7μ, outer 16μ in length. Leg 4 (fig. 98) a single seta 16μ long. These two legs lacking intercoxal plates.

Armature of legs 1–4 as follows (Roman numerals indicating spines, Arabic numerals setae):

P_1	protopod	0–0	1–0	exp	I–0	III,II,2
				end	0–0	I,1
P_2	protopod	0–0	1–0	exp	I–0	III,II,2
				end	0–0	I,II
P_3					2	
P_4					1	

In one female second segment of one endopod of leg 1 with an extra outer spine (I,I,1). In another female second segment of one exopod of leg 2 with an extra inner seta (III,II,3).

Leg 5 (fig. 99) without a free segment, and reduced to three setae, one dorsal 24μ, and two ventral 16μ and 18μ in length.

Color in life, in transmitted light, amber in cephalosome, rest of body translucent, eye red but indistinct.

Small immature male.—Body (fig. 100) elongated, rather vermiform, contractile, head region sometimes partly withdrawn into cephalosome and urosome often bent or contracted. Length (excluding setae on caudal rami) 1.17 mm (0.89–1.44 mm) and greatest width 0.26 mm (0.22–0.30 mm), based on 10 specimens not strongly contracted. Ratio of length to width of prosome about 2.61: 1. Segment of leg 1 fused with head.

Urosome (fig. 101) slender. Probably three postgenital segments, but their separation obscure, particularly between last two segments.

Caudal ramus (fig. 102) small, lobate, without distinct articulation with anal segment and bearing three spinules on dorsal surface (ventral surface smooth).

Surfaces of prosome and urosome apparently unornamented, though wrinkled condition of cuticula in preserved specimens makes this difficult to determine. Ratio of length of prosome to that of urosome (in specimen shown in fig. 100) about 1.40 : 1.

Rostrum (fig. 105) a tumid lobe as in female.

First antenna (fig. 103) 1-segmented, very short, about 44μ long, with 13 short terminal spines. Second antenna (fig. 104) probably 3-segmented (segmentation suggested by sclerites, no clear articulations present), about 64μ long. Last segment with eight short spines. External to base of second antenna and behind first antenna a conspicuous lobe (fig. 105), as in female.

Labrum a bulbous area between and behind second antennae, in ventral view (fig. 105) somewhat triangular and attached to a triangular sclerotized framework. Postlabral region forming a fold that slightly overlaps posterior end of labrum. Mouth region apparently located between labrum and postlabral fold. Mandibles, paragnaths, and first maxillae not discernible and apparently absent. Second maxilla (fig. 106) a well-sclerotized recurved hook with a broad base perhaps representing a basal segment. Maxilliped (figs. 107, 108) with a prominent 1-segmented basal area bearing a well-sclerotized short clawlike tip.

Legs 1 and 2 similar in form, each leg far removed from its opposite member, without an intercoxal plate. Leg 1 (fig. 109), located near maxilliped (see fig. 105), with an indefinitely defined protopodal area, a slender setiform unsegmented exopod, and a rather weakly sclerotized unsegmented endopod bearing a single blunt hyaline seta (its articulation indistinct). Leg 3 (fig. 110) consisting of a single seta 22μ in length. Leg 4 absent.

Leg 5 absent.

Leg 6 (figs. 101, 111) consisting of a posteroventral flap on genital segment bearing a well-sclerotized spinous process and two setae 16μ and 22μ in length.

Spermatophores not formed in bodies of these small males.

Color in life, in transmitted light, opaque and grayish, eye not clearly visible.

LARGE MATURE MALE.—In the following description features not mentioned may be regarded as similar to those of the small male already described.

Body (fig. 112) elongated, vermiform, and contractile as in small male. Length (without setae on caudal rami) 2.04 mm (1.86–2.21 mm) and greatest width 0.46 mm (0.41–0.51 mm), based on 10 specimens. (Two other specimens much smaller, 0.69 x 0.18 mm and 0.86 x 0.18 mm). Ratio of length of prosome to that of urosome about 2.60:1.

Four postgenital segments, their separation more distinct than in small male.

Caudal ramus resembling that of small male but a little longer.

Ratio of length of prosome to that of urosome (in specimen shown in fig. 112) about 1.43:1.

Rostrum (figs. 113, 114) similar to that in female and in small male.

First antenna, second antenna, labrum, and postlabral fold as in small male. Mandibles, paragnaths, and first maxillae absent. Second maxillae (figs. 113, 115) represented by small well-sclerotized spinous processes. Maxilliped absent.

Legs 1–3 as in small male. Legs 4 and 5 absent.

Leg 6 (fig. 112) protruding a little more laterally, edge of posteroventral flap less sclerotized, and two setae relatively shorter (15μ and 18μ) than in small male.

Spermatophores fairly well developed inside about two-thirds of large males.

Color in life in transmitted light similar to that of small male.

ETYMOLOGY.—The specific name *corallophilus*, from the Greek words κόραλλον=coral and φίλος=loving, alludes to the association of this species with a coral.

SPECIFIC IDENTITY OF FEMALES, SMALL MALES, AND LARGE MALES.—The differences in external anatomy between males and females of *Rhynchomolgus corallophilus* are so striking that the question arises whether or not they represent opposite sexes of the same species. One can not fail to be impressed by the great difference between the males and females in body form, the nature of the first and second antennae, the labrum, the mouthparts (with mandibles, paragnaths, and first maxillae absent in males), and the form of legs 1–5 (with legs 4 and 5 absent in males). The differences in the second maxillae and maxillipeds in the two kinds of males (with the maxillipeds absent in large males) also contribute to the impression that they represent separate forms.

Since no specimens in our collections were in amplexus, judgment in respect to their specific identity must be made on other grounds than sexual behavior.

We believe that the three groups of specimens represent one species, *R. corallophilus*, for several reasons based on their external anatomy. Both kinds of males and the females have a similar snoutlike rostrum and all possess a prominent lobe external to the base of the second antenna. The small males and large males, differing in their second maxillae (reduced to a spinous process in large males) and maxillipeds (absent in large males), are otherwise similar in their appendages. It is our opinion that the small males are immature, and represent the last pre-adult instar. This interpretation is based on the facts that in small males there seem to be, at most, three postgenital segments and the body does not contain formed spermatophores, while in large males there are four postgenital segments and there are often partly formed spermatophores within. A molt from the small immature male to the large mature male would have to be presumed in order to account for the reduction in the second maxilla and the loss of the maxilliped.

Further justification for considering all three groups as one species may be found in the circumstantial evidence of the numbers of specimens collected. It would seem unlikely, if the males and females represent separate species, that large numbers of females of one species and large numbers of males of the other species would occur together in the same host without there being at least a few of the opposite sex in each case. For this to happen it would be necessary to suppose a very unequal and improbable sex ratio. We therefore conclude that only one species is involved and that all the specimens represent *R. corallophilus.*

METHOD OF COLLECTION AND RELATION TO HOST.—*Rhynchomolgus corallophilus* apparently lives inside the polyps of the coral. When pieces of the coral were washed intact in alcoholized sea water within one or two hours after being brought into the laboratory, none of these copepods were obtained. After allowing the coral to remain overnight in the alcoholized sea water, considerable numbers were recovered from the sediment. After subsequently crushing the coral, still more *R. corallophilus* were found.

SYSTEMATIC POSITION OF THE NEW GENUS.—Several features of the female of *Rhynchomolgus* suggest that the genus belongs to the family Lichomolgidae. The mandible is lichomolgid in form, resembling rather closely that of *Lichomolgus rhadinus.* The second antenna, labrum, first maxilla, second maxilla, and maxilliped are also basically lichomolgid. The 5-segmented first antenna has fewer segments than in most other lichomolgid genera (where the number of segments is commonly seven). Apparently the reduction in the number of segments in *Rhynchomolgus* has involved the loss of segments 3 and 4, since the arrangement of the setae and aesthetes on the five segments corresponds rather closely (particularly on segments 3–5) to the pattern seen on segments 1, 2, 5, 6, and 7 of the 7-segmented first antenna of *Lichomolgus* and other lichomolgid genera.

There are obvious differences in legs 1–4 between the female of *Rhynchomolgus* and other lichomolgid genera, but these may be attributed to reduction associated with a parasitic way of life. Reduction of legs 1–4, so pronounced in both sexes of *Rhynchomolgus,* is known to occur to a lesser extent in certain other parasitic or associated lichomolgid genera, for example, in *Meomicola* Stock, Humes and Gooding, 1964, and in a new genus from zoanthid coelenterates whose description by Humes and Ho is in press.

Since the male of *Rhynchomolgus* lacks mandibles, paragnaths, and first maxillae, it is more difficult in this sex to demonstrate lichomolgid affinities. The sexual dimorphism seen in the first antenna, second antenna, second maxilla, and maxilliped makes comparison uncertain. However, following our opinion expressed above on the specific identity of the males and females, the males are included with the females as one species in the lichomolgid genus *Rhynchomolgus.* As far as known, no other genus of the Lichomolgidae lacks mandibles, paragnaths, and first maxillae in the male.

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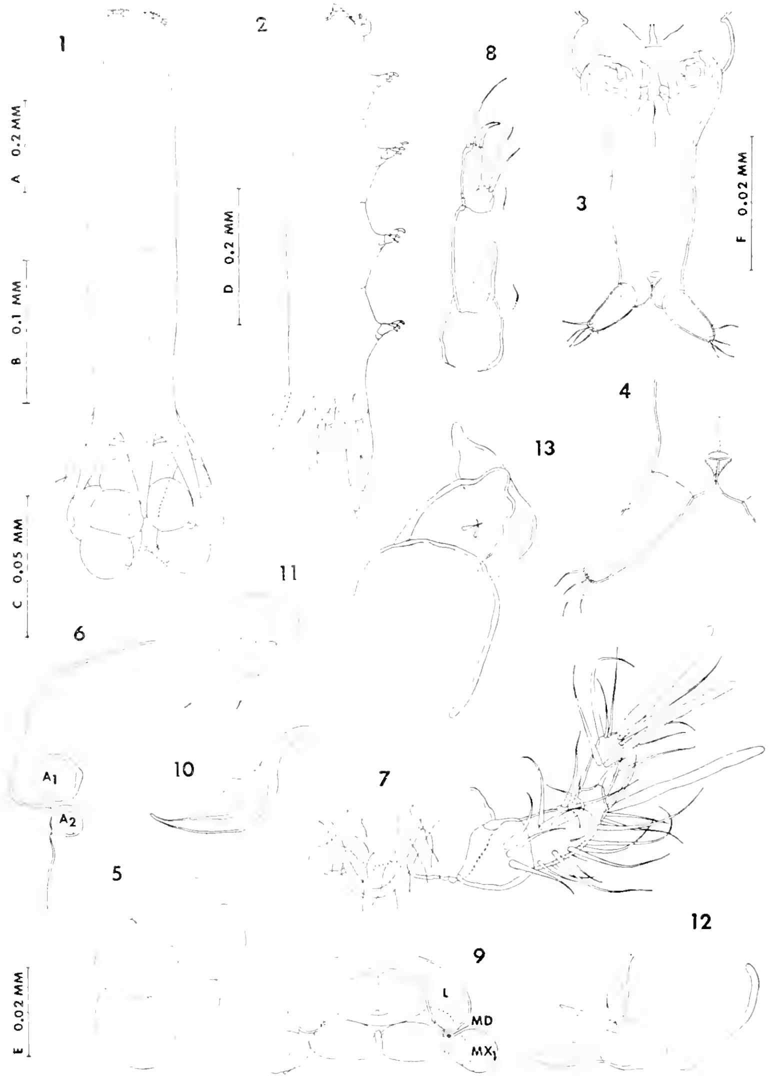
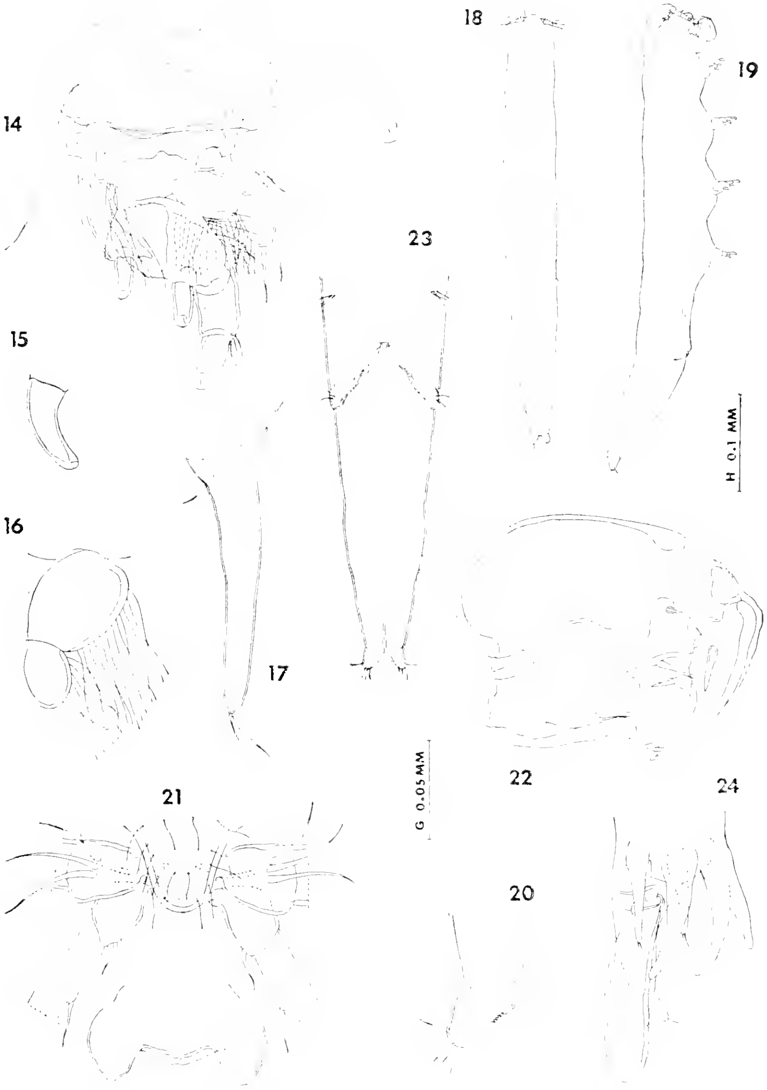
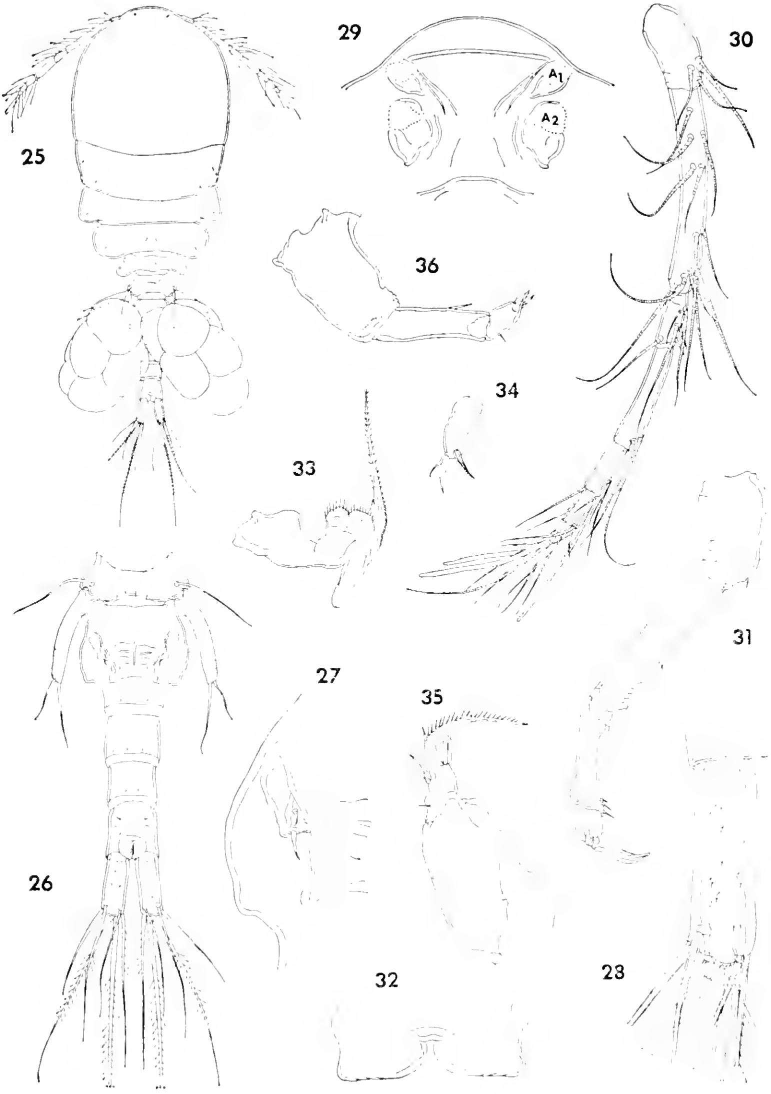


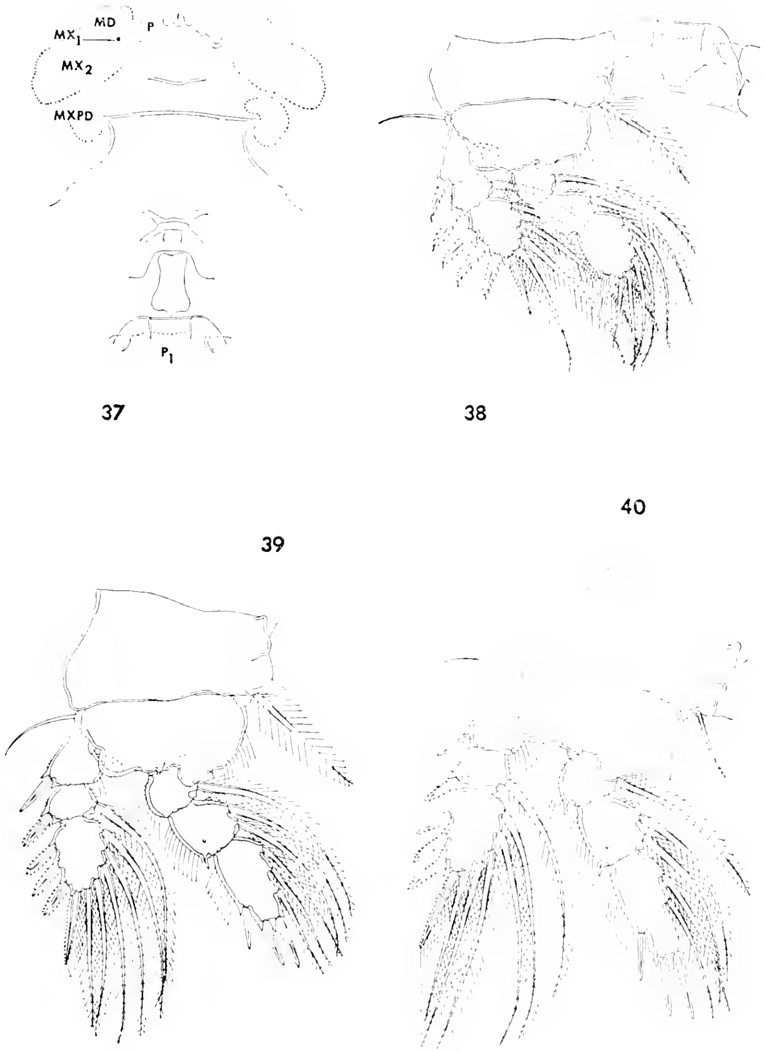
FIGURES 1–13.—*Xarifia diminuta,* new species, female: 1, dorsal (A); 2, lateral (A); 3, genital and postgenital segments, dorsal (B); 4, caudal ramus, dorsal (C); 5, egg sac, lateral (D); 6, outline of rostrum, lateral (C); 7, rostrum and first antenna, anterodorsal (E); 8, second antenna, lateral (E); 9, labrum, posteroventral (E); 10, mandible, anterior (F); 11, first maxilla, ventral (F); 12, second maxilla, anterior (F); 13, maxilliped, anterior (F).



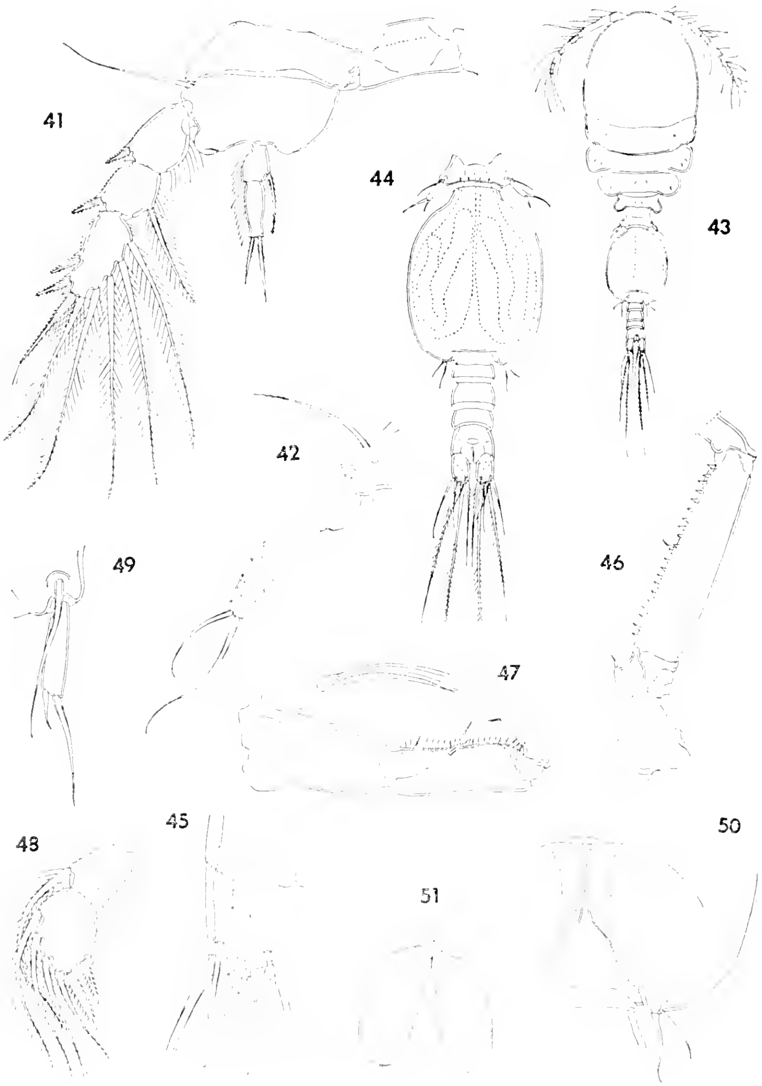
FIGURES 14–24.—*Xarifia diminuta*, new species, female: 14, leg 1 and intercoxal plate, posterior (E); 15, terminal spine on exopod of leg 1, lateral (E); 16, endopod of leg 3 posterior (F); 17, leg 5, medial (G). Male: 18, dorsal (A); 19, lateral (A); 20, caudal ramus, dorsal (C); 21, rostral area and labrum, anterior (E); 22, maxilliped, medial (E); 23, urosome, ventral (H); 24, spermatophore, attached to female, lateral (D).



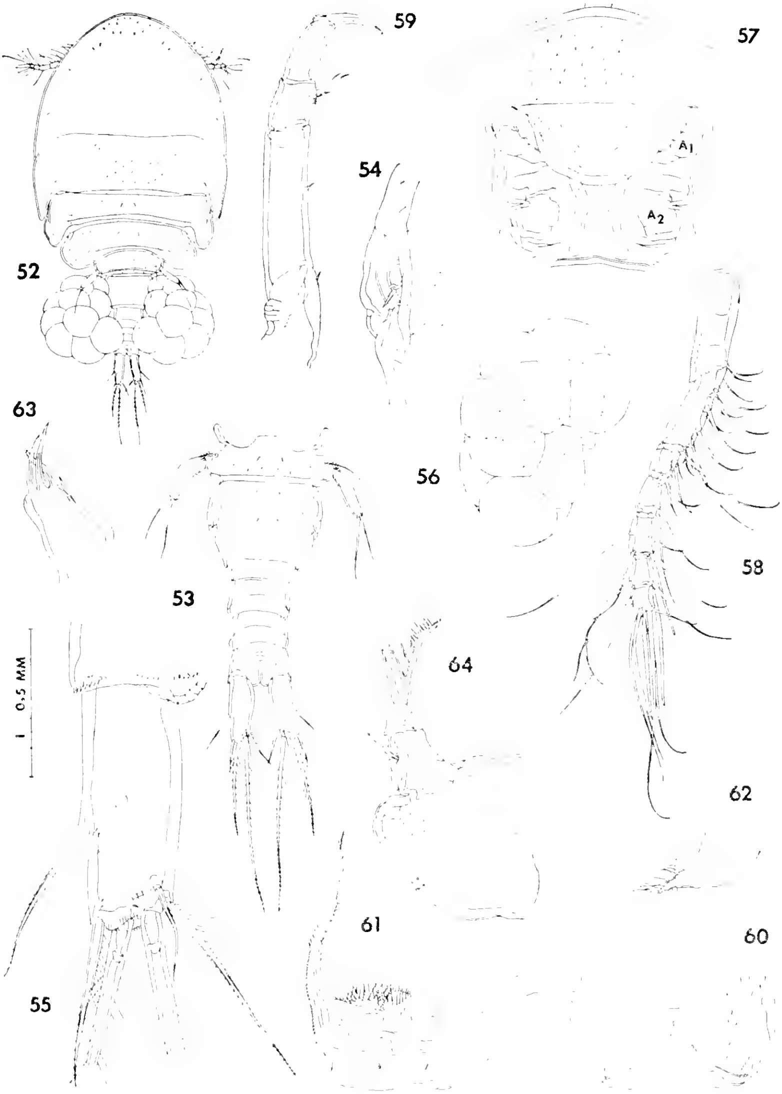
FIGURES 25–36.—*Lichomolgus rhadinus*, new species, female: 25, dorsal (A); 26, urosome, dorsal (H); 27, area of attachment of egg sac, dorsal (C); 28, caudal ramus, dorsal (C); 29, rostral area, ventral (B); 30, first antenna, dorsal (G); 31, second antenna, inner (G); 32, labrum, ventral (C); 33, mandible, anterior (C); 34, first maxilla, lateral (C); 35, second maxilla, anterior (C); 36, maxilliped, anterolateral (C).



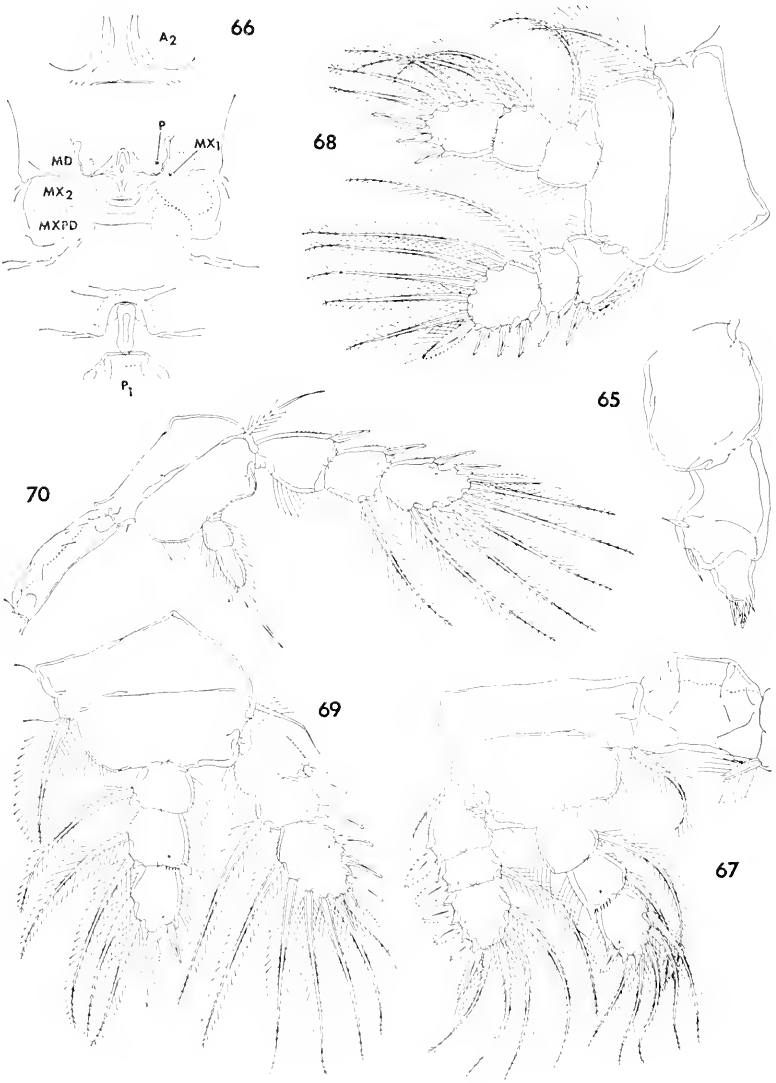
FIGURES 37–40.—*Lichomolgus rhadinus*, new species, female: 37, postoral area, ventral (G); 38, leg 1 and intercoxal plate, anterior (G); 39, leg 2, anterior (G); 40, leg 3, anterior (G).



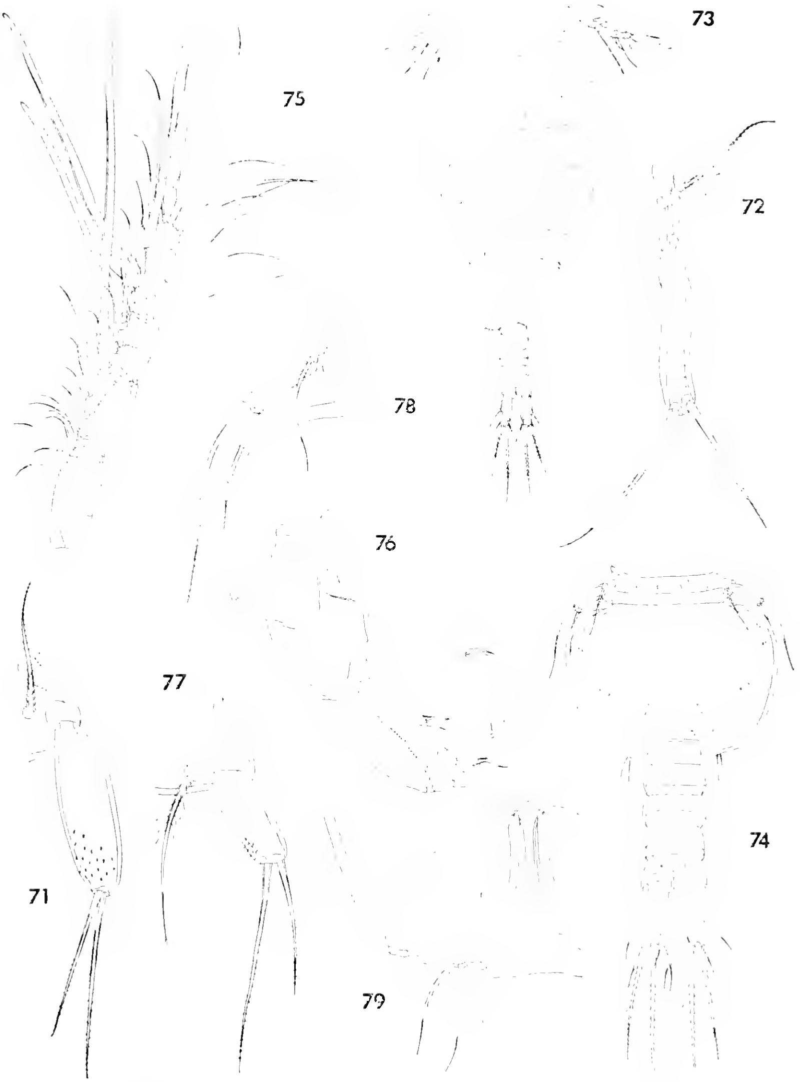
Figures 41–51.—*Lichomolgus rhadinus*, new species, female: 41, leg 4 and intercoxal plate, anterior (G); 42, leg 5, dorsal (G). Male: 43, dorsal (A); 44, urosome, dorsal (H); 45, caudal ramus, dorsal (E); 46, first two segments of second antenna, inner (C); 47, maxilliped, outer (G); 48, last two segments of endopod of leg 1, anterior (C); 49, leg 5, dorsal (E); 50, leg 6, ventral (C); 51, spermatophore, attached to female, lateral (H).



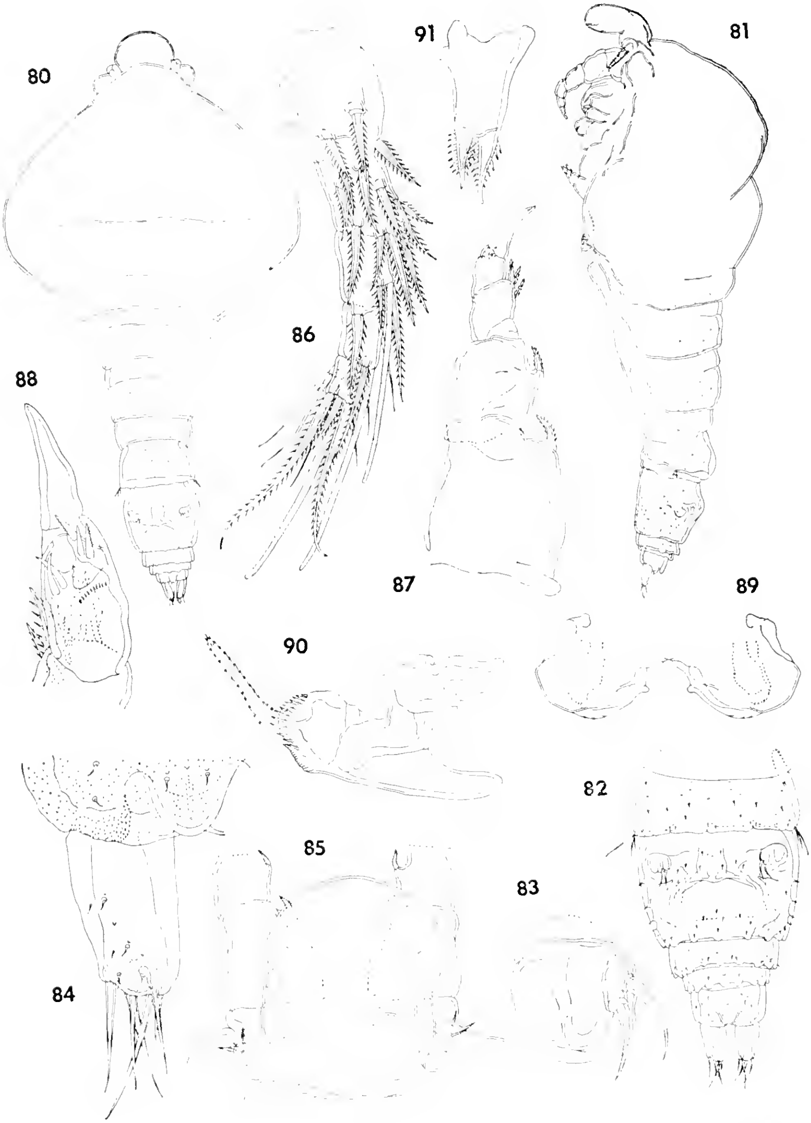
Figures 52–64.—*Monomolgus psammocorae*, new species, female: 52, dorsal (I); 53, urosome, dorsal (D); 54, area of attachment of egg sac, dorsal (C); 55, caudal ramus, dorsal (C); 56, egg sac, lateromedial (D); 57, rostral area, ventral (H); 58, first antenna, ventral (B); 59, second antenna, posterolateral (B); 60, labrum, ventral (G); 61, mandible, posterior (C); 62, paragnath, anterior (E); 63, first maxilla, posterior (C); 64, second maxilla, anterior (C).



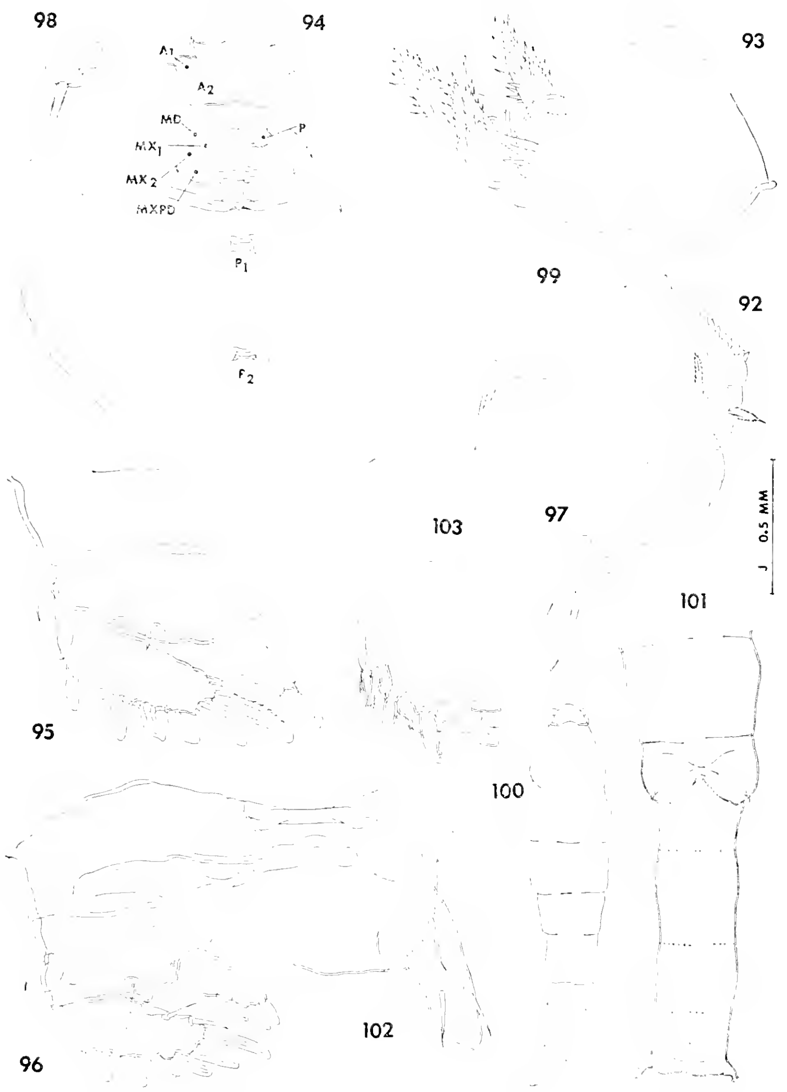
FIGURES 65–70.—*Monomolgus psammocorae*, new species, female: 65, maxilliped, anteromedial (C); 66, oral and postoral area, ventral (H); 67, leg 1 and intercoxal plate, anterior, (B); 68, leg 2, anterior (B); 69, leg 3, anterior (B); 70, leg 4 and intercoxal plate, anterior (B).



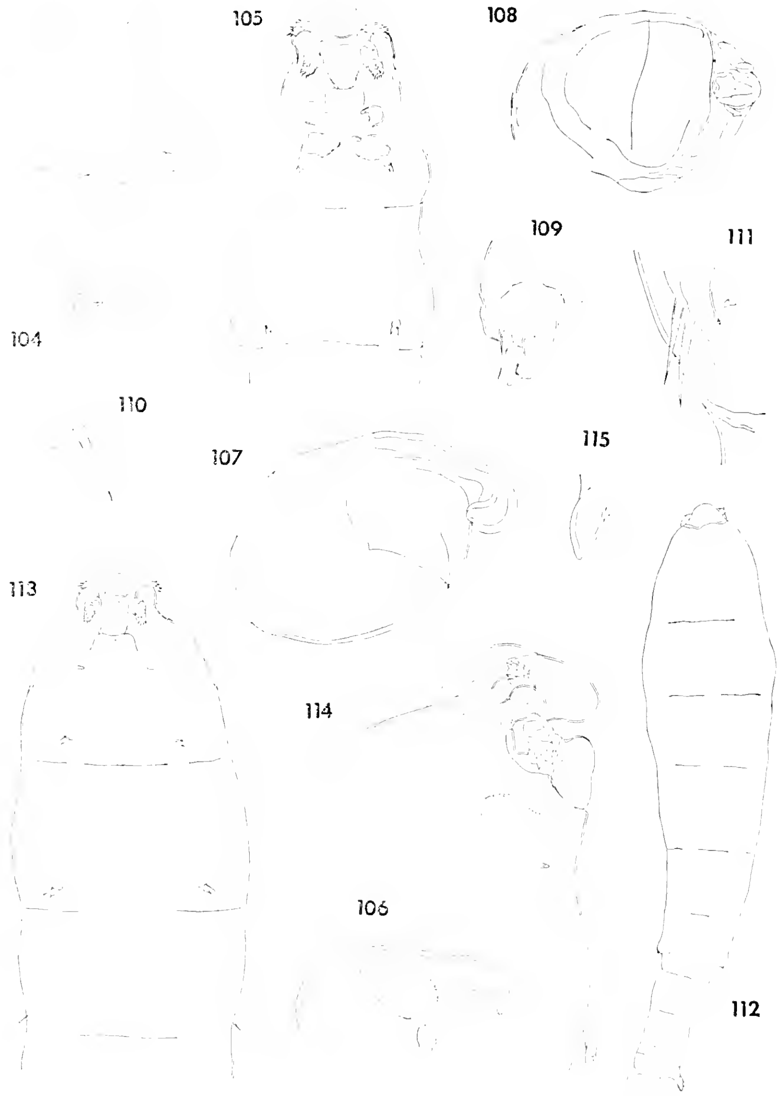
FIGURES 71–79.—*Monomolgus psammocorae*, new species, female: 71, leg 5, anterior (G); 72, leg 5, dorsal (G). Male: 73, dorsal (A); 74, urosome, dorsal (H); 75, first antenna, dorsal (G); 76, maxilliped, inner (C); 77, leg 5, somewhat anterior (C); 78, leg 5, dorsal (C); 79, leg 6, ventral (G).



Figures 80–91.—*Rhynchomolgus corallophilus*, new species, female: 80, dorsal (A); 81, lateral (A); 82, urosome, with postgenital segments telescoped, dorsal (H); 83, area of attachment of egg sac, dorsal (E); 84, caudal ramus, dorsal (E); 85, rostrum, dorsal (B); 86, first antenna, anterodorsal (E); 87, second antenna, anterior (G); 88, terminal segment and claw of second antenna, lateral (G); 89, labrum, ventral (G); 90, mandible, anterior (C); 91, first maxilla, anterior (E).



FIGURES 92–103.—*Rhynchomolgus corallophilus*, new species, female: 92, second maxilla, anterior (C); 93, maxilliped, posterior (E); 94, anterior part of body, ventral (D); 95, leg 1, anterior (E); 96, leg 2 and intercoxal plate, posterior (E); 97, leg 3, left side, ventral (E); 98, leg 4, left side, ventral (E); 99, leg 5, dorsal (E). Small immature male: 100, dorsal (J); 101, urosome, ventral (D); 102, caudal ramus, dorsal (E); 103, first antenna, ventral (E).



Figures 104–115.—*Rhynchomolgus corallophilus*, new species, small immature male: 104, second antenna, medial (E); 105, anterior part of body, ventral (D); 106, second maxilla, anterior (E); 107, maxilliped, ventral and slightly lateral (E); 108, maxilliped, ventra (E); 109, leg 1, ventral and somewhat anterior (E); 110, leg 3, ventral (E); 111, leg 6, ventral (E). Large mature male: 112, dorsal (J); 113, anterior part of body, ventral (A); 114, cephalosome, lateral (H); 115, second maxilla, ventral (E).

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A NEW GENUS AND THREE NEW SPECIES OF OSTRACODS WITH A KEY TO GENUS DACTYLOCYTHERE (OSTRACODA: ENTOCYTHERIDAE)

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The two genera treated here appear to be restricted to the eastern part of the United States. The new genus *Ornithocythere* is represented by a single species that ranges from the Dismal Swamp, Virginia, northward to the vicinity of Baltimore, Maryland, and, insofar as is known, is found only on burrowing crayfishes. The much more widely distributed *Dactylocythere* ranges from New Jersey and Kentucky southward to Alabama, where most of the species are known from the mountains, Cumberland Plateau, and the piedmont area. The range of the genus is perhaps more extensive than present records indicate, for one of the species described here is the first to be recorded from the lower coastal plain; its range extends from North Carolina to New Jersey. This ostracod, like the one mentioned above is known only from burrowing crayfishes. The third species, also a member of the genus *Dactylocythere*, is presently known from a single locality in the Greenbrier drainage system in West Virginia, where it was found on perhaps the commonest crayfish in the Appalachian Mountains, *Cambarus b. bartonii* (Fabricius).

Because no key exists to aid in the identification of the species of the genus *Dactylocythere*, an artificial one is presented as an introduction to the two members described here.

I wish to thank the following persons who have contributed specimens on which these three new species are based: Dr. Jean E. Pugh, Mr. C. W. Hart, Jr., Mr. Mark Odell, and Mr. John M. Rutherford.

***Ornithocythere*, new genus**

DIAGNOSIS.—Terminal tooth of mandible with cusps. Copulatory complex of male without finger guard; peniferum resembling inverted head of bird; ventral portion of peniferum with heavily sclerotized beaklike prominence directed anterodorsally; base of beak provided with subcircular aperture, through which presumably tip of penis emerges to surface. Penis complex with spermatic and prostatic portions contiguous throughout their length, not separated as in members of *Ascetocythere;* penis complex slightly longer than half anterior-posterior dimension of peniferum at level of base of penis. Clasping apparatus not clearly divisible into vertical and horizontal rami, with proximal and distal portions disposed at angle of approximately 60°; vertical ramus convex posteriorly with internal and external borders entire; horizontal ramus with external border entire and internal border with four evenly spaced teeth; ramus terminating in four denticles.

TYPE-SPECIES.—*Ornithocythere waltonae*, new species.

REMARKS.—The most distinctive feature of this monotypic genus is the sclerotized beaklike prominence of the peniferum (see "Relationships" under *O. waltonae*).

GENDER.—Feminine.

NAME.—From the Greek "ornis," meaning bird, plus generic name *cythere*, alluding to the resemblance of the peniferum to the head and neck of a bird.

***Ornithocythere waltonae*, new species**

MALE.—Eye present. Shell (fig. 1*b*) highest posterior to midlength with dorsal margin tapering ventrally only slightly less suddenly anteriorly than posteriorly; ventral margin of shell entire; submarginal setae rather evenly spaced anteriorly, ventrally, and posteriorly, very few dorsally.

Copulatory complex (fig. 1*a*): As described in generic diagnosis; in addition, dorsal finger moderately slender with apex reaching level of base of penis complex; ventral finger slender and subparallel to clasping apparatus, latter extending ventrally only slightly beyond ventral margin of peniferum.

FEMALE.—Eye present (not illustrated because destroyed in allotype). Shell of triunguis female (fig. 1*c*) distinctly larger than that of male with maximum height posterior to midlength; ventral margin of shell with distinct emargination just anterior to midlength;

submarginal setae as in male although somewhat more abundant anteriorly and posteriorly. Amiculum and J-shaped rod absent but posterodorsal area with papilla projecting into cuplike cavity containing material resembling that composing J-shaped rod of members of genus *Dactylocythere*.

MEASUREMENTS (in millimeters).—

	holotype	*males*	*allotype*	*females*
number of specimens		10		10
length (range)	0.49	0.47–0.50	0.52	0.49–0.52
average		0.49		0.51
height (range)	0.27	0.25–0.27	0.30	0.28–0.31
average		0.27		0.30

TYPE-LOCALITY.—Roadside ditch at Acerdale, 0.4 mile from junction of Great Bridge and Indian River, Princess Anne County, Virginia. Specimens removed from collection of crayfishes dug from burrows.

DISPOSITION OF TYPES.—The holotypic male, the allotypic female, and a dissected male paratype are deposited in the United States National Museum, 113472, 113473, 113474, respectively. Paratypes are in the collections of Mr. C. W. Hart, Jr., and in the joint collection of Miss Margaret Walton and the author.

RANGE.—In addition to the type-locality, *O. waltonae* is known from the following: (1) a roadside ditch across from Stumpy Lake on State Rte. 605, Virginia Beach, Princess Anne Co., Va.; (2) Landstown Road off Princess Anne Road, Virginia Beach, Princess Anne Co., Va.; (3) roadside ditch near Great Bridge, Norfolk Co., Va.; (4) Lyells, Rte. 202, Northumberland Co., Va.; (5) 2.5 mi. north of Davidsonville, Kings Branch at Sands Road, Ann Arundel Co., Md.; (6) 9.3 mi. east of Lyells, Rte. 202, Northumberland Co., Va.; (7) 6.4 mi. east of West Point on St. Rte. 14, King and Queen Co., Va.; (8) 9.5 mi. north of Surry Court House, Surry Co., Va.

HOSTS.—In the type-locality *O. waltonae* was found on *Procambarus a. acutus* (Girard) and *Cambarus d. diogenes* Girard. In all of the other localities it was found on the latter.

RELATIONSHIPS.—*Ornithocythere waltonae* seems to be most closely allied to *Okriocythere cheia* Hart (1964, p. 243) and to members of the genus *Geocythere*. The chief resemblance is in the penis complex, which consists of separated prostatic and spermatic elements. In all of these species the two elements, although distinct, are intimately associated throughout the length of the prostatic element. Somewhat more distantly related are the members of the genera *Ascetocythere* and *Plectocythere*. It differs from all of them in possessing a beaklike prominence on the antrodistal extremity of the peniferum.

OSTRACOD ASSOCIATES.—This species was associated with *Dactylocythere jeanae*, new species, in several of the localities cited above and with *Okriocythere cheia* in the Landstown locality.

Name.—This ostracod is named in honor of my good friend and fellow student of crayfishes and entocytherid ostracods, Miss Margaret Walton.

Dactylocythere Hart

Dactylocythere Hart, 1962, Proc. Acad. Nat. Sci. Philadelphia, vol. 114, no. 3, p. 129.

With the description of the 2 new species included here, 18 species have been referred to this genus, which ranges from Kentucky and West Virginia to Alabama and from New Jersey to South Carolina. The following key will assist in the recognition of these ostracods.

Key to Species of *Dactylocythere*

1 Ventral portion of peniferum with two or more small acute projections; finger guard very slender and tridentate; clasping apparatus almost U-shaped with subterminal flare; accessory groove reduced or obsolete. **leptophylax** (Crawford, 1961, p. 238)

1′ Ventral portion of peniferum without projections; finger guard seldom slender, if tridentate, comparatively stocky; clasping apparatus variable but never with subterminal flare; accessory groove well developed 2

2(1′) Apex of clasping apparatus without denticles 3

Apex of clasping apparatus with two or more denticles 4

3(2) Clasping apparatus scythelike, sometimes with a single tooth on internal border of horizontal ramus, otherwise unadorned. **falcata** (Hobbs and Walton, 1961, p. 379)

3′ Clasping apparatus without teeth but with two or three grooves appearing to encircle distal portion of horizontal ramus. **striophylax** (Crawford, 1959, p. 157)

4(2′) Shell with posteroventral projection 18

4′ Shell without posteroventral projection 5

5(4′) Accessory groove extending dorsally much beyond level of dorsal extremity of spermatic loop 6

5′ Accessory groove never extending dorsally more than slightly beyond level or dorsal extremity of spermatic loop, sometimes not reaching loop 8

6(5) Vertical ramus of clasping apparatus distinctly arched 7

6′ Vertical ramus of clasping apparatus almost straight. **mecoscapha** (Hobbs and Walton, 1960, p. 19)

7(6) Proximal and distal ends of clasping apparatus subparallel. **prionata** (Hart and Hobbs, 1961, p. 178)

7′ Proximal and distal ends of clasping apparatus at angle of 50° to 70° to each other 19

8(5′) Dorsal margin of accessory groove not reaching spermatic loop . . 20

8′ Dorsal margin of accessory groove reaching spermatic loop, almost to or slightly beyond dorsal extremity 9

9(8′) Width of clasping apparatus at major bend more than 1.5 times least width (excluding proximal articulation) of vertical ramus 10

9′ Width of clasping apparatus at major bend less than 1.5 times least width (excluding proximal articulation) of vertical ramus 13

10(9) Horizontal ramus of clasping apparatus with one tooth on internal border . . . . **chalaza** (Hobbs and Walton, 1962, p. 45)

10′ Horizontal ramus of clasping apparatus with more than one tooth on internal border 11

11(10′) Width of clasping apparatus at major bend less than two times least width of vertical ramus . . . . **runki** (Hobbs, 1955, p. 330)

11′ Width of clasping apparatus at major bend more than two times least width of vertical ramus 12

12(11′) Peniferum with prominent hump on posterior margin paralleling accessory groove; posterior margin of finger guard strongly concave, distal end with single emargination.
xystroides (Hobbs and Walton, 1963, p. 460)

12′ Peniferum without prominent hump on posterior margin paralleling accessory groove; posterior margin of finger guard only slightly concave, distal end with two emarginations.
pachysphyrata (Hobbs and Walton, 1966, p. 3)

13(9′) Finger guard with three distinct distal tubercles 14

13′ Finger guard with less than three distinct distal tubercles 15

14(13) Posterodistal thickening of peniferum distinctly rounded with opening of peniferal groove directed anteriorly; apical portion of clasping apparatus serrate . . . . **suteri** (Crawford, 1959, p. 162)

14′ Posterodistal thickening of peniferum angular with opening of peniferal groove directed anteroventrally; apical portion of clasping apparatus with teeth but not serrate . . . **chelomata** (Crawford, 1961, p. 242)

15(13′) External border of vertical ramus of clasping apparatus with angular shoulder 16

15′ External border of vertical ramus of clasping apparatus entire, rounded. 17

16(15) Internal border of horizontal ramus of clasping apparatus with four teeth, distal extremity with two . . . . **phoxa,** new species

16′ Internal border of horizontal ramus of clasping apparatus with two teeth, distal extremity with three . . . . **jeanae,** new species

17(15′) Vertical ramus of clasping apparatus wider than horizontal ramus, extremities directed subparallel to each other.
steevesi (Hart and Hobbs, 1961, p. 180)

17′ Vertical ramus of clasping apparatus not wider than horizontal ramus, extremities directed at angle of 35° to 50°.
ungulata (Hart and Hobbs, 1961, p. 177)

18(4) Shell with anteroventral protuberance.
amphiakis Hart and Hart (1966, p. 3)

18′ Shell without anteroventral protuberance.
daphnioides (Hobbs, 1955, p. 325)

19(7′) Three proximal teeth on internal border of horizontal ramus of clasping apparatus subequal in size and equally spaced.
arcuata (Hart and Hobbs, 1961, p. 177)

19′ Proximal tooth on internal border of horizontal ramus of clasping apparatus much larger than following two and widely separated from them.
amicula Hart and Hart (1966, p. 1)

20(8) Height of horizontal ramus of clasping apparatus at level of proximal tooth almost twice that of height at level of third tooth.
brachystrix Hobbs and Walton (1966, p. 2)

20′ Height of horizontal ramus of clasping apparatus at level of proximal tooth only slightly more than that of height at level of third tooth.
exoura Hart and Hart (1966, p. 5)

***Dactylocythere jeanae*, new species**

MALE.—Eye present. Shell (fig. 1*h*) highest posterior to midlength, much higher posteriorly than anteriorly; ventral margin with very shallow excavation just anterior to midlength; submarginal setae present except dorsally and closer together anteriorly and posteriorly than ventrally.

Copulatory complex (fig. 1*g*): Peniferum with thickened, rounded, ventral extremity; accessory groove extending posterodorsally to level of dorsal extremity of spermatic loop; penis L-shaped with bulbous area in horizontal position and subequal in length to slender, terminal vertical portion. Finger guard essentially bifid with anterior ramus longer than posterior. Dorsal finger comparatively heavy with apical part appearing bifid (probably spatulate); ventral finger slender and gently curved to base of terminal "segment." Clasping apparatus with extensions of two rami forming angle of 60° to 80° and without thickening at their junction; vertical ramus with angular prominence just proximal to midlength of posterior surface, anterior border entire; horizontal ramus with external (ventral) border entire and internal border with two teeth on distal third; apex with three dorsodistally directed denticles.

FEMALE.—Eye present. Shell (fig. 1*i*) highest posterior to midlength and much higher posteriorly than anteriorly, ventral margin with distinct concavity anterior to midlength. Submarginal setae present except dorsally from level of eye to amiculum. Amiculum and J-shaped rod present; however, latter often resembles inverted L more than usual J.

MEASUREMENTS (in millimeters).—

	holotype	*males*	*allotype*	*females*
number of specimens		10		10
length (range)	0.50	0.46–0.51	0.56	0.49–0.56
average		0.49		0.50
height (range)	0.29	0.27–0.29	0.34	0.26–0.34
average		0.28		0.30

TYPE-LOCALITY.—Roadside ditch in Virginia Beach on Rte. 605, near Stumpy Lake, Princess Anne County, Virginia. Specimens removed from crayfishes dug from burrows.

DISPOSITION OF TYPES.—The holotypic male, and allotypic female (113475) and a dissected paratypic male (113476) are deposited in the United States National Museum. Paratypes are in the collection of Mr. C. W. Hart, Jr., and in the joint collection of Miss Margaret Walton and the author.

RANGE.—Other localities from which specimens were collected are: (1) 3.5 mi. north of Snow Hill on Rte. 258, Greene Co., N.C.; (2) Landstown Road, off Princess Anne Road, Virginia Beach, Princess

Anne Co., Va.; (3) Acerdale, Princess Anne Co., Va.; (4) 9.5 mi. north of Surry Court House, Surry Co., Va.; (5) underground spring near

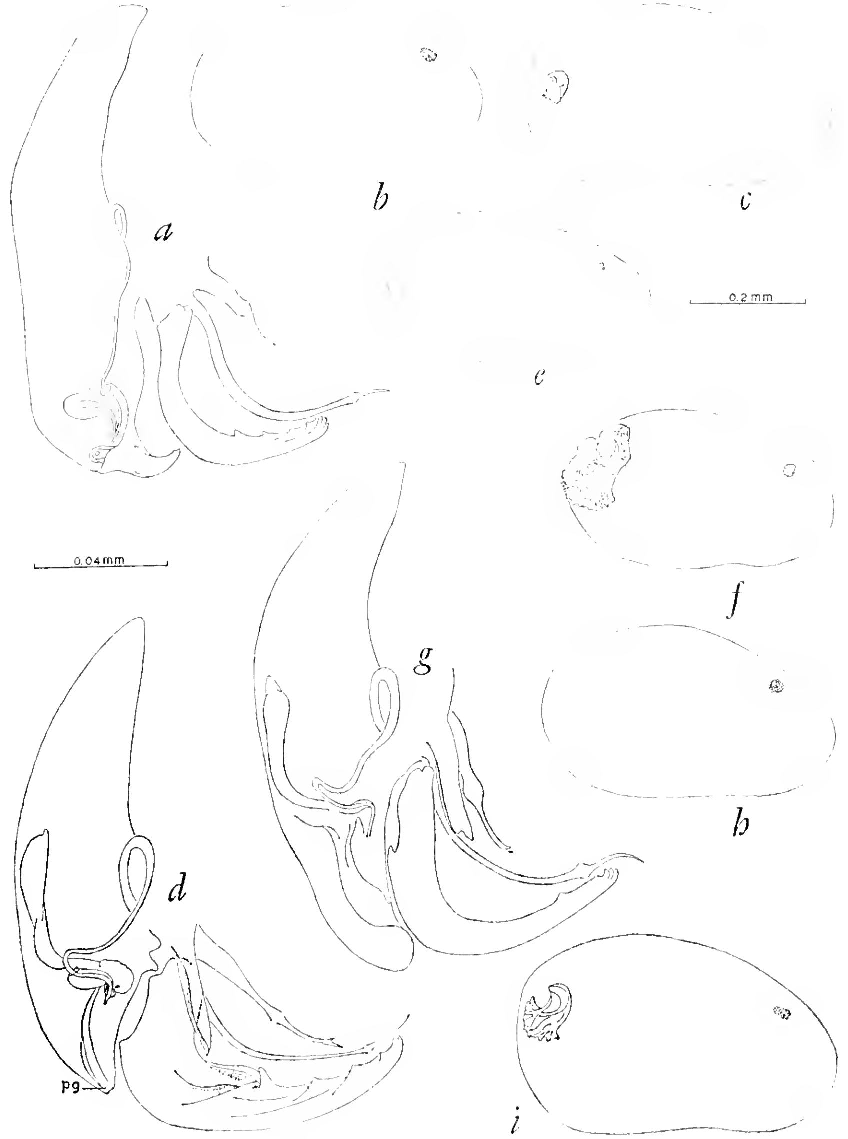

Figure 1.—*Ornithocythere waltonae*, new species: *a*, copulatory complex; *b*, right valve of holotype; *c*, right valve of allotype. *Dactylocythere phoxa*, new species: *d*, copulatory complex; *e*, right valve of holotype; *f*, right valve of allotype. *Dactylocythere jeanae*, new species: *g*, copulatory complex; *h*, right valve of holotype; *i*, right valve of allotype.

James River, James City Co., Va.; (6) 6.4 mi. east of West Point on St. Rte. 14, King and Queen Co., Va.; (7) backwater of South Anna

River on Rte. 22, Louisa Co., Va.; (8) Lyells, Rte. 202, Northumberland Co., Va.; (9) Seaview, Northampton Co., Va.; (10) "1 mile above D.C.," Fairfax Co., Va. (11) Howard University Reservoir, Washington, D.C.; (12) tributary to east branch of the Potomac, Burville, D.C.; (13) Plummer's Island, Potomac River, Montgomery Co., Md.; (14) Laurel, Prince Georges Co., Md.; (15) 7 mi. west of Bridgeton, Cumberland Co., N.J.

HOSTS.—*Cambarus diogenes diogenes* Girard was the host, or one of the hosts, in all of the localities cited, and in the type-locality *D. jeanae* was also found on *Procambarus acutus acutus* (Girard).

OSTRACOD ASSOCIATES.—In the type-locality and in localities 2, 3, 4, 6, and 8, listed above, *D. jeanae* was associated with *Ornithocythere waltonae* and in locality 2 with *Okriocythere cheia* Hart (1964, p. 243). At locality 13 it was found with *Ankylocythere tridentata* Hart (1964, p. 245).

RELATIONSHIPS.—Without a doubt, *Dactylocythere jeanae* has its closest affinities with *D. suteri* (Crawford, 1959, p. 162). Their penifera are distinctly similar and the tapering, L-shaped clasping apparatus without a thickening at the junction of the two rami is found in only two other species of the genus, *D. chelomata* (Crawford, 1961, p. 242) and *D. striophylax* (Crawford, 1959, p. 157). The structure of the penifera of the latter two, however, suggests that *D. jeanae* is not nearly so closely related to them as to *D. suteri*. The combination of an angular hump on the posterior side of the vertical ramus of the clasping apparatus, two teeth on the internal border of the horizontal ramus, a bifid finger guard, and a rounded anteroventral portion of the peniferum is unique in *D. jeanae*.

NAME.—This species is named in honor of its discoverer and a member of my academic family, Dr. Jean E. Pugh, who through her contribution of many crayfishes and ostracods to the national collection has added much to our knowledge of both groups.

***Dactylocythere phoxa*, new species**

MALE.—Eye present. Shell (fig. 1*e*) highest posterior to midlength, dorsal margin tapering ventrally much more suddenly posteriorly than anteriorly; ventral margin of shell with only a slight concavity just anterior to midlength; submarginal setae evenly spaced except dorsally where absent; length 0.46 mm, height 0.26 mm.

Copulatory complex (fig. 1*d*): Peniferum with ventrally and slightly anteriorly directed subacute apex; apical portion of peniferal groove (pg) directed more strongly ventrally than that in other members of the genus, width of groove at apex about ⅛ of maximum anterior-posterior diameter of vertical ramus of clasping apparatus; accessory groove extending posterodorsally to level of dorsal extremity of spermatic loop; penis L-shaped, with bulbous area in horizontal plane and distinctly longer than slender vertical portion. Finger guard simple with distinct groove extending from base to distal end along posterior surface. Dorsal finger comparatively slender with bifid tip; ventral finger gently curved but with long, nearly straight portion just proximal to bulbous area. Clasping apparatus L-shaped with subangular hump at posterior junction of two rami; external borders of both rami and internal border of vertical ramus entire. Internal border of horizontal ramus with comparatively long conical tooth near midlength and three low, but pointed, teeth along distal half; apex of ramus with two teeth.

Female.—Eye present. Shell (fig. 1*f*) subreniform with proximal emargination ventrally; submarginal setae present except dorsally between levels of eye and amiculum, nowhere conspicuously abundant. Amiculum and J-shaped rod present; amiculum, although partially obscured by adhering debris, fully ruffled and extending beyond posterodorsal margin of shell; length 0.46 mm, height 0.28 mm.

Type-locality and range.—Known only from a small stream immediately east of Maxwelton, Greenbrier County, West Virginia.

Disposition of types.—The unique holotypic male and allotypic female are deposited in the United States National Museum, 113477 and 113478, respectively.

Host.—*Cambarus b. bartonii* (Fabricius) was the only crayfish present in the collection from which the type specimens were removed.

Ostracod associates.—None.

Relationships.—*Dactylocythere phoxa* is most closely related to *D. daphniodes* and *D. runki* but differs from both in possessing a short vertical ramus of the clasping apparatus, and the proximal tooth on the internal border of the horizontal ramus is conical rather than saw-toothed. The narrow, almost ventrally directed peniferal groove is not found in any other member of the genus.

Name.—From the Greek "phoxas," meaning pointed, so named because of the prominent pointed proximal tooth on the internal border of the horizontal ramus of the clasping apparatus.

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VARIATION AND DISTRIBUTION OF THE PELAGIC AMPHIPOD CYPHOCARIS CHALLENGERI IN THE NORTHEAST PACIFIC (GAMMARIDEA: LYSIANASSIDAE)

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The most common epipelagic gammaridean amphipod in Subarctic Water of the North Pacific is *Cyphocaris challengeri* Stebbing (1888, pp. 661–664, pl. 17). Other species of *Cyphocaris* occur in the North Pacific but are usually found at deeper levels than *C. challengeri.*

Altho the original description by Stebbing was detailed and well illustrated, it was based on a single juvenile specimen only about 5 mm long. The species was subsequently reported from the North and South Atlantic, the South Pacific, and the Indian Ocean but was not again recorded from the North Pacific until Thorsteinson (1941) reported its presence at Nanaimo, British Columbia. Its occurrence in the western North Pacific has been discussed recently by Birstein and Vinogradov (1955, 1958), who provided a map showing its worldwide distribution (1955, fig. 33).

In addition to recording the presence of *C. challengeri* at Nanaimo and giving some data on its variation with age, Thorsteinson described *C. kincaidi* from the Gulf of Alaska. Thorsteinson's new species was said to differ from *C. challengeri* in the more sharply produced pereonite 1, the more numerous setae on the gnathopods, the longer and narrower process of the basis of pereopod 5, and the longer telson.

It has been shown that certain characters of *C. challengeri* change with age: (1) In all species of *Cyphocaris* the head is directed downward and partly covered above by the long pereonite 1, which is produced anteriorly into a process. The process varies in shape from low and bluntly rounded to long and sharply pointed. The process is most acute in young specimens and becomes more rounded as a *Cyphocaris* ages (Schellenberg, 1926b). (2) The number of teeth on the posterior margin of the basis of pereopod 5 decreases with age (Chevreux, 1916; Schellenberg, 1926a; Thorsteinson, 1941). (3) The length of the process of the basis of pereopod 5 increases in proportion to the rest of the limb (Thorsteinson, 1941). (4) The length of the telson increases relative to the length of uropod 3 (Schellenberg, 1926b).

In consideration of the variation with age detailed above, Shoemaker (1945) reduced *C. kincaidi* to a junior synonym of *C. challengeri*, an action accepted by subsequent authors (Birstein and Vinogradov, 1955, 1958, 1960; Gurjanova, 1962). In recent years, however, we have examined numerous samples collected with plankton nets and Isaacs-Kidd midwater trawls off the west coast of North America, containing larger numbers of *Cyphocaris* than had been available previously. The fact that almost all of the specimens could be assigned without difficulty to either *C. challengeri* or *C. kincaidi* as defined by Thorsteinson indicated the desirability of a reassessment of Shoemaker's decision to lump them, especially since in our collections the two forms were separated geographically as well as morphologically.

We wish to thank William Aron, then of the Department of Oceanography, University of Washington, for sending us representative samples of amphipods from M/V *Brown Bear* Cruises 199 and 202, and Bruce L. Wing, U.S. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska, for midwater trawl collections from Lynn Canal, in the Alexander Archipelago, Southeast Alaska.

Distribution in the North Pacific

Since the form of the body of *C. challengeri* (sensu latu, including both *C. challengeri* and *C. kincaidi* sensu Thorsteinson) is correlated with its neritic-oceanic distribution, the neritic and oceanic distributions will be considered separately.

OCEANIC DISTRIBUTION.—Figure 1 shows the offshore distribution of *C. challengeri*, based largely on Cruises 1, 5, and 9 of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) in 1949 and Cruises 199 and 202 of the University of Washington M/V *Brown Bear* in 1958. A few records from collections by the U.S. Bureau of Fisheries Steamer *Albatross* have been included.

Altho the CalCOFI cruises extended south about to the latitude of Punta Eugenia, Baja California, almost all the stations positive for

Cyphocaris occurred north of Cape Mendocino, Calif. (about 40.3°N). Likewise, *Brown Bear* Cruise 199 occupied stations south to about 32°N, or just south of the latitude of San Diego, but collected very few *Cyphocaris* south of 38°N, the approximate latitude of San Francisco.

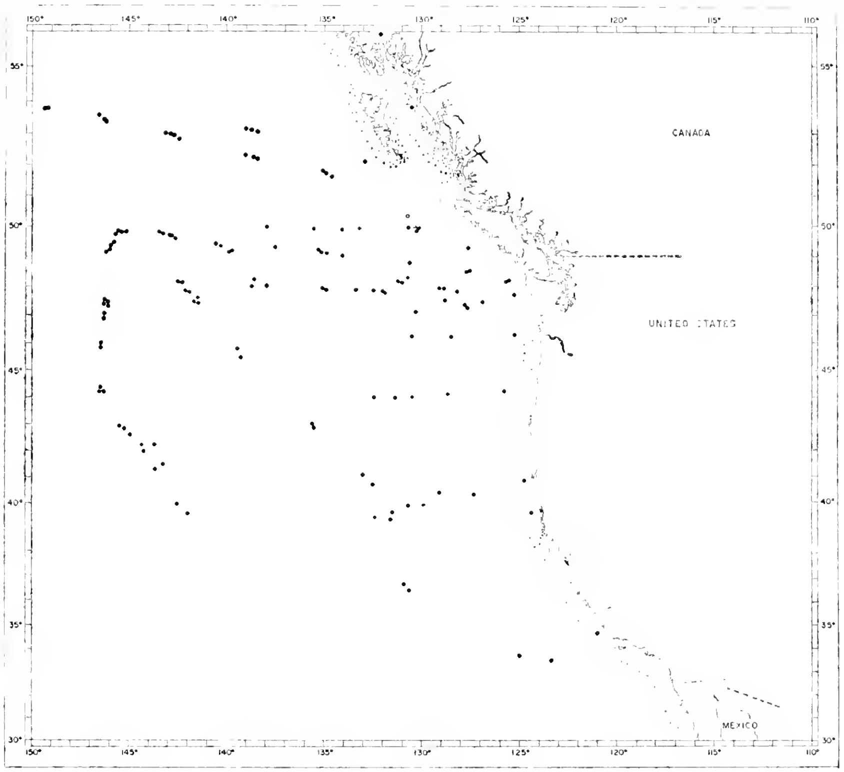

FIGURE 1.—Offshore distribution records of *Cyphocaris challengeri* in the northeastern Pacific.

The southern boundary of *C. challengeri* in the northeastern Pacific is comparable to that of other subarctic plankters: the euphausiids *Thysanoessa longipes* and *Tessarabrachion oculatus* (Brinton, 1962), and the chaetognath *Sagitta elegans* (Bieri, 1959). West of 150°W the southern boundary is not known, but presumably, as in other subarctic plankters, it runs parallel to and somewhat north of the North Pacific Drift. In the northwestern Pacific Bogorov (1958) lists *C. challengeri* as a characteristic species of the boreal plankton, the southern boundary of which approximates the convergence of the Oyashio and Kuroshio systems.

Little information is available on the depth distribution of *C. challengeri* in Subarctic Water. Birstein and Vinogradov (1955, fig. 32) show it ranging from near the surface down to 500–2000 m and possibly deeper. Bogorov (1958) refers to it as a surface zone (0–200 m) species. In CalCOFI Cruises 5 and 9, which sampled the upper 70 m with 1-m plankton nets, *C. challengeri* was taken mainly at night. Five of the six positive stations of Cruise 5 (July 1949) were night stations; an average number of 16/1000 m³ was taken at the night stations, and 1/1000 m³ at the day station. Of the 13 positive stations on Cruise 9 (November 1949), 12, with an average catch of 12/1000 m³, were night stations, whereas only 1/1000 m³ was caught at the day station. There is clearly an upward movement of the population at night.

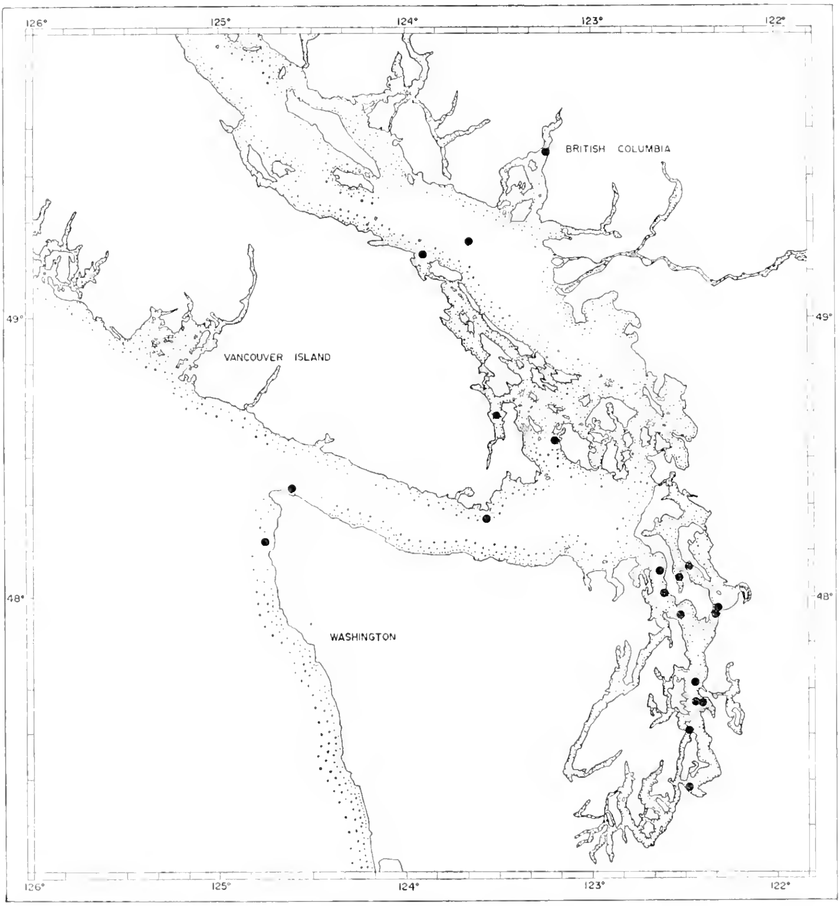

FIGURE 2.—Distribution records of *Cyphocaris challengeri* in the Puget Sound region.

Neritic distribution.—As shown in figure 2, *C. challengeri* is widespread in the Puget Sound region. To the north it also occurs in Hecate Strait and in at least some of the straits between the islands of the Alexander Archipelago. Details of its vertical distribution are poorly known, but large numbers were taken with Isaacs-Kidd trawls in the upper 100 m in Lynn Canal, Alexander Archipelago.

Global Distribution

The world-wide distributional pattern of *C. challengeri* outside of the North Pacific, shown in figure 3, is puzzling. Many zooplankton species inhabiting Subarctic Water do not occur elsewhere, for example: the polychaete worm *Tomopteris pacificus* (Tebble, 1962); the copepods *Calanus cristatus*, *C. plumchrus*, *Eucalanus bungii bungii*, *Candacia columbiae*, and others (Brodsky, 1957; Johnson, 1941; Omari, 1965); the euphausiids *Euphausia pacifica*, *Tessarabrachion oculatus*, and *Thysanoessa longipes* (Brinton, 1962); and the hyperiid amplipod *Parathemisto pacifica* (Bowman, 1960). As far as we know, none of the subarctic epipelagic plankters has a global distribution comparable to that of *C. challengeri*. It is perhaps significant that almost all the collections outside of the North Pacific were made with nets that had been lowered to considerable depths, mainly 1000–3000 m. Altho these were not closing nets and the depth of capture is uncertain, it is possible that *C. challengeri* undergoes a submergence at lower latitudes. An alternative possibility, that more than one species is involved, cannot be properly evaluated until abundant material from all parts of the geographic range becomes available.

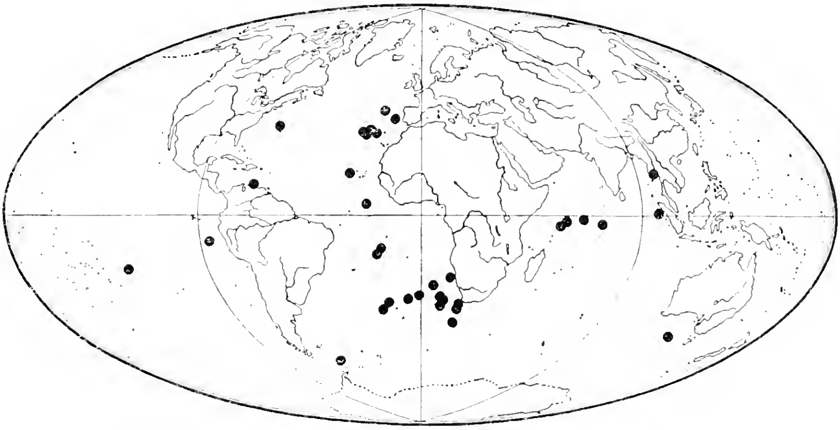

Figure 3.—World distribution records of *Cyphocaris challengeri* outside of the North Pacific.

Morphological Variation

Shape of pereonite 1.—All of the oceanic specimens had the more sharply produced pereonite 1 described by Thorsteinson for *C. kincaidi*. In profile it is very sharp and high in small specimens and as the animal grows the process becomes more rounded and lower. A series of profiles of pereonite 1 from representative growth stages is shown in figure 4. In a similar series from inshore populations collected in the Puget Sound region, pereonite 1 is also more produced in small specimens, but it does not approach the condition in oceanic specimens. Specimens from Lynn Canal and Revillagigedo

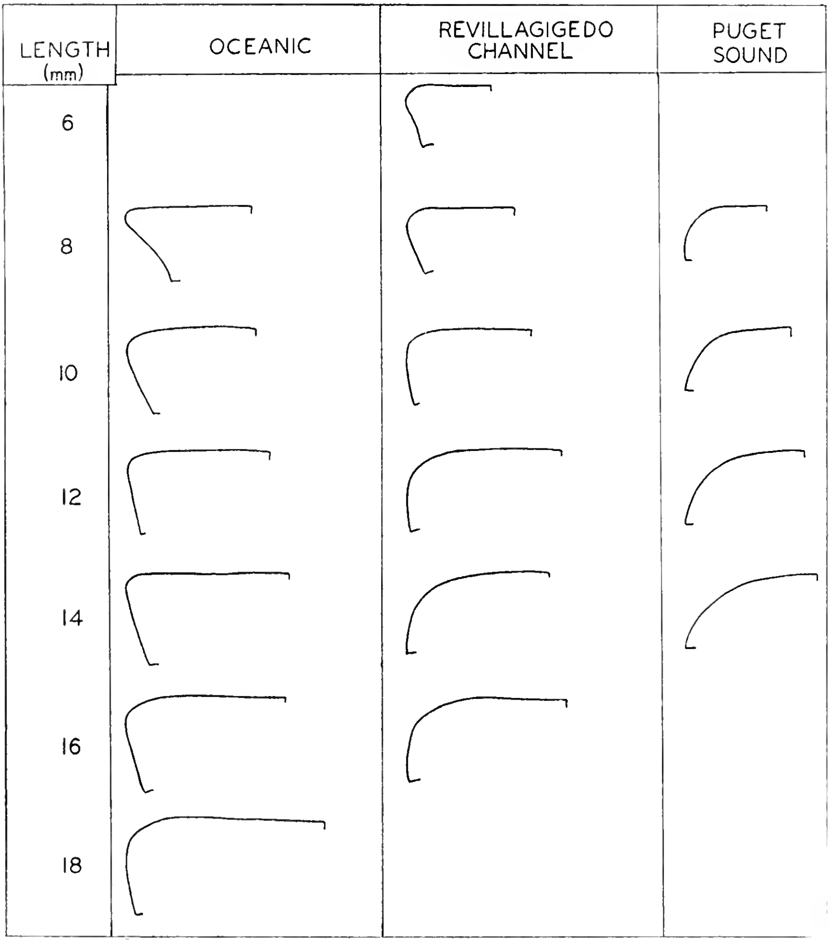

Figure 4.—Profiles of pereonite 1 of three populations of *Cyphocaris challengeri*, showing variation with age.

Channel, Alexander Archipelago, are intermediate, but appear to show more resemblance to the Puget Sound than to the oceanic specimens.

In order to express quantitatively the shape of pereonite 1, a simple index has been devised. The straight-line distance between the anterodorsal and posterodorsal margins, viewed laterally, is divided into the longest perpendicular from this line to the dorsal margin (fig. 5). The quotient is multiplied by 100 to give an index which may be termed the "cyphos index" (from κυφος="hump," the first part of the generic name *Cyphocaris*="hump-head"). In figure 6, cyphos indices are plotted against body length for the oceanic

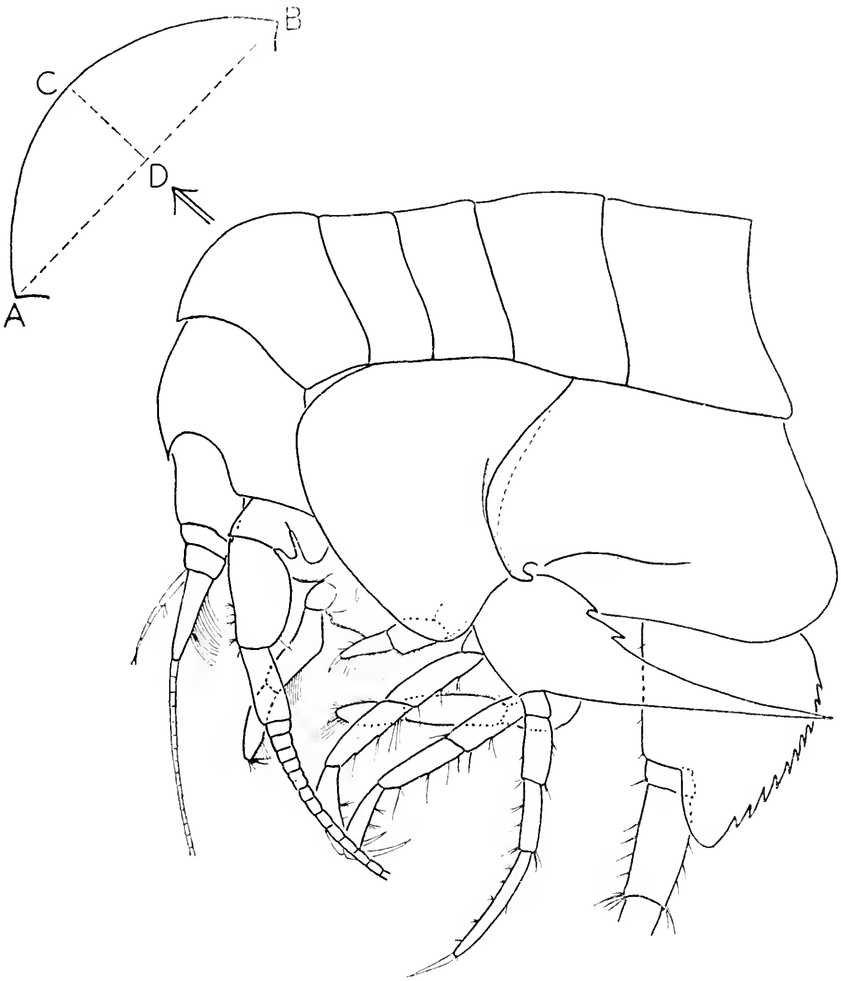

FIGURE 5.—Anterior end of *Cyphocaris challengeri*, lateral $\left(\frac{CD}{AB}\times 100=\text{cyphos index}\right)$.

form and for neritic populations from Puget Sound and Alexander Archipelago. The change with age to a flatter pereonite 1 is evident; the figure also demonstrates that in this character the Alexander Archipelago population is intermediate between the oceanic and Puget Sound populations, but is closer, as might be expected, to the other neritic population from Puget Sound.

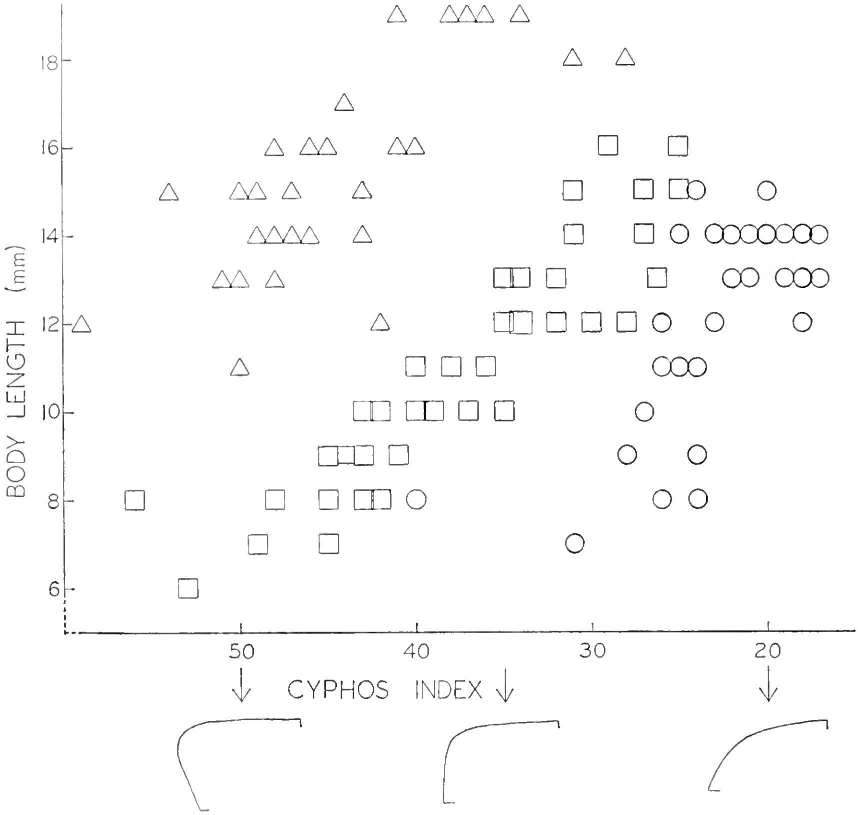

Figure 6.—Relation between cyphos index and body length in oceanic (triangles), Puget Sound (circles), and Revillagigedo Channel (squares) populations of *Cyphocaris challengeri*.

Length of process of pereopod 5 basis.—In figure 7 the ratio of the length of the process of the basis to the length of the distal segments of the limb is plotted against body length. The ratio is clearly higher in the oceanic form and does not appear to vary with age. In figure 8 the ratios obtained for the three populations, lumping all growth stages, are represented according to the graphical method of Hubbs and Hubbs (1953). The wide separation of the oceanic from the two neritic populations is evident. The difference between the means of the latter populations is statistically significant (t=2.6) but small compared to their divergence from the oceanic population. Note that in this character the Puget Sound population is intermediate, whereas the Revillagigedo Channel population was intermediate with respect to the cyphos index.

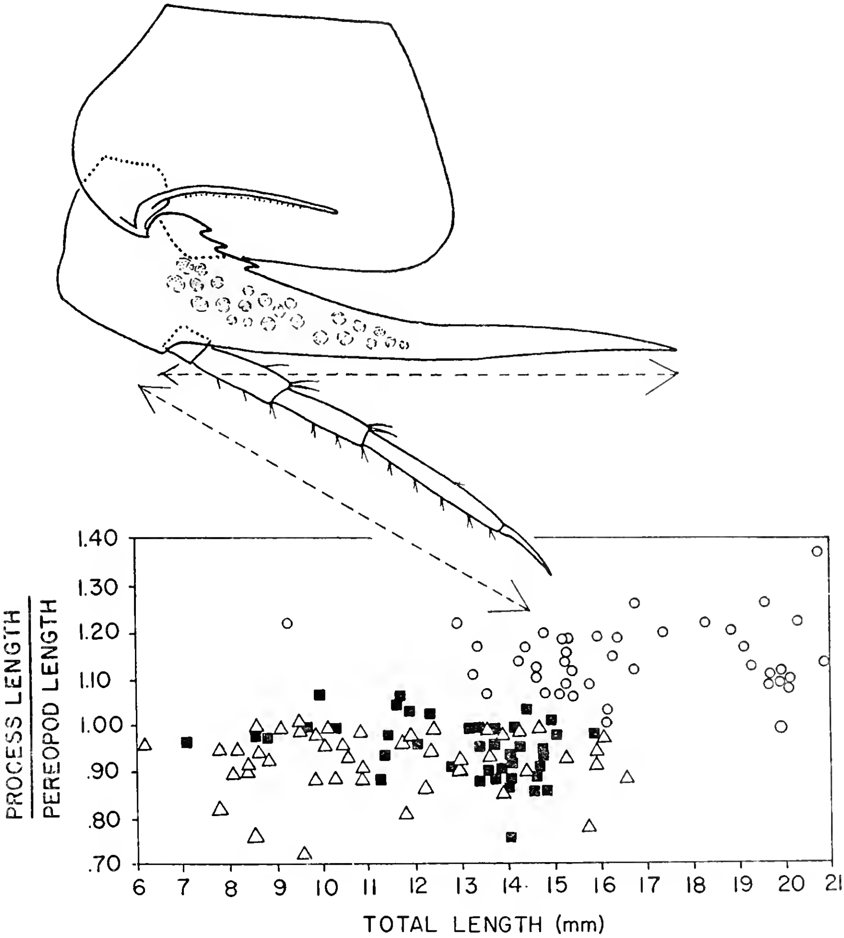

Figure 7.—Ratio of length of basal process to that of distal segments in pereopod 5 plotted against body length in oceanic (circles), Puget Sound (solid squares), and Revillagigedo Channel (triangles) populations of *Cyphocaris challengeri.*

Ratio of length of 3rd uropod to length of telson.—In figure 9 the ratio of the length of uropod 3 to that of the telson is plotted against body length. Altho there is considerable variation, it can be seen that the ratio decreases from 1.4–1.8 in juveniles to 1.0–1.2 in adults. The rate at which the ratio decreases is approximately equal in all three populations, but for a particular body length the ratio tends to be lower in the Puget Sound population, the adults of which are smaller than those of the other two populations.

Origin of Variation in *Cyphocaris challengeri*

Movement of Subarctic Water is from west to east, via the Subarctic or Aleutian Current (Sverdrup, Johnson, and Fleming, 1942). As this current approaches the American coast, it divides into the Alaska Current, which moves north into the Gulf of Alaska, and the California Current, which flows south along the coast of California. From the direction of the currents it is assumed that the coastal population of *C. challengeri* has been derived from the oceanic population. Any large contribution of individuals to the oceanic population from the coastal population is precluded by the circulation in the coastal inlets. The inlets are deep estuaries, with a surface layer of low salinity water formed by river runoff overlying a deep layer of denser high salinity water. The surface water flows seaward and deep water enters the inlets from the ocean. (Waldichuk, 1957; Herlinveaux and Tully, 1961; Pickard, 1961). The effects of tides and other factors complicate the picture, but if it is assumed that *Cyphocaris* avoids the low salinity surface layer, the circulation would tend to hinder its seaward movement. Hence, any genetic changes that might accumulate in the coastal populations would not affect the oceanic population.

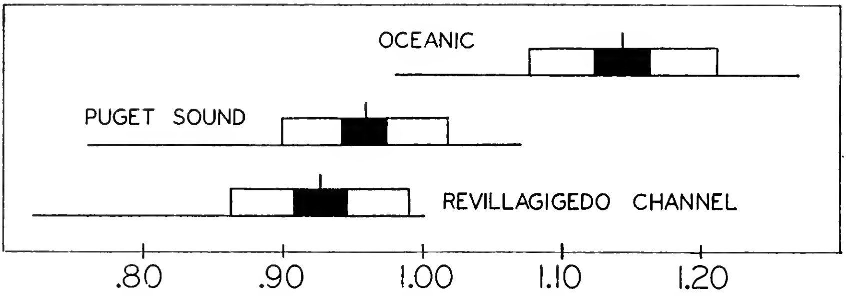

Figure 8.—Ratio of length of basal process to that of distal segments of pereopod 5 for three populations of *Cyphocaris challengeri* (for each diagram the horizontal line represents the sample range, the vertical line the sample mean, and the black rectangle the value of 2 standard errors on each side of the mean; the distance from a mean to the edge of a white rectangle equals the value of 1 standard deviation).

The origin of the coastal forms can be explained by the mechanism proposed by Buzzati-Traverso (1958) and used by McGowan (1963) to explain the distribution of two forms of the pteropod *Limacina helicina* in the subarctic North Pacific.

When the inlets were first invaded by *Cyphocaris,* only those individuals genetically pre-equipped to endure the unaccustomed coastal conditions were able to survive and breed successfully. As the coastal populations multiplied in the new environment, selection and adaptation proceeded until the morphologically distinct coastal forms evolved. Altho immigrants continued to arrive from the the oceanic population, most of them could not compete successfully under coastal conditions. Populations in Puget Sound and the inlets of the Alexander Archipelago evolved independently and now have demonstrable morphological differences. It is possible that other coastal populations, now unstudied, will also show recognizable differences.

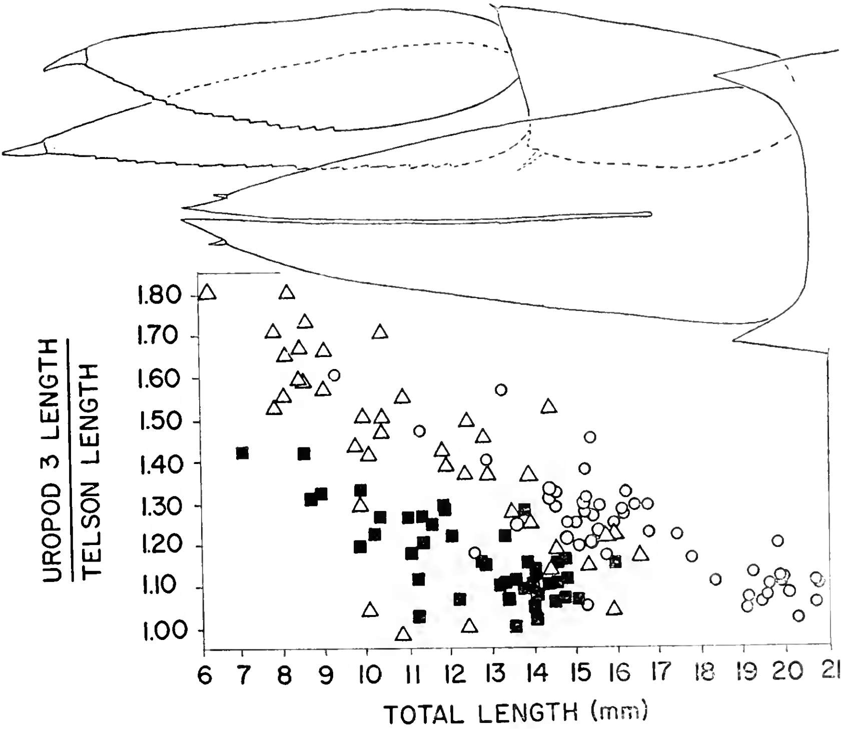

FIGURE 9.—Ratio of length of uropod 3 to that of telson plotted against body length for oceanic (circles), Puget Sound (solid squares), and Revillagigedo Channel (triangles) populations of *Cyphocaris challengeri.*

From the foregoing analysis it is clear that the northeast Pacific population of *Cyphocaris challengeri* includes an oceanic form in Subarctic Water and inshore forms inhabiting coastal waters of western North America from Puget Sound northward. The oceanic form, considered a new species, *C. kincaidi*, by Thorsteinson, is distinguished by its larger size, more produced pereonite 1 (higher cyphos index) and a longer process on pereopod 3 than populations from Revillagigedo Channel and Lynn Canal, Alexander Archipelago. The two inshore forms are morphologically more similar to each other than to the oceanic form.

We are now faced with the problem of whether Thorsteinson's *C. kincaidi* should be reestablished as a species distinct from *C. challengeri*. First, however, we must consider to which form Stebbing's *C. challengeri* belongs. Unfortunately, Stebbing's single type specimen was so immature (about 5 mm) that morphological characters cannot be relied upon. Concerning the type-locality Stebbing states: "The label on the mounted specimen states that it was taken 400 miles north of the Sandwich [=Hawaiian] Islands; probably near station 256." Murray (1895) lists it as a constituent of the surface plankton of Station 256, located at 30°22′N, 154°56′W. At our request Mr. E. C. Jones, Bureau of Commercial Fisheries Biological Laboratory, Honolulu, examined a number of plankton samples collected near the type-locality, but none of these samples contained *Cyphocaris*. Mr. Jones agrees with us that *C. challengeri* is a subarctic species and would not be expected to occur in Central Water. It is not unreasonable to suspect that the type specimens of *C, challengeri* may have been collected farther north than Station 256. perhaps during the traverse of H.M.S. *Challenger* across the North Pacific from Japan.

Despite the uncertainty of the exact position of the type-locality, it must be presumed that *C. challengeri* is the oceanic form, with the more produced pereonite 1. But, as we have seen, Thorsteinson described the oceanic form as a new species, *C. kincaidi*, and assigned the Puget Sound form to *C. challengeri*. Hence, *C. kincaidi* is a junior synonym of *C. challengeri*, and, if the inshore form (*C. challengeri* sensu Thorsteinson) should be considered to be specifically or subspecifically distinct, a new name would be required.

Because the differences between the oceanic and coastal forms are much less than those separating the known species of *Cyphocaris* from one another and because these differences vary from one coastal population to another, we have chosen not to consider the two forms as distinct species. For the present it seems most convenient to refer to "oceanic" and "coastal" forms and to further designate the coastal form populations by locality.

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NOTES ON THE GENUS MANNINGIA WITH DESCRIPTION OF A NEW SPECIES (CRUSTACEA: STOMATOPODA)

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One of the recent trends in the study of stomatopod crustaceans has been a critical re-evaluation of generic characters (Serène, 1962; Manning, 1963; Holthuis, 1964). In setting this trend, Serène (1962) reviewed the genus *Pseudosquilla* Dana and showed it to be a conglomerate of several groups of species that should be recognized as distinct genera. One of the genera erected by Serène was the monotypic *Manningia,* which originally contained only *Pseudosquilla pilaensis* de Man.

In a recent study of three specimens of *Manningia* from Australia, I re-examined five of the seven specimens of *Manningia* reported in the literature. The Australian specimens proved to be a distinct species, *M. notialis,* which has been described elsewhere (Manning, 1966). The present paper includes comments on specimens from other localities in the Indo-West Pacific area.

Since its description by de Man in 1888, *Pseudosquilla pilaensis* has been recorded only six times from widely scattered areas in the Indo-West Pacific. The following specimens are known (those marked with an asterisk were illustrated):

original reference	*sex, size*	*location*	*present identification*
de Man, 1888	1(?), TL 88.0	Elphinstone Island, Mergui Archipelago	*M. pilaensis*
Nobili, 1906	1 ♀, broken	Gulf of Aden	*Manningia*, new species?
Kemp, 1913	1 ♀, TL 48.0	Elphinstone Island, Mergui Archipelago	*M. pilaensis*
Schmitt, 1929	1 ♂, TL 58.0*	Amoy, China	*M. pilaensis*
Gravier, 1937	1 ♂, TL 32.0*	Viet Nam	*M. serenei*, new species
Dollfus, 1938	1 ♂, TL 63.0*	Amoy, China	*M. pilaensis*
Stephenson, 1953	1 ♂, TL 50.0	Queensland, Australia	*M. notialis*

Other authors, including Serène (1962) and Ingle (1963), re-illustrated parts of one or more of the above specimens. A comparison of these illustrations revealed several discrepancies, some of which are cited below.

Gravier (1937) figured a small specimen from the Poulo Condore Islands in which the third lateral carinae of the telson were subdivided into three erect spines; Serène (1962) refigured Gravier's specimen and showed an uninterrupted carina terminating in a single spine. Gravier's specimen has a rounded lobe between the spines of the basal prolongation of the uropod; the lobe is lacking in the Chinese specimen of *M. pilaensis* figured by Schmitt (1929) and Ingle (1963). These are among the discrepancies noted in the literature.

All but the two specimens of *M. pilaensis* from Elphinstone Island have been examined for this study. *M. pilaensis* is redescribed, a new species from the Poulo Condore Islands, *M. serenei*, is described, and the single, mutilated specimen from the Gulf of Aden, which probably represents a new species, is briefly characterized but not named.

The descriptions given herein do not include generic characters, which are summarized separately in the generic definition. Synonymies include all references in the literature. Measurements of total length (TL) are made along the midline, from the apex of the rostral plate to the bases of the movable submedian teeth of the telson. Telson length is also measured to the bases of the submedian teeth. Carapace length (CL) is measured along the midline and does not include the rostral plate. In general, appendage setation is not shown in the illustrations; on most of the specimens the setae are badly damaged.

I would like to thank R. W. Ingle of the British Museum (Natural History) (BMNH) and J. Forest of the Muséum National d'Histoire Naturelle, Paris (MNHNP), for making available on loan specimens from their institutions. The illustrations are from the pen of my wife, Lilly. Support of the National Science Foundation under grant GB–1602 is gratefully acknowledged.

Manningia Serène, 1962

Manningia Serène, 1962, p. 20.—Manning, 1963, p. 313.

Definition.—Size moderate, TL 90 mm or less; body smooth, depressed but compact; eyes of moderate size, cornea bilobed, set very obliquely on stalk, outer margin of stalk longer than inner; rostral plate usually pentagonal, apical spine present or absent; antennal protopod with papillae; carapace narrowed anteriorly, unarmed, cervical groove indicated on lateral plates only; carapace with marginal carinae, not reflected, along posterior margins of lateral plates; thoracic somites with at most 1 pair of lateral dorsal carinae, lateral margins of sixth and seventh somites rounded; eighth thoracic somite with low, short, median ventral keel; 5 epipods present; mandibular palp present; propodi of last 3 thoracic appendages as long as or longer than broad, that of last appendage with ventral brush of setae; raptorial claw stout, dactylus armed with 4 teeth, outer margin of dactylus with strong basal notch; propodus stout, fully pectinate, with 3 movable spines at base, proximal one longest; dorsal ridge of carpus divided into 2 strong teeth; merus stout, much shorter than ischium, with or without inferodistal spine; endopods of walking legs 2-segmented, elongate; abdomen depressed, smooth, second to fourth somites each with obscure longitudinal lateral grooves; fifth and sixth abdominal somites carinate, sixth with 3 pairs of dorsal spines; telson much broader than long, with median carina and 5 pairs of lateral carinae on dorsal surface; submedian teeth of telson with bases appressed, apices movable; submedian denticles absent, 2 broad intermediate denticles and 1 broad lateral denticle present, outer intermediate and lateral denticle each with ventral spinule; basal segment of uropod with dorsal and lateral carinae, dorsal terminating in distal spine; distal segment of exopod longer than proximal; endopod elongate; basal prolongation produced into 2 spines, inner longer, with or without intervening lobe; inner margin of basal prolongation with spinules.

Type-species.—*Pseudosquilla pilaensis* de Man, 1888, by monotypy.

Discussion.—Within the *Pseudosquilla* complex of genera including *Pseudosquilla*, *Pseudosquillopsis*, *Parasquilla*, *Manningia*, *Coronidopsis*, *Eurysquilloides*, and *Eurysquilla*, discussed by Manning (1963), *Manningia* seems to be most closely related to *Coronidopsis* Hansen. Both of these genera share an eye with bilobed cornea and an outer margin longer than the inner; a raptorial claw with four teeth on the dactylus and two dorsal teeth on the carpus; a relatively broad, flattened body, with the abdomen partially carinate; a telson broader than long, with submarginal intermediate and lateral denticles; and a basal prolongation of the uropod with the inner spine the longer, armed with spinules on its inner margin. The single species of *Coronidopsis*, *C. biscuspis* Hansen, differs from the three species now recognized in *Manningia* in having an anteriorly bifurcate rostral plate and numerous dorsal spinules on the telson.

The terminology of the carinae of the telson proposed by Kemp (1913, p. 13, text-fig. 4) and currently used in this and related genera is illogical in that dorsal carinae may bear names different from the marginal teeth on which they occur. Thus, as used by Kemp, the intermediate dorsal carina extends onto the submedian marginal tooth and the first lateral carina extends onto the intermediate marginal tooth. In the carinal nomenclature used herein by me, the name of a dorsal carina is derived from that of the marginal tooth onto which it extends. The proposed nomenclature of the carinae of the telson in *Manningia* and related genera compared with that proposed by Kemp (1913) is as follows:

Kemp, 1913	*present*	*remarks*
submedian	accessory median	parallel to median carina
second submedian	second accessory median	paralled to median carina, present in *Odontodactylus* only
intermediate	submedian	on submedian marginal tooth
first lateral	intermediate	on intermediate marginal tooth
second lateral	lateral	on lateral marginal tooth
marginal	marginal	

Key to Species of *Manningia*

1. Rostral plate pentagonal 2
   Rostral plate ovate . . . . **Manningia** species (p. 5)
2. Rostral plate lacking apical spine; merus of raptorial claw lacking inferodistal spine . . . . **M. notialis** Manning, 1966 [Australia]
   Rostral plate with apical spine; merus of raptorial claw with inferodistal spine 3
3. Intermediate carinae of telson entire; basal prolongation of uropod without broad, rounded lobe between apical spines . . . . . **M. pilaensis** (p. 6)
   Intermediate carinae of telson divided into spined lobes; basal prolongation of uropod with rounded lobe between apical spines.
   M. serenei, new species (p. 9)

Manningia species

FIGURE 1

Pseudosquilla pilaensis.—Nobili, 1906, p. 336.—Dawydoff, 1952, p. 146 [discussion; not *P. pilaensis* de Man, 1888].
Manningia pilaensis.—Serène, 1962, text-fig. 5D.

MATERIAL.—1 broken ♀, CL 7.0; Djibouti or Obock, French Somaliland, Gulf of Aden; Dr. Jousseaume, collector; MNHNP.

DESCRIPTION.—Rostral plate ovate, anterolaterally rounded; apical spine absent (possibly broken).

Antennal scale slender, margin complete setose; antennal peduncle with one ventral papilla.

Walking legs slender, endopod increasing in length posteriorly.

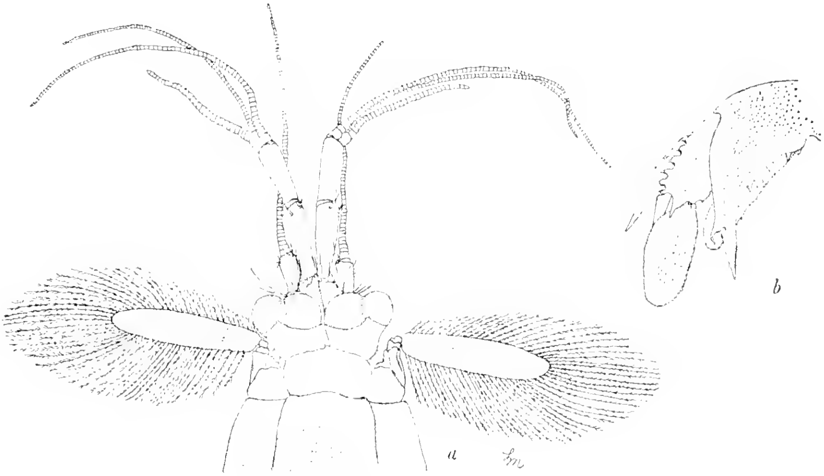

FIGURE 1.—*Manningia* species, female, Gulf of Aden: *a*, anterior portion of body; *b*, basal prolongation of uropod, ventral view (uropodal setae damaged, omitted).

Fifth abdominal somite with posterolateral spines, 3 lateral carinae present on each side, upper and lower subparallel and as long as somite, middle carina shorter; sixth somite with 6 pairs of posterior spines, with unarmed accessory carina present dorsally between submedian and intermediate carinae as well as between intermediates and laterals.

Uropodal exopod with 8–9 movable spines on outer margin of penultimate segment, last spine extending past midlength of distal segment; basal prolongation of uropod with 6 spinules on inner margin and poorly marked lobe present between distal spines.

COLOR.—Completely faded.

MEASUREMENTS.—Summarized in table 1.

DISCUSSION.—This small, fragmented specimen, which lacks a telson and raptorial claws, resembles *M. pilaensis* in most features, but differs as follows: (1) the rostral plate is ovate rather than pentagonal and is broadly rounded anterolaterally instead of angled; (2) there is but one papilla on the antennal protopod; and (3) there is a small, rounded lobe present between the spines of the basal prolongation of the uropod.

A small irregular area on the left side of the rostral plate indicates that it has been damaged and a rostral spine may have been present.

Because of its small size, poor condition, and apparent distinctness from the other species of *Manningia*, it seems best not to discuss this specimen under *M. pilaensis* but to treat it separately in order to call attention to it. Additional specimens from the Gulf of Aden are needed to determine the identity of this specimen.

DISTRIBUTION.—Known only from the single specimen collected at Djibouti or Obock, French Somaliland, in the western Gulf of Aden.

***Manningia pilaensis* (de Man)**

FIGURE 2

Pseudosquilla pilaensis de Man, 1888, p. 296.—Bigelow, 1894, p. 499 [key only].—Kemp, 1913, p. 105.—Schmitt, 1929, p. 140, pl. 19, figs. 12-14.—Dollfus, 1938, p. 201, text-fig. 10.—Ingle, 1963, p. 22.

Not *Pseudosquilla pilaensis*.—Nobili, 1906, p. 336 [= new species from Gulf of Aden discussed above].—Gravier, 1937, p. 193, text-fig. 13 [=*M. serenei*, new species].—Stephenson, 1953, p. 144.—Stephenson and McNeill, 1955, p. 245 [= *M. notialis* Manning].

Manningia pilaensis.—Serène, 1962, p. 20 et seq. [part].—Manning, 1963, p. 313 [discussion].

MATERIAL.—1 ♂, 54.8; Liawutien, on mainland near Amoy, China; May 27, 1923; S. F. Light, collector; USNM 62190. 1 ♂, 61.7; Tsimei, Amoy, China; S. F. Light, collector; BM(NH) Reg. No. 1924.5.27.2.

DESCRIPTION.—Eyes not extending beyond midlength of first segment of antennular peduncle; ocular scales low, rectangular, partially fused along midline.

Antennular peduncle more than ⅔ as long as carapace.

Antennal scale not markedly curved, short, little more than ½ as long as carapace, margins completely setose; antennal protopod with one mesial and one ventral papilla.

Rostral plate pentagonal, with long apical spine.

Merus of raptorial claw with inferodistal spine.

Fifth thoracic somite with inconspicuous lateral processes; sixth and seventh somites with prominent lateral carina on each side; last thoracic somite with blunt lateral lobes; endopods of walking legs increasing in length and slenderness posteriorly.

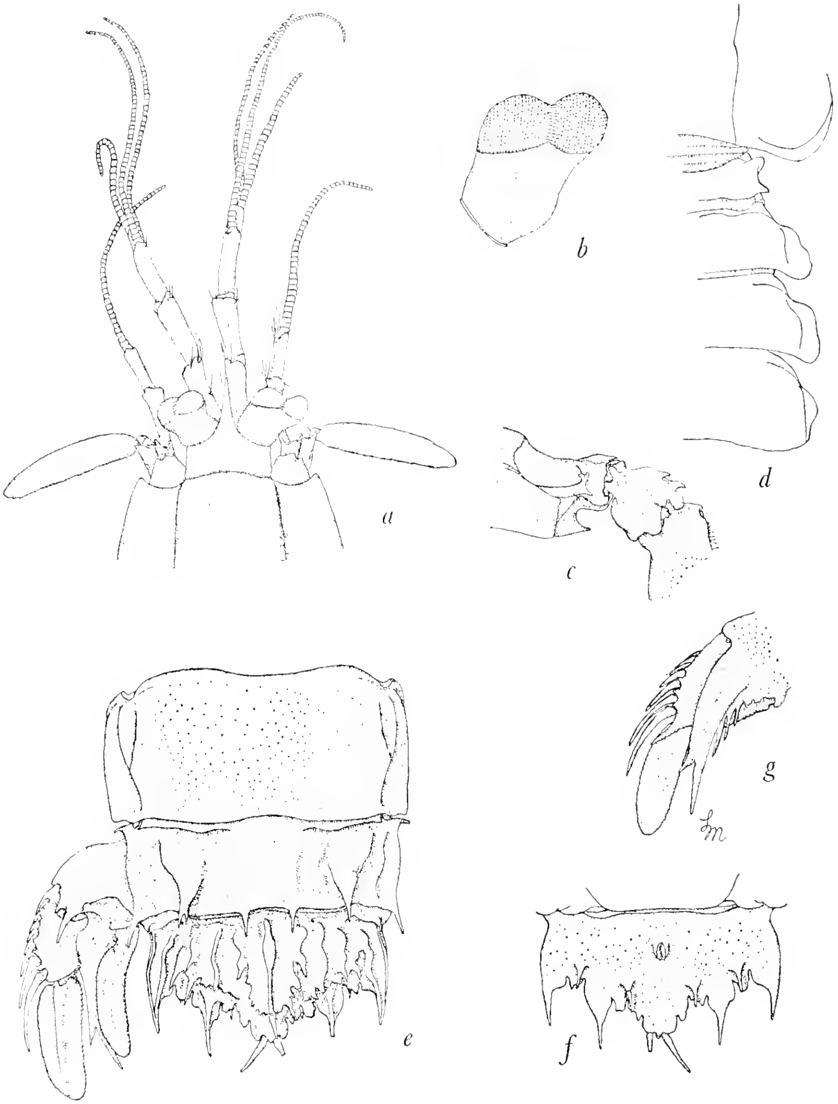

FIGURE 2.—*Manningia pilaensis* (de Man), male, Liawutien, China: *a*, anterior portion of body; *b*, eye; *c*, carpus of raptorial claw; *d*, lateral processes of exposed thoracic somites; *e*, posterior portion of body; *f*, telson, ventral view; *g*, basal prolongation of uropod, ventral view (setae omitted).

Abdomen with longitudinal grooves on second to fifth somites; fifth somite with 3 broad carinae, upper short, parallel to body line, middle oblique, extending to posterior margin, lower swollen, subparallel with upper; posterolateral margin of fifth somite (occasionally fourth) armed with small spine; sixth somite with 6 carinate marginal spines; broad, unarmed accessory carinae present between submedian and intermediate carinae as well as between intermediates and laterals; submedian carinae slender; intermediate carinae very broad, widening anteriorly, sides sharp; lateral carinae swollen, inconspicuous; sixth somite with small lateral spine anterior to articulation of each uropod.

Telson less than twice as broad as long; accessory median carinae subdivided into 3–6 lobes, each armed with slender spine; submedian dorsal carinae with 1–2 denticles ventral to apical spine; intermediate carinae with 1–2 inner and one outer lobes or spinules ventral to each apical spine, outer and/or inner connected to low ridge extending anteriorly around apex; lateral carinae uninterrupted dorsally, with 1–2 subterminal tubercles or spinules; marginal carinae irregular but entire; anterior surface of telson with 1 pair of dorsal, submedian, rounded tubercles; submedian and intermediate marginal teeth with short dorsal carinae.

Table 1.—*Measurements (in mm) of four specimens of* Manningia

	M. pilaensis		*M. serenei*	*Manningia* species Gulf of Aden
Sex	♂	♂	♂	♀
Total length	61.7	54.8	31.5	–
Carapace length	11.6	10.7	5.8	7.0
Rostral length	4.3	4.0	2.2	1.2
Rostral width	3.7	3.4	2.0	2.2
Cornea width	2.5	2.5	1.6	2.2
Antennal scale length	6.1	5.0	2.5	3.7
Antennal peduncle length	8.7	7.9	5.1	–
Fifth abdominal somite width	12.1	10.8	6.5	7.1
Telson length	5.3	4.8	2.7	–
Telson width	9.6	8.8	4.8	–

Uropodal exopod with 8 slender movable spines on outer margin of proximal segment, distal extending past midlength of distal segment; endopod slender, curved; basal prolongation lacking lobe between apical spines; inner margin of basal prolongation with 5 slender spinules.

Color.—The color pattern is completely faded in the USNM specimen, but some chromatophores are visible on the one from the British Museum. There are dark chromatophores along the abdominal pleura, with the ventral margin of each pleuron black; the anterior edge of the merus of the claw is black; and the posterior margin of the carapace, last abdominal somite, and telson are outlined in dark pigment.

Measurements.—Summarized in table 1.

Discussion.—The presence of the following features will distinguish *M. pilaensis* from the other species of the genus: (1) a slender rostral spine; (2) one mesial and one ventral papilla on the antennal protopod; (3) the inferodistal spine on the merus of the raptorial claw; and (4) the uninterrupted intermediate carinae of the telson. *M. pilaensis* agrees with *M. notialis* and differs from *M. serenei*, new species, as well as the undescribed species from the Gulf of Aden in lacking a rounded lobe between the spines of the basal prolongation of the uropod.

Although de Man (1888) did not illustrate the type, from Elphinstone Island, Mergui Archipelago, he did provide a long and detailed description with which the present specimens agree in all respects.

Remarks.—The specimens available differ in minor details of telson ornamentation, particularly in the numbers of subterminal tubercles and spinules on the submedian and intermediate dorsal carinae. On the USNM specimen, the right lateral carina recurves anteriorly and terminates in a spine; on the left side a short, spined carina is present in the same location, but it is not connected to the lateral. The left intermediate spine of the sixth abdominal somite is bifurcated on the USNM specimen.

Distribution.—*M. pilaensis* is known from the two specimens from Amoy, China, discussed herein, and from two other specimens collected at Elphinstone Island, Mergui Archipelago, eastern Indian Ocean.

***Manningia serenei*, new species**

Figure 3

Pseudosquilla pilaensis.—Gravier, 1937, p. 193, text-fig. 13 [not *P. pilaensis* de Man, 1888].

Manningia pilaensis.—Serène, 1962, text-figs. 4, 5C.

Holotype.—1 ♂, 31.5; reefs, Poulo Condore Island, Viet Nam; Dawydoff, collector; March–April 1931; MNHNP.

Description.—Eyes not extending to end of first segment of antennular peduncle; ocular scales low, rectangular, partially fused along midline.

Antennular peduncle ⅚ as long as carapace.

Antennal scale slender, slightly curved, less than ½ as long as carapace, margins completely setose; antennal protopod with one ventral papilla.

Rostral plate pentagonal, longer than broad, with long apical spine extending to end of cornea.

Merus of raptorial claw with inferodistal spine.

Lateral process of fifth thoracic somite blunt, inconspicuous; lateral processes of next 2 somites rounded, anterolaterally flattened; no dorsal carinae visible on thoracic somites; endopods of walking legs slender, 2-segmented, increasing in length posteriorly, that of first leg broadest.

Second to fifth abdominal somites each with shallow longitudinal grooves laterally; fifth somite with 3 low lateral carinae, upper and lower parallel with body line, middle carina oblique, connected to neither upper nor lower; posterolateral angles of fourth somite acute, those of fifth spined; sixth somite with 3 pairs of marginal spines; submedians each on low carina not extending to anterior margin of somite; intermediates on broad triangular swellings, margins sharp; blunt longitudinal carina present between each intermediate and lateral carina; sixth somite with inconspicuous spine or lobe anterior to articulation of each uropod.

Telson less than twice as broad as long; accessory median carinae interrupted, divided into 3 spined lobes (anterior lobe subdivided on one side); submedian carinae uninterrupted, terminating in strong spines; intermediate carinae divided into at least 2 lobes, posterior spined, with lateral and dorsal subapical denticles; lateral carinae entire; submedian and intermediate marginal teeth each with short dorsal carina.

Uropods broad, curved; proximal segment with strong dorsal and lateral carinae, distal dorsal spine broken on both sides in holotype; proximal segment of outer branch with 8 movable spines, last extending to midlength of distal segment; proximal segment of exopod shorter than distal; endopod curved mesially, tapering distally; basal prolongation with rounded lobe between spines; inner spine of basal prolongation with 5–6 fixed spinules on inner margin.

COLOR.—Completely faded in the holotype.

MEASUREMENTS.—Summarized in table 1.

DISCUSSION.—The chief diagnostic features of *M. serenei* are the interrupted intermediate carinae of the telson, each of which is divided into at least two spined lobes. This feature and the broad, rounded lobe present between the spines of the basal prolongation of the uropod will distinguish *M. serenei* from *M. pilaensis* and *M. notialis*. *M. serenei* resembles *M. pilaensis* and differs from *M. notialis* in having the rostral plate armed anteriorly and in having an inferodistal spine

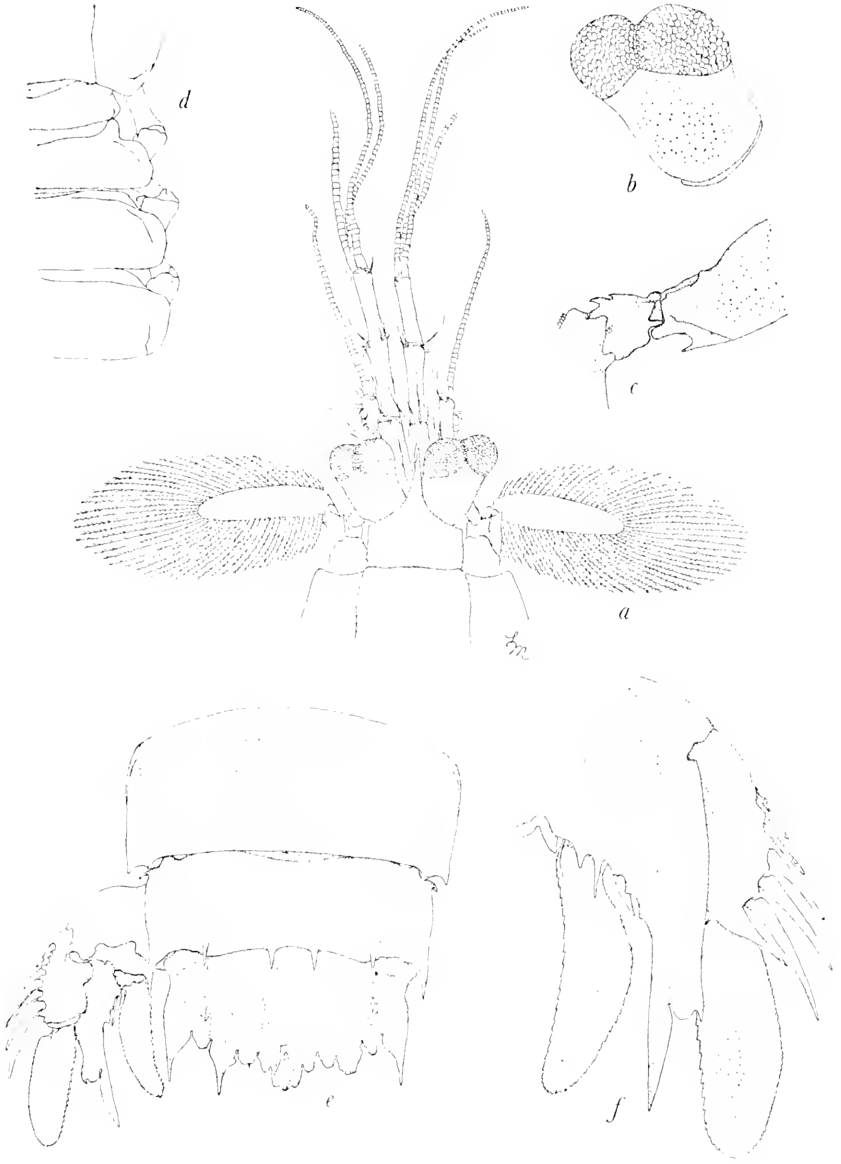

FIGURE 3.—*Manningia serenei*, new species, male holotype, Viet Nam: *a*, anterior portion of body; *b*, eye; *c*, carpus of raptorial claw; *d*, lateral processes of exposed thoracic somites; *e*, posterior portion of body; *f*, basal prolongation of uropod, ventral view, enlarged (setae omitted where damaged).

on the merus of the raptorial claw. *M. serenei* resembles the small fragmented specimen from the Gulf of Aden in having but one papilla on the antennal protopod and in having the rounded lobe between the spines of the basal prolongation of the uropod; the rounded lobe is much better developed in the holotype of *M. serenei* than in the Gulf of Aden specimen.

Remarks.—This species is named for Raoul Serène in recognition of his studies on the Stomatopoda of the Indo-West Pacific.

Distribution.—Known only from the type-locality, the Poulo Condore Islands, off Viet Nam.

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NEOTROPICAL MICROLEPIDOPTERA, XIII[1]

REVIEW OF GENUS LOXOTOMA (LEPIDOPTERA: STENOMIDAE)

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This paper represents a part of a continuing study of the moths of the family Stenomidae in the Neotropical Region. The genus *Loxotoma* Zeller as herein defined consists of two species that present rather contrasting pictures when viewed in the light of previous and present knowledge. One, *L. elegans* Zeller, is widely distributed throughout the Neotropics, reasonably well represented in major collections, and has been alluded to in the literature a number of times since its original description; the other, *L. seminigrescens* Meyrick, is known only from the type-locality, represented only by

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a type that is without abdomen and is recorded in the literature only by its original description, which consists of three and one-half lines.

In this paper the genus is redefined, the two species redescribed and illustrated, and comparative remarks made on both the generic and specific levels.

The author wishes to acknowledge with thanks the cooperation and aid of the following persons who have allowed him to study the types and specimens in their charge: Mr. P. E. S. Whalley and Mr. Alan Watson of the British Museum (Natural History); Dr. J. G. Franclemont of Cornell University; Dr. Klaus Sattler, Zoologische Sammlung des Bayerischen Staates, Munich; and Dr. Fritz Kasy of the Naturhistorisches Museum, Vienna.

The author also wishes to acknowledge the assistance of Mrs. Sandra Duckworth in all phases of the study. The map and line drawings were done by Mr. Andre Pizzini and the photographs by Mr. Jack Scott.

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History

The genus *Loxotoma* was proposed by Zeller (1854, p. 383) to accommodate a single Neotropical species, *elegans*. Busck (1909, p. 213) in his remarks concerning a new species, *Stenoma loxotoma*, stated: "This species would, on account of the striking wing form and the peculiarly thickened front tarsi, fall in Zeller's genus *Loxotoma*, which I, however, am unable to consider a good genus." Busck failed, however, to transfer *L. elegans* to *Stenoma*, and *Loxotoma* continued to exist in the literature as a monobasic genus. Walsingham (1913, p. 158) formally placed *Loxotoma* in synonymy with *Stenoma* without comment, probably an indication that he was following Busck's earlier opinion. Meyrick (1915, p. 382), apparently not in agreement with Busck's comments on the validity of *Loxotoma*, removed it from synonymy and added another species, *rhodanthes*, which he described from British Guiana. One year later, Meyrick (1916, p. 509) stated that he had erred in describing *rhodanthes* and that further study revealed the specimen to be an extreme form of *elegans*, thus requiring that it be placed in synonymy. In a list of species of Microlepidoptera collected in Brazil by Dr. H. Zerny, Meyrick (1930, p. 237) recorded *L. elegans* from Taperinha and mentioned that it was also known from Colombia, Venezuela, Guiana, and Peru. Two years later, Meyrick (1932, p. 288) very briefly described another species, *L. seminigrescens*, from a single female specimen collected in Petrópolis, Brazil, by J. G. Foetterle. Busck (1934, p. 18), apparently having reversed his earlier opinion, listed *Loxotoma* in the Stenomidae part of the "Lepidopterorum Catalogus" series with three included species, *elegans*, *seminigrescens*, and *liniella* (Busck), the latter a species that Busck (1910, p. 80) had described and placed in *Stenoma*. Clarke (1955, p. 223) illustrated the wings and genitalia of the type of *rhodanthes* Meyrick and reiterated its synonymy with *L. elegans*. Duckworth (1962, p. 113) transferred *liniella* (Busck) from *Loxotoma* to *Timocratica*, thus reducing the number of species of *Loxotoma* to the two covered in this paper.

Genus *Loxotoma* Zeller

Loxotoma Zeller, 1854, p. 383.

Type-species: *Loxotoma elegans* Zeller, by monotypy.

Head rough, lateral tufts somewhat spreading. Labial palpus large, sharply recurved; second segment thickened ventrally with appressed scales; apical segment acute, shorter than second. Forewing with costa arched sharply at midpoint then tapering to apex, apex sharply rounded, termen slightly oblique, tornus rounded; with 12 veins, all separate, 3 and 4 approximate, 6 and 7 approximate, 7 to apex, 12 somewhat sinuate due to sharp arch in costa. Hindwing broader than forewing; with eight veins, 3 and 4 connate or stalked, 5 approximate to 3 and 4, 6 and 7 stalked. Abdomen of males with strong, eversible pair of hair pencils contained in an elongate cuplike pocket on first sternum.

Male genitalia: Harpe broad, rounded at apex, saccular margin with numerous short, heavy setae; anellus with four lateral lobes that adhere closely to aedeagus; uncus broad, slightly recurved, with setiferous dorsal hump at apex; arms of gnathos separate.

Female genitalia: Ovipositor lobes long, narrow; tergite and sternite of eighth abdominal segment fused laterally forming a complete ring; anterior apophyses short, heavy, laterally curved; ductus bursae, corpus bursae, membranous; signum consisting of two heart-shaped dentate plates connected by a narrow sclerotized band.

This genus is easily recognized on the basis of its size and wing shape. It is related to the genus *Timocratica* in both superficial characters and structures of the genitalia; however, it is readily separated by the separate gnathos in the male genitalia and the fusion of the eighth tergite and sternite in the female genitalia.

Key to Species of *Loxotoma* Based on Color

Hindwing whitish with rosy overcast at apex, which may extend over entire wing; ground color of forewing yellow brown . . . . **elegans** Zeller

Hindwing dark gray on basal half, becoming rosy brown posteriorly; ground color of forewing orange brown . . . . **seminigrescens** Meyrick

Loxotoma elegans **Zeller**

Plate 1 (fig. 1); Figures 1–9; Map 1

Loxotoma elegans Zeller, 1854, p. 384.
Loxotoma rhodanthes Meyrick, 1915, p. 382.

Alar expanse 30–48 mm.

Antenna brown. Head yellow brown with slight rosy overcast; second segment of labial palpus yellow brown overcast with rose exteriorly, apical segment yellow brown. Forelegs with femur and tibia red, tarsi fuscous overcast with rose; mid- and hindlegs white with first tarsal segment shaded with rose dorsally. Thorax and tegula yellow brown with darker raised median line. Forewing light yellow brown; dorsum edged with brown; costa edged with rosy brown on basal and apical fourths; a faint brown outwardly curved transverse line from costa to dorsum at apical fourth; a faint transverse linear brown mark at end of cell; a faint brown line from costa at basal fourth slanting outward toward dorsum to fold; a triangular black spot on middle of costa; termen narrowly brown; cilia rosy shaded with brown, above apex shortly suffused with fuscous. Hindwing whitish with rosy overcast from apex varying from slight to entire wing; cilia light rosy at anal angle to red at apex.

Male genitalia (slide WDD 3320): Arms of gnathos somewhat variable in shape and setation (see figures); anellar lobes consisting of two ventral fleshy digitate setiferous lobes and two dorsal medially curved bladelike lobes; aedeagus with area of small spines near apex, vesica without cornuti.

Female genitalia (slide WDD 3645): Eighth sternite with a median groove extending to ostium, fused laterally with eighth tergite forming sclerotized cylinder; ostium V-shaped; ostium bursae extremely small, sclerotized; inception of ductus seminalis very near ostium.

Type: In the Zoologisches Museum der Humboldt-Universität zu Berlin.

Type-locality: Orinoco, Colombia (*elegans*); Bartica, British Guiana (*rhodanthes*).

Distribution: Guatemala: Cayuga (no date). British Honduras: Punta Gorda (August). Panama: Barro Colorado Island (March–May). Colombia: Orinoco (no date). Venezuela: Las Quiguas, Esteban Valley (March–November); Palma Sola (no date); La Vuelta, Cauro Río (May). Trinidad: Caparo (November). British Guiana: Potaro (April); Tumatumari, Potaro River (June); Demerara River (no date); Omai (no date); Christianburg, River Demerara (no date); River Demerara (no date); Bartica (December). Surinam: Aroewarwa Kreek, Maroewym Valley (April–June); Paramaribo (November). French Guiana: St. Jean, Maroni (no date); Godebert, Maroni (February); Nouveau Chantier (no date); St. Laurent (no date). BRAZIL: Manacapuru (June); Hyutanahãn, Rio Purus (January, February); Nova Olinda, Rio Purus (May); Santo Antônio do Javary (June); Teffé (January, September); Fonte Boa (May); Ponte Nova, Rio Xingu (no date); Nova Teutônia (October); Sta. Catharina (no date); Rio Madeira, 300 mi. up river (no date); Maués (no date). PERU: Yahuarmayo (April); Tingo María (November, December); Pumayaca (no date); La Oroya, Río Inambari, 3100 ft. (January, March). BOLIVIA: Chaparé-Gebiet, Río Chipiriri, 400 m. (October, November); Río Yacuma, Santa Rosa, 250 m. (December); Rurrenobaque (October).

I have examined the male genitalia of a large series of specimens from localities throughout the range of this species and find that the variation in shape and setation of the gnathal arms is random and not of specific or subspecific significance. The same is true of the degree of rose shading on the hindwing.

The color characters given in the key serve to distinguish *L. elegans* from *L. seminigrescens;* however, further comparative remarks are impossible until additional specimens of *L. seminigrescens* are obtained.

***Loxotoma seminigrescens* Meyrick**

PLATE 1 (FIG. 2); MAP 1

Loxotoma seminigrescens Meyrick, 1932, p. 288.

Alar expanse 37 mm.

Antenna brown. Head orange brown overcast with rose; second segment of labial palpus brown overcast with rose exteriorly, apical segment brown. Forelegs reddish brown deepening to fucous at last tarsal segment; midlegs white with dorsum of tibia, entire tarsi brown, hindlegs missing. Thorax, tegula, forewing as in *elegans* except ground color orange brown. Hindwing dark gray on basal half, becoming rosy brown posteriorly; cilia rose basally, brown beyond.

Male genitalia; Unknown.

Female genitalia: Unknown

Type: In the Naturhistorisches Museum, Vienna.

Type-locality: Petrópolis, Brazil.

Distribution: Known only from the type-locality.

Through the kindness of Dr. Fritz Kasy and the Naturhistorisches Museum, Vienna, I have had the opportunity to study the type of this species, a female, which is the only specimen known and which is without abdomen. The orange color and dark hindwings afford separation from *L. elegans;* however, final judgment concerning its validity must be reserved pending the acquisition of additional material and study of the genitalia.

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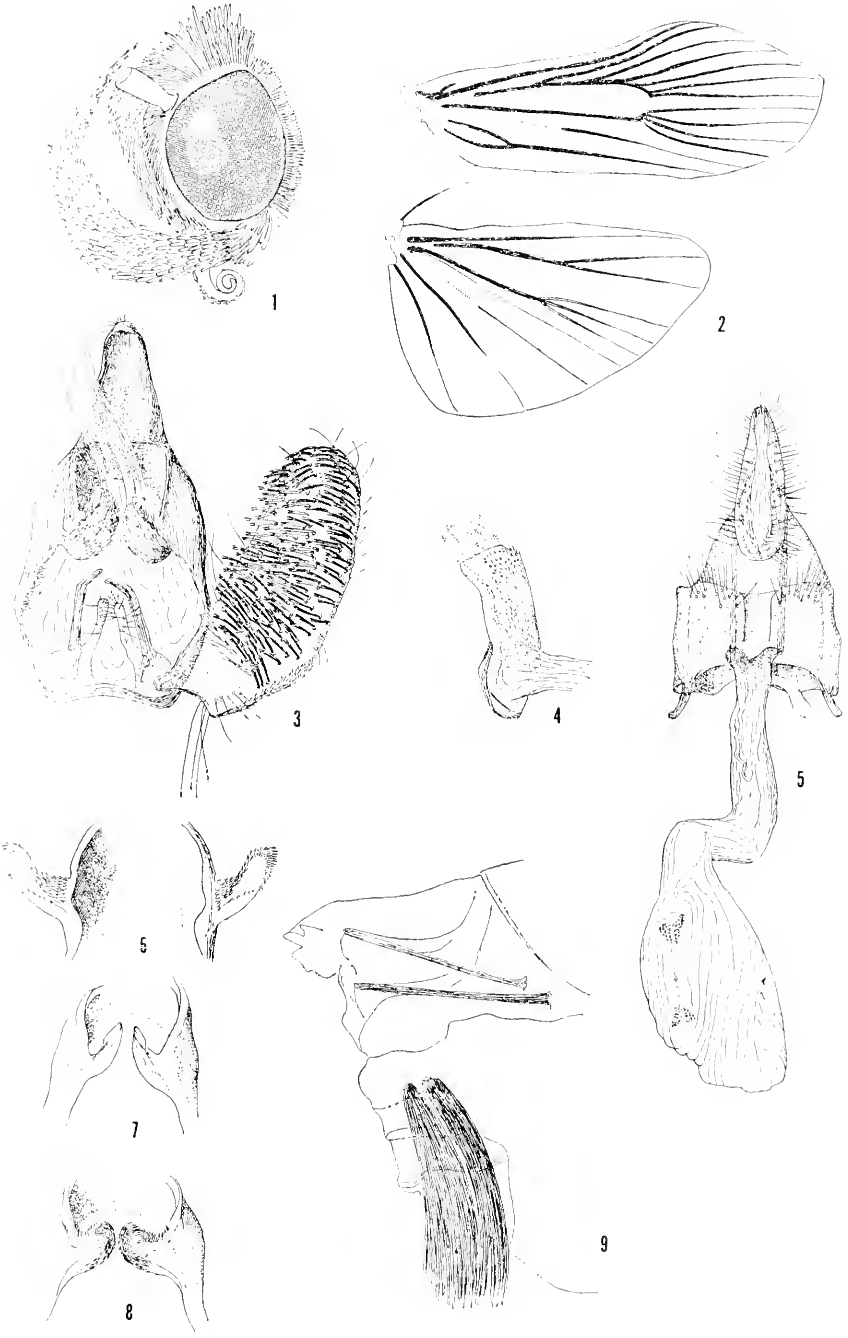

FIGURES 1–9.—*Loxotoma elegans* Zeller: 1, lateral view of head; 2, wing venation; 3, ventral view of male genitalia with left harpe and aedeagus removed; 4, aedeagus; 5, female genitalia; 6–8, variation in gnathal arms; 9, lateral view of abdominal hair pencils.

Map 1.—Distribution of species.

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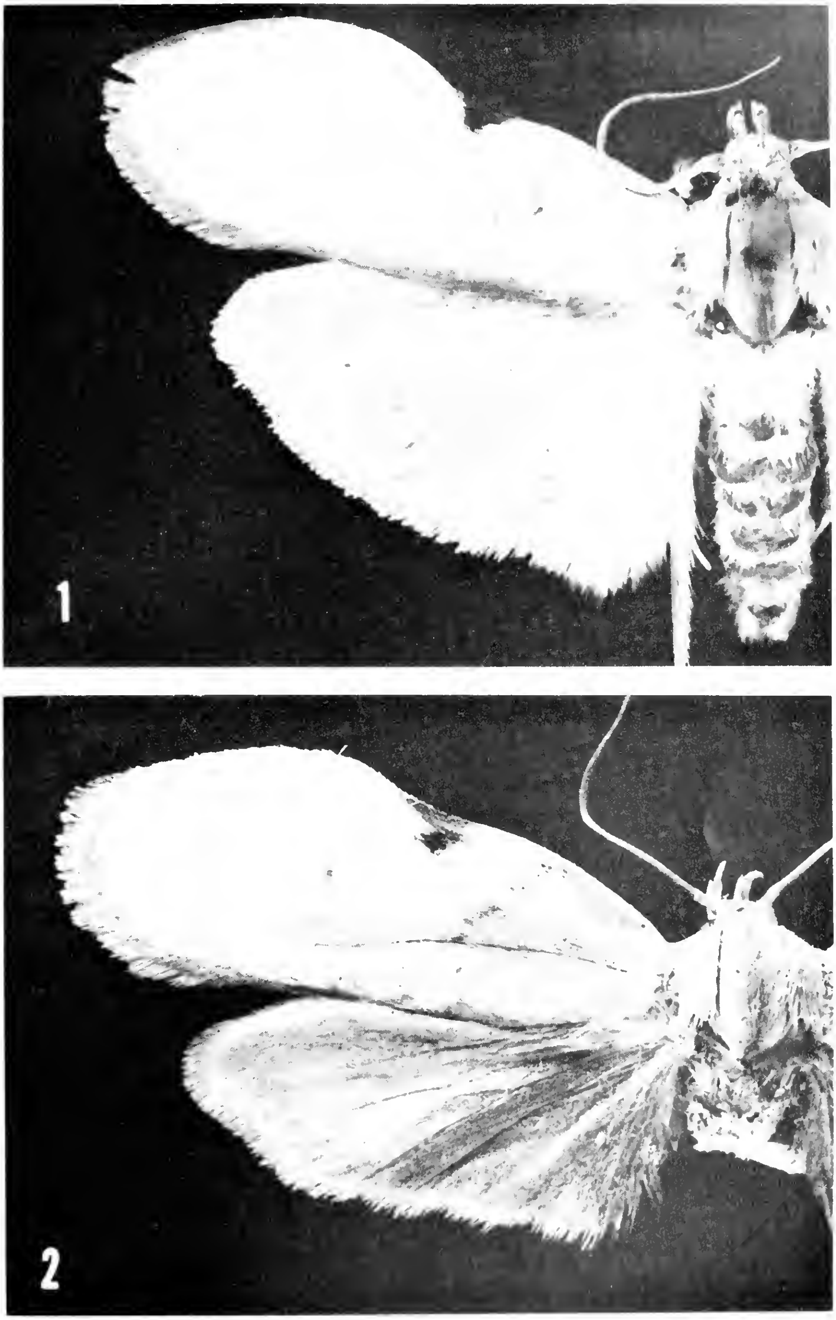

Left wings: 1, *Loxotoma elegans* Zeller; 2, *L. seminigrescens* Meyrick.

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NEOTROPICAL MICROLEPIDOPTERA, XIV[1]

CHILEAN MICROLEPIDOPTERA DESCRIBED BY EMILIO BLANCHARD

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Through the courtesy of Dr. Pierre Viette, Museum Nationale d'Histoire Naturelle, Paris, I have enjoyed the privilege of examining some of the types of Chilean Microlepidoptera described by Emilio Blanchard in 1852. The species recorded in this paper, the types of which I have examined, are *Epigraphia albella, Palpula variegella, Aecophora candidella, Elachista rubella, E. cupreella, E. aureella*, and *E. maculella*. Apparently the type of *Elachista obscurella* (the fifth species described in the latter genus) has been lost or destroyed.

All of the above were described as "Tineidas" and, as far as I am able to ascertain, no attempt has been made to assign these species to

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[1] Prepared with the aid of a National Science Foundation Grant. Previous parts of this same series are: I and II, Clarke, 1962, Proc. U.S. Nat. Mus., vol. 113, no. 3457, pp. 373–388; III, Clarke, 1964, ibid., vol. 115, no. 3480, pp. 61–84; IV, Duckworth, 1964, ibid., vol. 116, no. 3497, pp. 97–114; V, Obraztsov, 1964, ibid., vol. 116, no. 3501, pp. 183–196; VI, Clarke, 1964, ibid., vol. 116, no. 3502, pp. 197–204; VII, Obraztsov, 1966, ibid., vol. 118, no. 3527, pp. 221–232; VIII, Duckworth, 1966, ibid., vol. 118, no. 3531, pp. 391–404; IX, Obraztsov, 1966, ibid., vol. 118, no. 3535, pp. 577–622; X, Duckworth, 1966, ibid., vol. 119, no. 3540, pp. 1–6; XI, Obraztsov, 1966, ibid., vol. 119, no. 3543, pp. 1–12; XII, Duckworth, 1967, ibid., vol. 122, no. 3585, pp. 1–38; XIII, Duckworth, 1967, ibid., vol. 122, no. 3590, pp. 1–8.

appropriate families and genera; indeed, no references to these have been made by modern workers including Meyrick, who apparently never recognized any of the species.

For the most part the types are not in sufficiently good condition to encourage photography; they are either covered with mold or are glued to small pieces of celluloid. The pattern on some of them is clearly visible, but on the others it is obscured. By cleaning a forewing it was possible to make a fairly accurate drawing of the pattern of *Epigraphia albella*—certainly an adequate procedure for identification when taken together with the figure of the genitalia.

Oecophoridae

Epigraphia albella Blanchard

FIGURE 1

Epigraphia albella Blanchard, 1852, *in* Gay, Historia fisica and politica de Chile, Zoologia, vol. 7, p. 107.

This species is clearly oecophorid but is improperly placed in *Epigraphia.* The type is covered with mold, but the following characters are visible: Antenna ciliate. Labial palpus recurved, second and third segments of about equal length. Forewing with 12 veins; 2 remote from 3; 3, 4, and 5 about equidistant; 7 and 8 stalked,

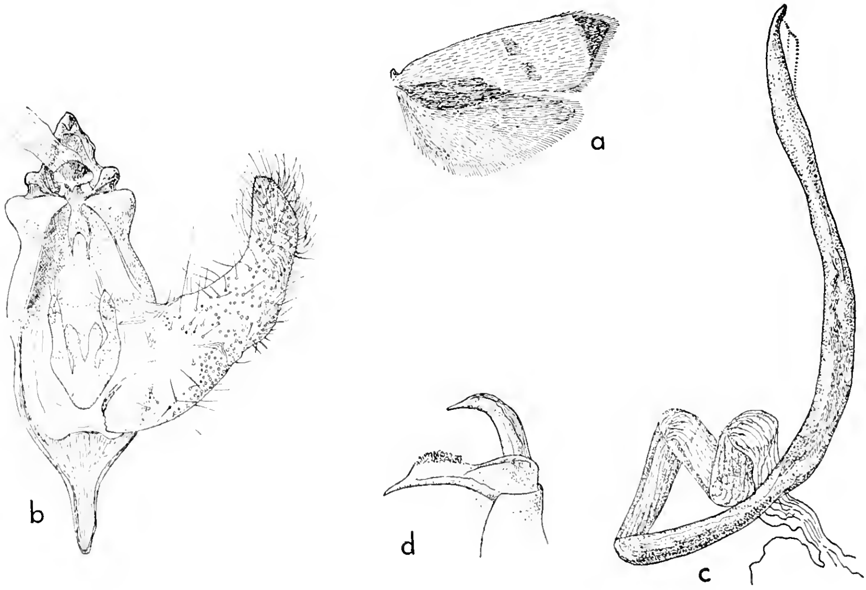

FIGURE 1.—*Epigraphia albella* Blanchard: *a*, right wings showing pattern; *b*, ventral view of male genitalia with left harpe and aedeagus removed; *c*, aedeagus; *d*, lateral aspect of uncus and gnathos.

7 to termen just below apex. Hindwing with 8 veins; 2 remote from 3; 3 and 4 connate; 4, 5, and 6 about equidistant, well separated. Abdomen spined.

Male genitalia figured from slide JFGC no. 11257.

The proper generic placement of this species must await exhaustive studies in southern hemisphere Oecophoridae.

Hyponomeutidae

Eucalliathla, new genus

Type-species: *Aecophora candidella* Blanchard, 1852 *in* Gay, Historia fisica y politica de Chile, Zoologica, vol. 7, p. 109.

Head smooth except posteriorly; face smooth; ocelli absent; tongue well developed; maxillary palpus obsolete. Antenna with pecten on scape. Labial palpus long, slender; second segment with slightly rough scaling beneath; third segment slightly longer than second, acute. Posterior tibia smooth-scaled. Forewing with 12 veins, all veins separate; stigma present; 2 from angle of cell; 2 to 10 approximate; 11 from slightly before middle of cell; accessory cell present. Hindwing with 8 veins; 3 and 4 connate; 5 and 6 long stalked; 6 and 7 nearly parallel. Female genitalia with signum. Male unknown.

This genus is closely allied to *Calliathla* Meyrick but differs from it by the absence of ocelli, smooth head and face, the close proximity of veins 2, 3, and 4 of forewing and the connate condition of veins 3 and 4 of hindwing. In addition, the third segment of labial palpus is longer than the second in *Eucalliathla* but shorter than second in *Calliathla*.

In describing *Calliathla*, Meyrick stated: "Hindwings . . . 5 to 7 nearly parallel." This is not the case; 5 and 6 are stalked, and 6, 7, and 8 are nearly parallel.

Eucalliathla candidella (Blanchard), new combination

FIGURE 2

Aecophora candidella Blanchard, 1852, *in* Gay, Historia fisica y politica de Chile, Zoologica, vol. 7, p. 109.

The type of this small species, in very good condition, is glued by the left side to a piece of celluloid. I removed one pair of wings and the abdomen to make the necessary preparations so the species could be placed properly. The remaining wings are in excellent condition with the upper surfaces exposed. Both wings are shiny white, the forewing with a slight tinge of ocherous.

Female genitalia and wing venation figured from slide JFGC no. 11263.

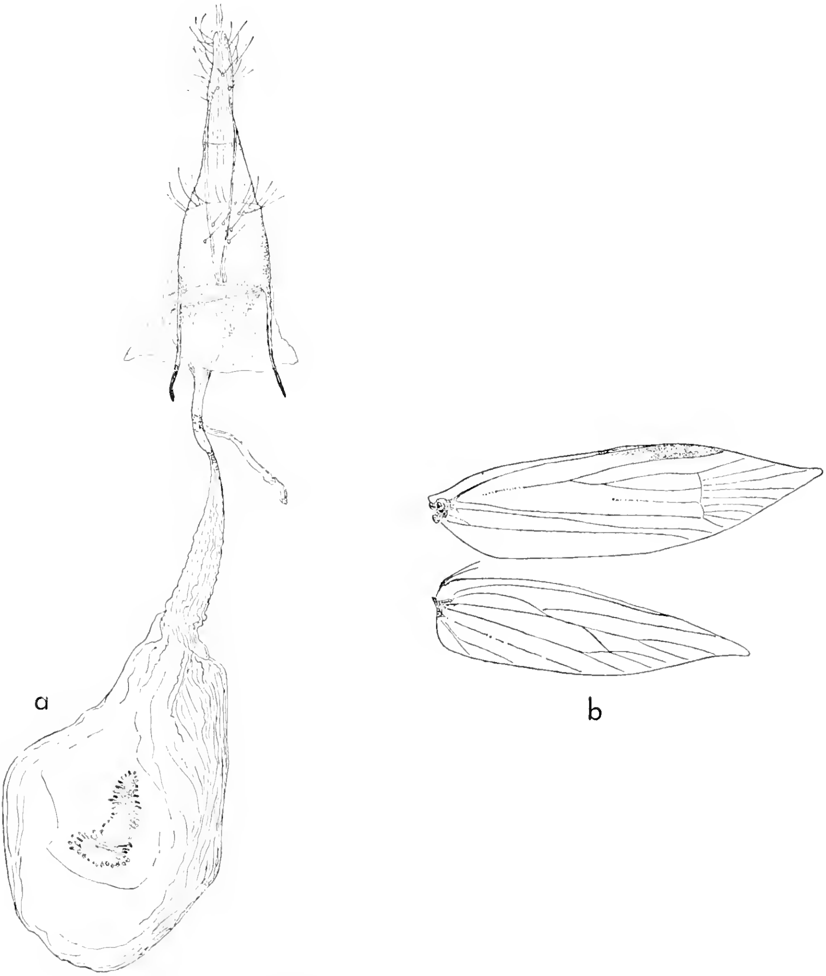

FIGURE 2.—*Eucalliathla candidella* (Blanchard): *a*, ventral view of female genitalia; *b*, venation of right wings.

Acrolepia aurcella (Blanchard), new combination

FIGURE 3

Elachista aurcella Blanchard, 1852, *in* Gay, Historia fisica y politica de Chile, Zoologica, vol. 7, p. 110.

I have before me 13 ♂♂ and 17 ♀♀ (Chile, Llanquihue, Peulla, 7–9.III.1959, JFGClarke) which I have been able to identify as this species. The type, labeled "Chile, Valdivia," although unspread and glued to a piece of celluloid, is in reasonably good condition, and the female genitalia are identical to those of females of my series.

Female genitalia figured from the type, slide JFGC no. 11367.

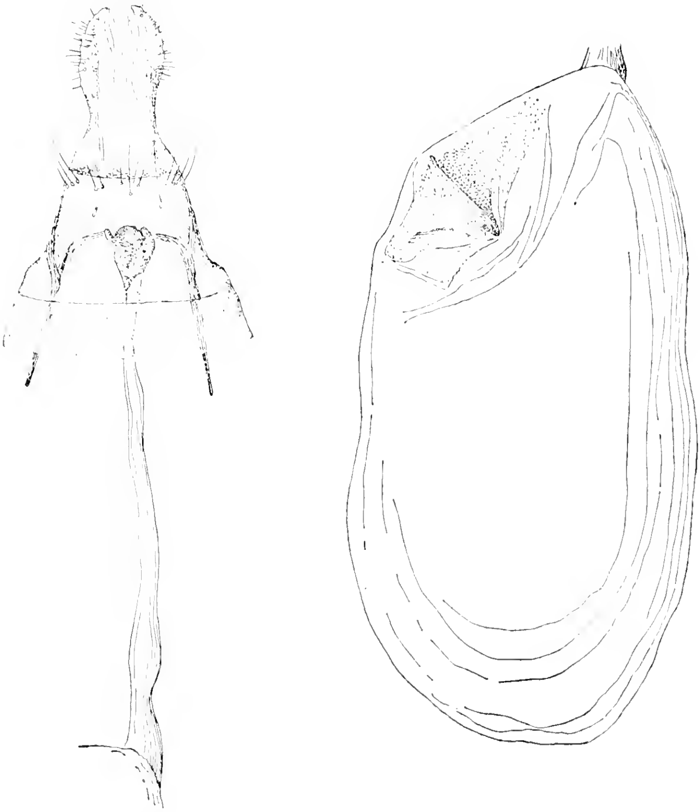

FIGURE 3.—*Acrolepia aureella* (Blanchard): ventral view of female genitalia with bursa copulatrix on right.

Acrolepia maculella (Blanchard), new combination

Elachista maculella Blanchard, 1852, *in* Gay, Historia fisica y politica de Chile, Zoologica, vol. 7, p. 111.

The type, from San Carlos, lacks its abdomen but the species is clearly a hyponomeutid belonging to *Acrolepia*. Actually, *maculella* resembles *aureella* but there are sufficient points of distinction to separate the two. A complete, narrow, transverse, white fascia, at about apical third of forewing, is the most conspicuous feature separating *maculella* from *aureella*.

Elachistidae

Elachista cupreella Blanchard

FIGURE 4*b*

Elachista cupreella Blanchard, 1852, *in* Gay, Historia fisica y politica de Chile, Zoologica, vol. 7, p. 110.

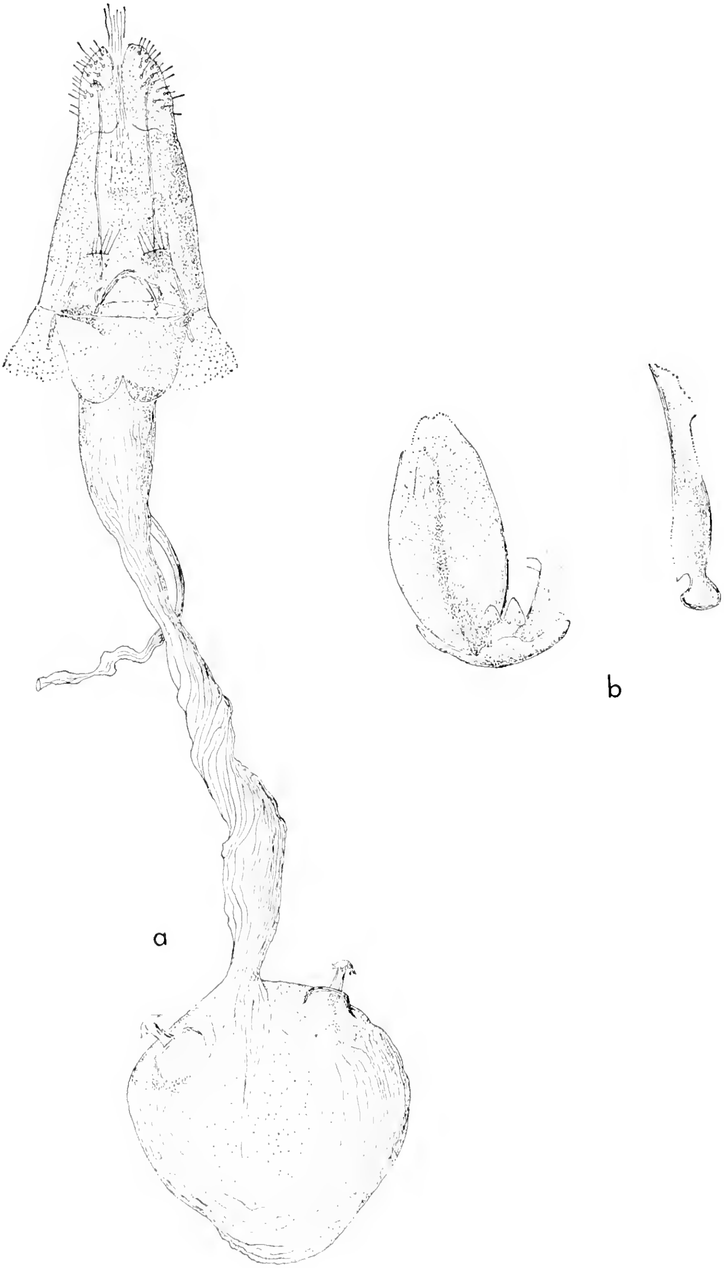

Figure 4.—*Elachista rubella* Blanchard: *a*, ventral view of female genitalia. *Elachista cupreella* Blanchard: *b*, ventral view of male genitalia (fragmentary) with aedeagus to right.

The posterior portion of the abdomen of the type has been damaged by pests, and an insufficient part of the genitalia remains to permit accurate placement of this species. Most of the vinculum, one harpe, part of the aedeagus and the anellus are preserved. The anellus is comparable to that of other species of *Elachista*, and the habitus and pattern of this brilliant little moth recommend its retention in this genus. The type is labeled "Carelmapu."

The male genitalia (partial) are figured from the type slide, JFGC no. 11368.

Elachista rubella Blanchard

FIGURE 4*a*

Elachista rubella Blanchard, 1852, *in* Gay, Historia fisica y politica de Chile, Zoologia, vol. 7, p. 110.

This colorful little species has the fascies of a heliodinid, but the female genitalia rule out placement in that family as we know it. The two peculiar signa are reminiscent of some species of *Phyllocnistis*, but otherwise, *rubella* has no characters in common with species of that genus. The type is labeled "Chile" and recorded from Valdivia.

Female genitalia figured from the type, slide JFGC no. 11369.

Tineidae

Lindera tessellatella Blanchard

FIGURE 5

Lindera tessellatella Blanchard, 1852, *in* Gay, Historia fisica y politica de Chile, Zoologia, vol. 7, p. 106.

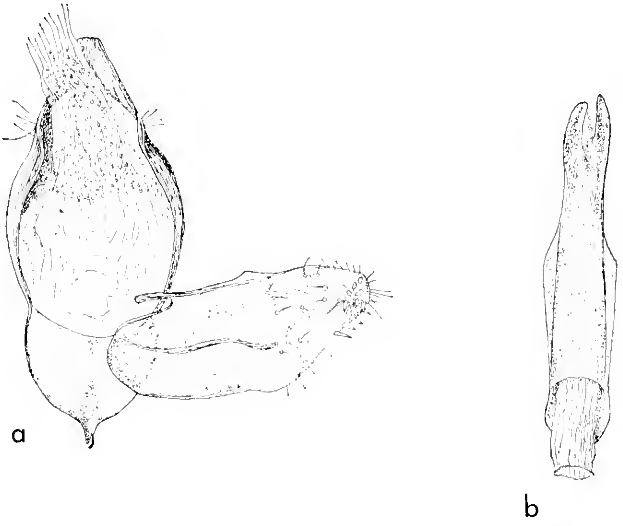

FIGURE 5.—*Lindera tessellatella* Blanchard: *a* (type of *Palpula variegella* Blanchard), ventral view of male genitalia with left harpe and aedeagus removed; *b*, aedeagus.

Palpula variegella Blanchard, 1852, *in* Gay, Historia fisica y politica de Chile, Zoologia, vol. 7, p. 108. [New synonymy.]

Although *tessellatella* has long been recognized, *variegella* has never been associated with it. The type of *variegella* is badly covered with mold and is superficially unrecognizable, but it was possible to obtain an adequate preparation of the genitalia to insure identification. The specimen is a male, and there is no doubt about the synonymy.

Male genitalia figured from slide JFGC no. 11262.

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THE PSOLID HOLOTHURIAN GENUS LISSOTHURIA

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The holothurians of the family Psolidae are unique in that they have adopted an essentially sedentary mode of existence. The body is more or less flattened and strongly bilaterally symmetrical. While the dorsal surface of the body is generally invested in an armor of imbricating calcareous scales, the ventral surface is a soft thin sole surrounded by tube feet that enable the animal to cling to a hard substrate.

These holothurians may be regarded as "pelmatozoans," while the majority of the other holothurian groups are essentially "eleutherozoan" or free-living. As in other groups of sedentary marine animals, the mouth and anus are on the same side of the body, in this case the dorsal surface, and the gut describes a U-shaped course. Among other echinoderms the U-shaped, pelmatozoan-type gut is found in many Paleozoic groups (including crinoids, blastoids, cystoids, and edrioasteroids); crinoids are the only surviving members of these groups. While the modifications resulting from the adoption by psolids of a sedentary existence show some similarities to those in the extinct edrioasteroids (see Fell, 1965), it is believed that the psolids themselves are not an ancient group of holothurians. Although they are strongly bilaterally symmetrical, their internal anatomy reflects a former radial symmetry, and it seems probable that psolids arose from an ancestral stock that was radially symmetrical. This topic is discussed briefly elsewhere (Pawson, 1966) and it is hoped that a full discussion will arise from research now in progress.

Gross features of the internal anatomy of psolids are similar to those in other dendrochirotid holothurians; such modifications as are present can be explained readily in terms of the altered shape of the body. The calcareous ring, for example, lies inside the mouth as usual, but, as the mouth is turned dorsally, the calcareous ring is oriented in the anteroposterior plane, so that the posterior edge of the ring is now ventral. Tube feet are very numerous on the ventral surface of the body and restricted to the radii, forming a continuous fringe around the sole. The midventral radius is usually naked in *Psolus* but carries a varying number of feet in other members of the family. Dorsal tube feet are reduced (as in *Psolidium*, *Stolinus*, *Lissothuria*) or absent altogether (as in *Psolus*).

Within the family Psolidae the genus *Psolus* seems to be the most highly modified. Other genera, especially *Psolidium* and *Lissothuria*, show more features in common with other dendrochirotids, and within the genus *Psolidium* it is difficult to determine whether or not some species should be regarded as members of the Psolidae; they might be referred equally well to one or another family elsewhere in the Order Dendrochirotida.

An attempt is being made to revise the entire family Psolidae. The present paper comprises a revision of the small genus *Lissothuria*, which is restricted to the eastern Pacific Ocean and the Caribbean Sea region.

I would like to thank Dr. Willard D. Hartman of the Peabody Museum, Yale University, for many kindnesses, Drs. Bent Hansen and F. Jensenius Madsen of the Zoological Museum, Copehagen, for their help during my visit to that museum in the summer of 1965, and Captain Fred C. Ziesenhenne of the Allan Hancock Foundation, Los Angeles, for facilitating my study of the collections at that institution.

Status of the Genus *Thyonepsolus* Clark

H. L. Clark (1901a, p. 167) described a new holothurian from the coast of California. The species differed from all other psolids known to Clark at that time in possessing calcareous deposits of a unique type on the dorsal surface of the body. In addition to the overlapping scales characteristic of psolids, the dorsal surface carried hourglass-shaped and tower-shaped calcareous deposits. In view of the nature of these deposits, Clark proposed a new genus, *Thyonepsolus nutriens*, to accomodate this species.

In an article on the echinoderms of the Panama region, Verrill (1867, p. 322) had diagnosed and described *Lissothuria ornata* on the basis of one specimen collected from Panama. Verrill's description was inadequate in some respects, and subsequent authors generally regarded *Lissothuria* as a synonym of *Psolus*, noting that the species required reexamination. Deichmann (1937, p. 172), in describing the new species *Thyonepsolus beebei* from Lower California, suggested that "Verrill's imperfectly described *Lissothuria ornata* (1867) from Panama may quite well be this species."

I have reexamined the type-specimen of *Lissothuria ornata*. The deposits of the dorsal surface of the body of this specimen include hourglass-shaped deposits and towers, which are diagnostic characters of *Thyonepsolus*. In the Zoological Museum, Copenhagen, six other specimens of *L. ornata* from Panama were found. All of this material is described below. It is evident that *Thyonepsolus* is a junior synonym of *Lissothuria*, and it is here proposed that the generic name *Lissothuria* be resurrected as a senior synonym.

Lissothuria Verrill

Lissothuria Verrill, 1867, p. 322.

Thyonepsolus H. L. Clark, 1901a, p. 167. [Type-species: *T. nutriens*, original designation.]

Thionepsolus Delage and Herouard 1903, p. 320. [Error for *Thyonepsolus*.]

Diagnosis.—Psolids with tube feet on dorsal surface of body and in midventral interradius. Dorsal scales few or numerous, imbricating, covered by an external layer of deposits that include hourglass-shaped bodies and towers; one of these types may be absent. Sole deposits are knobbed or smooth plates; in some species shallow or deep cups also present.

Type-species.—*Lissothuria ornata* Verrill (original designation, by monotypy).

Content of genus.—Verrill (1867) described *Lissothuria ornata*. In 1901, H. L. Clark described *Thyonepsolus nutriens*. Deichmann (1930) referred Theel's (1886) species *Psolus braziliensis* to *Thyonepsolus* and later (Deichmann, 1937) described a new species, *T. beebei*, from the Gulf of California. Again, Deichmann (1941) described two other new species, *T. veleronis* from the Galapagos Islands and *T. hancocki* from Lower California. Thus, at the commencement of this study, six species had been named. In this paper, two of the original six species (*Lissothuria ornata* and *Thyonepsolus beebei*) are regarded as synonyms and three species are described as new, so that eight species may now be listed under the genus *Lissothuria*.

Key to Species of Genus *Lissothuria*

1. Dorsal scale covering incomplete . . . . **nutriens** (Clark)
   Dorsal scale covering complete 2
2. Rosettes present in tentacles 3
   Rosettes absent from tentacles 5
3. Sole deposits include cups; plates in sole knobbed . . **antillensis,** new species
   Sole deposits plates only; plates smooth or with inconspicuous knobs . . 4
4. Hourglass-shaped deposits closely resemble cups; average height of towers 0.1 mm. Caribbean . . . . **braziliensis** (Theel)
   Hourglass-shaped deposits of "typical" form; average height of towers 0.27 mm. Eastern Pacific . . . . **ornata** Verrill
5. Deposits in sole include strongly knobbed plates that tend to become 2-layered **deichmannae,** new species
   No such plates in sole 6
6. Sole deposits include cups; hourglass deposits absent. **mortenseni,** new species
   Cups absent from sole; hourglass deposits present 7
7. Towers absent; 7–8 scales between oral and anal apertures. **veleronis** (Deichmann)
   Towers present; ca. 14 scales between oral and anal apertures. **hancocki** (Deichmann)

DISTRIBUTION.—The eight known species in the genus resemble each other in so many respects that it seems likely that the genus is a relatively young one, arising (perhaps from some *Psolidium*-like ancestor) in the Caribbean or Eastern Pacific and dispersing across the Isthmus of Panama when it was below sea level, perhaps during the early Tertiary. At the present time, six species are known from the Eastern Pacific and two from the Caribbean region. This suggests that the migration was from west to east. The distribution of this genus is paralleled by other genera in the Holothuroidea, and it is known that at least 10 species of holothurians are common to the Pacific and Atlantic sides of the Isthmus of Panama.

Lissothuria ornata Verrill

FIGURES 1, 2F–L

Lissothuria ornata Verrill, 1867, p. 322.
Psolus ornatus.—Theel, 1886a, p. 127.—Ludwig, 1892, p. 350.
Thyonepsolus beebei Deichmann, 1937, p. 172, fig. 3; 1938, p. 382; 1941, p. 139, pl. 28 (figs. 1–3).

DIAGNOSIS.—Dorsal scale covering complete. Deposits of dorsal surface are perforated plates, towers, and hourglass-shaped deposits; no cups. Deposits of sole are perforated plates, which are smooth or with a few rounded knobs. Tentacles with rosettes.

DESCRIPTION OF HOLOTYPE.—Specimen cut transversely at middle of body. Total length 51 mm, greatest breadth 18 mm, height at center 10 mm. Mouth anterodorsal, anal aperture posterodorsal. Oral aperture surrounded by numerous irregular valves with sharp points on free edges. Arrangement of valves indeterminable. Dorsal surface completely covered by imbricating scales, through and between which pass inconspicuous tube feet. Finely papillate integument containing calcareous deposits overlies scales. Sole elongate, oval, fringed by 5–6 rows of closely crowded tube feet, which form a continuous margin. Midventral radius with 3–5 rows of tube feet throughout. Sole leathery, opaque. Tentacles richly branched. Color in alcohol yellowish white overall.

Calcareous deposits of dorsal surface (apart from scales) are towers, hourglass-shaped deposits, and some flat plates. Towers complex, height ranging from 0.25 to 0.40 mm, diameter at base 0.15 to 0.20 mm. Tops of towers irregular, not carrying distinct teeth (fig. 1F). Hourglass deposits fragile, with numerous perforations, varying greatly in size and shape; length ranges from 0.08 to 0.15 mm (fig. 1B). Flat plates with larger central perforations and smaller marginal perforations present; diameter ranges from 0.05 to 0.3 mm (figs. 1D,E). Plates fragile, often broken.

Sole with flat perforated plates of varying shape (fig. 1C), greatest length 0.17 to 0.22 mm. Margins of plates smoothly indented; some plates with low rounded knobs.

Tentacles with minute rosettes that vary greatly in size and degree of complexity (fig. 1G), also curved or flat perforated plates and rods (fig. 1A). Tube feet with end plates; feet supported by narrow perforated rods of average length 0.19 mm (fig. 1H).

Color.—Verrill (1867, p. 322) noted that the color in alcohol of this specimen was "light purple, whitish beneath, disk [sole] purple, with a yellowish white ring around the mouth; tentacles purple at base, the subdivisions yellowish." At the time Verrill described the specimen, it had been in alcohol for less than six months, and thus apparently the color had faded very little. No trace of this striking original coloration now can be found.

Holotype.—Peabody Museum of Natural History, Yale University, YPM no. 5327.

Type-locality.—Pearl Island Panama; collected by F. H. Bradley, December 1866.

Additional material.—A collection of six specimens from Taboga, Panama, was examined in the Zoological Museum, Copenhagen. Some information on the internal anatomy of the species is given below.

Total length 27–37 mm. Midventral radius with 3–5 rows of tube feet anteriorly and posteriorly, but at center of radius rows, without exception, double. Dorsal surface of body with 8–10 scales between oral and anal apertures. Mesentery of posterior loop of intestine lies in left ventral interradius. Gonad a large mass of long unbranched cacea. A single bulbous Polian vesicle; respiratory trees flattened tubes with long simple branches. Ventral retractor muscles smaller than dorsal muscles (perhaps an artifact of preservation). Calcareous ring simple, interradial pieces bluntly pointed anteriorly, radial pieces notched anteriorly for attachment of radial muscles. Posterior margin of calcareous ring undulating, lacking projections.

In smaller specimens towers not nearly as well developed as in holotype (fig. 2K); deposits in sole tend to have a more regularly indented margin (fig. 2F).

REMARKS.—*Lissothuria beebei* (Deichmann) is regarded here as a synonym of *L. ornata*. No significant differences between these species can be found; in her original description of *L. beebei*, Deichmann (1937, p. 174) called attention to the possibility that the species were synonymous (see above). *L. ornata* may be distinguished readily from other Eastern Pacific species since it is the only species that possesses rosettes in the tentacles.

DISTRIBUTION.—The species has been recorded from the following localities: Pearl Island, Gulf of Panama (type-locality; Verrill, 1867, p. 322); Taboga, Panama, coast under stones at low water, collected by Th. Mortensen, Nov. 7, 1915; off Arena Bank, 23°26′ N, 109°24′30″ W, 2.5 fathoms, in *Pocillopora ligulata* (type-locality of *L. beebei;* Deichmann, 1937, p. 173); Tangola-Tangola, Mexico, 15°46′ N, 96°06′ W, 15–20 fathoms (Deichmann, 1941, p. 140); Thurloe Bay, west coast of Lower California, 8–10 fathoms (Deichmann, 1941, p. 140); Situatanejo Bay, Mexico, 17°37′ N, 101°34′ W, shore (Deichmann, 1938, p. 382); Jasper Island, Gulf of Nicoya, Costa Rica, 9°46′ N, 84°54′ W, shore (Deichmann, 1938, p. 382). The species thus ranges from Lower California to Panama in depths of 0–36 meters and has been found on two occasions in association with corals.

Lissothuria nutriens (Clark)

Thyonepsolus nutriens H. L. Clark, 1901a, p. 169, figs. 6–14; 1901b, p. 491; 1923, p. 161.—Deichmann, 1937, p. 174; 1941, p. 138, pl. 26 (figs. 1–5).

DIAGNOSIS.—Dorsal scale covering incomplete. Deposits of dorsal surface are towers and hourglass-shaped deposits; no cups. Deposits of sole are perforated plates with raised marginal projections and small cups. Tentacles lack rosettes.

MATERIAL EXAMINED.—Allan Hancock Foundation: Velero Sta. 1447–42, Point Arguello Boat Station, outside of breakwater, among loose rock in tide pools, collected Mar. 13, 1942, by F. C. Ziesenhenne, 1 specimen; Velero Sta. 1575–46, 6.7 miles south of surf, Pedernales Point, Santa Barbara Co., Calif., intertidal, Dec. 7, 1946, 1 specimen; Velero Sta. 1576–46, 0.5 mile north of Cayucos, San Luis Obispo Co., Calif., intertidal, Dec. 8, 1946, 1 specimen.

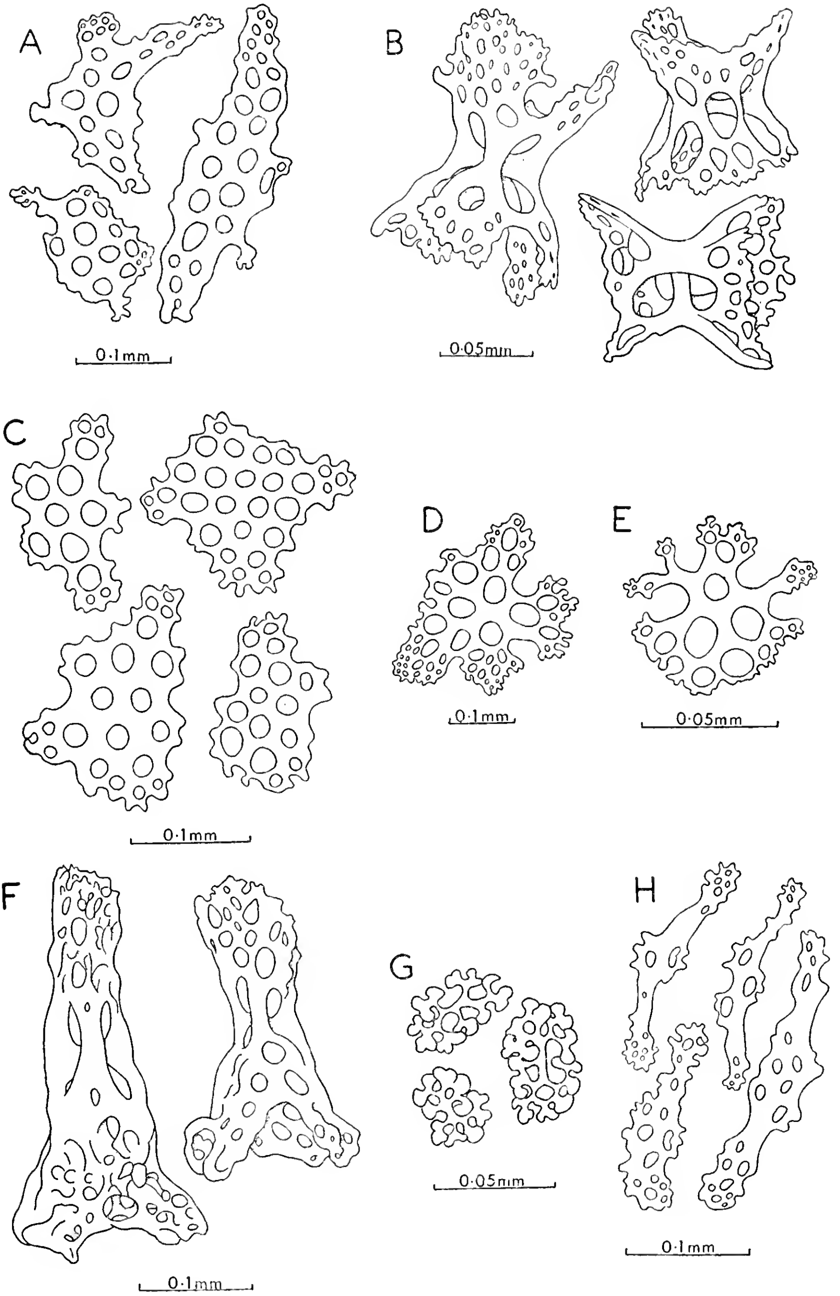

FIGURE 1.—*Lissothuria ornata* Verrill, holotype: A, plates from tentacles; B, hourglass-shaped deposits from dorsal body wall; C, perforated plates from sole; D, portion of larger plate from dorsal body wall; E, smaller plate from dorsal body wall; F, towers from dorsal body wall; G, rosettes from tentacle; H, deposits from tube feet.

Remarks.—This relatively common species is bright red in life, and the female broods its eggs on the dorsal surface of the body (Clark, 1901a; Deichmann, 1941). The brooding habit is unknown in other members of the genus.

Distribution.—*L. nutriens* is known only from the coast of California, where it ranges from Pacific Grove in the north to the Gulf of Santa Catalina in the south in depths of 0–20 m. Deichmann (1941) examined a specimen of this species labeled "Galapagos Is." but believed that the labeling was erroneous.

Lissothuria braziliensis (Theel)

Figures 2a–e

Psolus braziliensis Theel, 1886b, p. 15, fig. 7.
Thyonepsolus braziliensis Deichmann, 1930, p. 192, pl. 21 (figs. 1–6).—Clark, 1933, p. 117.—Deichmann, 1954, p. 401.

Diagnosis.—Dorsal scale covering complete. Deposits of dorsal surface are perforated plates, hourglass-shaped deposits resembling cups, and towers. Deposits of sole are perforated plates, which are smooth but with raised marginal projections. Tentacles with rosettes.

Material examined.—Museum of Comparative Zoology, Harvard University, no. 348, Porto Seguro, Brazil, 2 specimens (syntypes).

Description.—Larger specimen 32 mm in total length, tentacles expanded. Smaller specimen 14 mm in total length, tentacles retracted. Mouth anterodorsal, anus posterodorsal. Oral aperture surrounded by numerous sharply pointed valves. Tentacles richly branched. Dorsal scales numerous, approximately 8–10 between mouth and anus. No obvious skin overlies scales. (For additional anatomical details, see Theel, 1886, p. 15; Deichmann, 1930, p. 192; and Deichmann, 1954, p. 401.) Sole deposits are plates with irregularly indented edges, around which projections are slightly upraised to give appearance of small knobs (fig. 2b). Rosettes in tentacles not complex (fig. 2e); also present in tentacles are perforated plates of two types, and rods. Larger plates of average length 0.47 mm are long, broad, with numerous perforations (fig. 2c); smaller plates and rods of average length 0.16 mm are narrow, with few perforations (fig. 2d). Ventral tube feet have well-developed end plates and contain elongate, often curved, perforated supporting rods of average length 0.18 mm (fig. 2a).

Lectotype.—I select the larger specimen (total length 32 mm) of the two syntypes as the lectotype of this species.

Remarks.—In possessing rosettes in the tentacles, *L. braziliensis* falls close to *L. antillensis*, new species (see below), but it differs from that species in lacking cups in the sole.

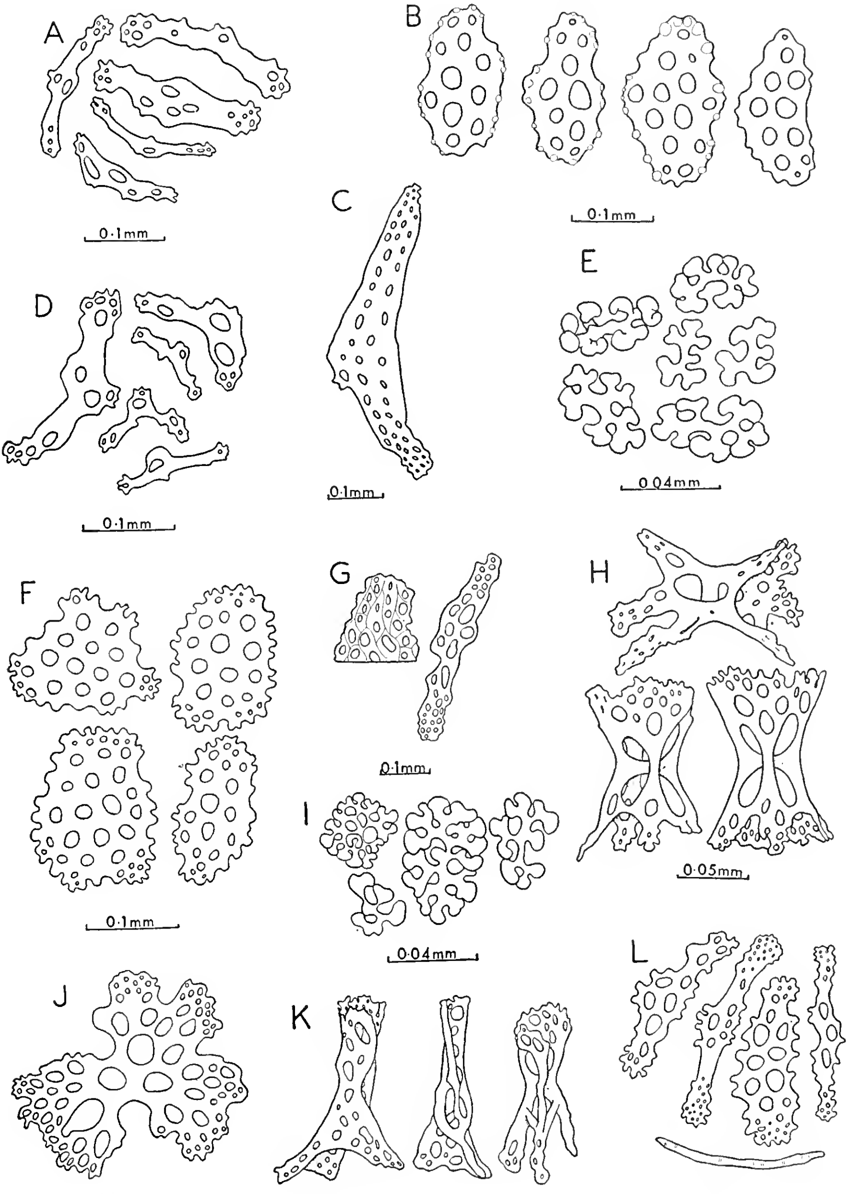

FIGURE 2.—*Lissothuria braziliensis* (Théel), paratype: A, deposits from tube feet; B, perforated plates from sole; C, larger plate from tentacle; D, smaller rods and plates from tentacle; E, rosettes from tentacle. *L. ornata* Verrill, paratype: F, perforated plates from sole; G, plates from tentacle; H, hourglass-shaped deposits from dorsal body wall; I, rosettes from tentacle; J, plate from dorsal body wall; K, towers from dorsal body wall; L, deposits from tube feet.

Distribution.—The species has been reported from the type-locality (Théel, 1886b, p. 15), Porto Seguro, Brazil. Deichmann (1930, p. 193) recorded numerous specimens from Buccoo Bay, Tobago, British West Indies. In a later publication Deichmann (1954, p. 401) noted that this species occurs in "shallow water, attached to rocks or seaweeds."

***Lissothuria antillensis*, new species**

Figure 3

Diagnosis.—Dorsal scale covering complete. Deposits of dorsal surface are perforated plates, towers, and cups; no hourglass-shaped deposits. Deposits of sole are knobbed plates and cups. Tentacles with rosettes.

Description.—Body elongate, about twice as long as broad, mouth anterodorsal, anus dorsal. Dorsal surface of body arched, sole flat, rectangular. Dorsal surface with thick imbricating scales approximately 1.5 mm in diameter; 7 scales between mouth and anus. Scales perforated for passage of tube feet, which are scattered over dorsal surface; sometimes 4–5 feet pass through one scale. Oral valves of varying shape, sharply pointed distally, interradial valves larger than radial valves. Scales overlaid by thick soft integument filled with calcareous deposits.

Sole with 2–3 rows of larger tube feet along left and right ventral radii (in addition to single row of smaller marginal feet). Midventral radius with tube feet throughout, 3 rows anteriorly and posteriorly, 1–2 rows near center of sole.

Color in alcohol light to dark brown; tentacles dark brown. Internal anatomy not examined.

Calcareous deposits of dorsal surface (apart from scales) are perforated plates, towers, and cups. Perforated plates small, smooth, average greatest length 0.1 mm (fig. 3E); larger plates occasionally found. Towers complex, with dentate apex; average height 0.18 mm, average diameter of base 0.15 mm (fig. 3G). Deep cups (fig. 3A) common on dorsal surface; cups typically with 4 large perforations and 4 conspicuous knobs projecting from underside. Cup rim of variable shape, with numerous irregular projections. No hourglass-shaped deposits found.

Sole deposits are plates and cups. Plates 0.1 to 0.12 mm in length, oval to rectangular, perforated, with low rounded knobs around margin and in center (fig. 3B). Cups of average diameter 0.074 mm, shallow, resembling buttons, with 4 larger perforations and some scattered smaller perforations; margin and center of each cup with low rounded projections (fig. 3F).

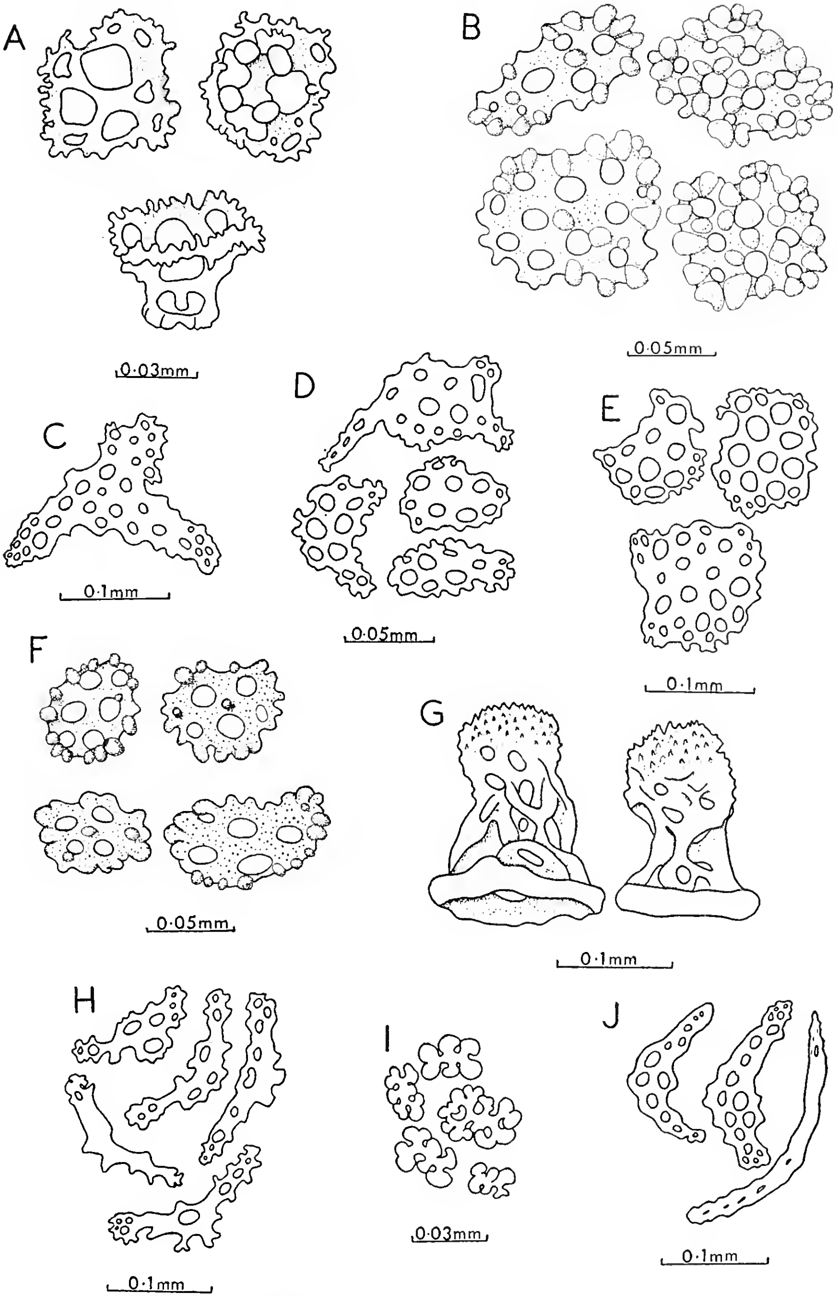

FIGURE 3.—*Lissothuria antillensis*, new species: A, cups from dorsal body wall; B, perforated plates from sole; C, rare larger plate from tentacle; D, small plates from tentacle; E, plates from dorsal body wall; F, cups from sole; G, towers from dorsal body wall; H, deposits from ventral tube feet; I, rosettes from tentacle; J, curved perforated rods from tentacle

Dorsal and ventral tube feet with end plates 0.21 mm in diameter, and curved perforated supporting rods and plates of average greatest length 0.15 mm. Tentacles with numerous rosettes (fig. 3I), larger curved perforated rods (fig. 3J) and plates (fig. 3C), and smaller plates (fig. 3D). Larger perforated plates uncommon.

HOLOTYPE.—Complete specimen, expanded, total length 10 mm, greatest breadth 4.5 mm, height 4 mm. Lodged at Universitetets Zoologiske Museum, Copenhagen, Denmark.

TYPE-LOCALITY.—St. Thomas, Virgin Islands (date and depth unknown); collected by A. A. Riise.

PARATYPES.—Three specimens 9 x 5 mm (length x greatest breadth), 12 x 5 mm, 9 x 4 mm. Locality and depository as above.

REMARKS.—While examining collections in the Zoological Museum at Copenhagen, I found the above specimens labeled "*Psolus antillensis* Lütken." I know of no reference to this species in the literature. Drs. Bent Hansen and F. Jensenius Madsen agreed that the labels with the specimens were written by Dr. C. F. Lütken during the latter part of the 19th century, and it appears that *Psolus antillensis* is one of several of Lütken's manuscript names. The name is validated here.

Lissothuria antillensis differs from its Caribbean congener *L. braziliensis* in having shallow cups among the deposits of the sole.

Lissothuria mortenseni, new species

FIGURE 4

DIAGNOSIS.—Dorsal scale covering complete. Deposits of dorsal surface are towers and a few small plates; no cups, no hourglass-shaped deposits. Deposits of sole are shallow cups and, rarely, small smooth plates. Tentacles lack rosettes.

DESCRIPTION.—Body approximately two-thirds as broad as long. Mouth and anus dorsal, each surrounded by numerous sharply pointed valves. Dorsal surface of body covered by imbricating scales approximately 1.5 mm in diameter; approximately 6 scales between oral and anal apertures. Scales covered by dense coat of small granules. Dorsal tube feet few, minute, passing through and between scales. Tentacles richly branched.

Sole transparent, surrounded by double row of tube feet. Single or triple rows not uncommon in smaller and larger specimens respectively. Midventral radius naked or with 1 or a few tube feet in larger specimens. Specimens 8–9 mm in total length already sexually mature. Sexes separate, eggs less than 0.5 mm in diameter.

Calcareous deposits of dorsal surface (apart from scales) are almost exclusively towers of approximately same size and shape; average height 0.13 mm, average diameter of base 0.13 mm (figs. 4A,B).

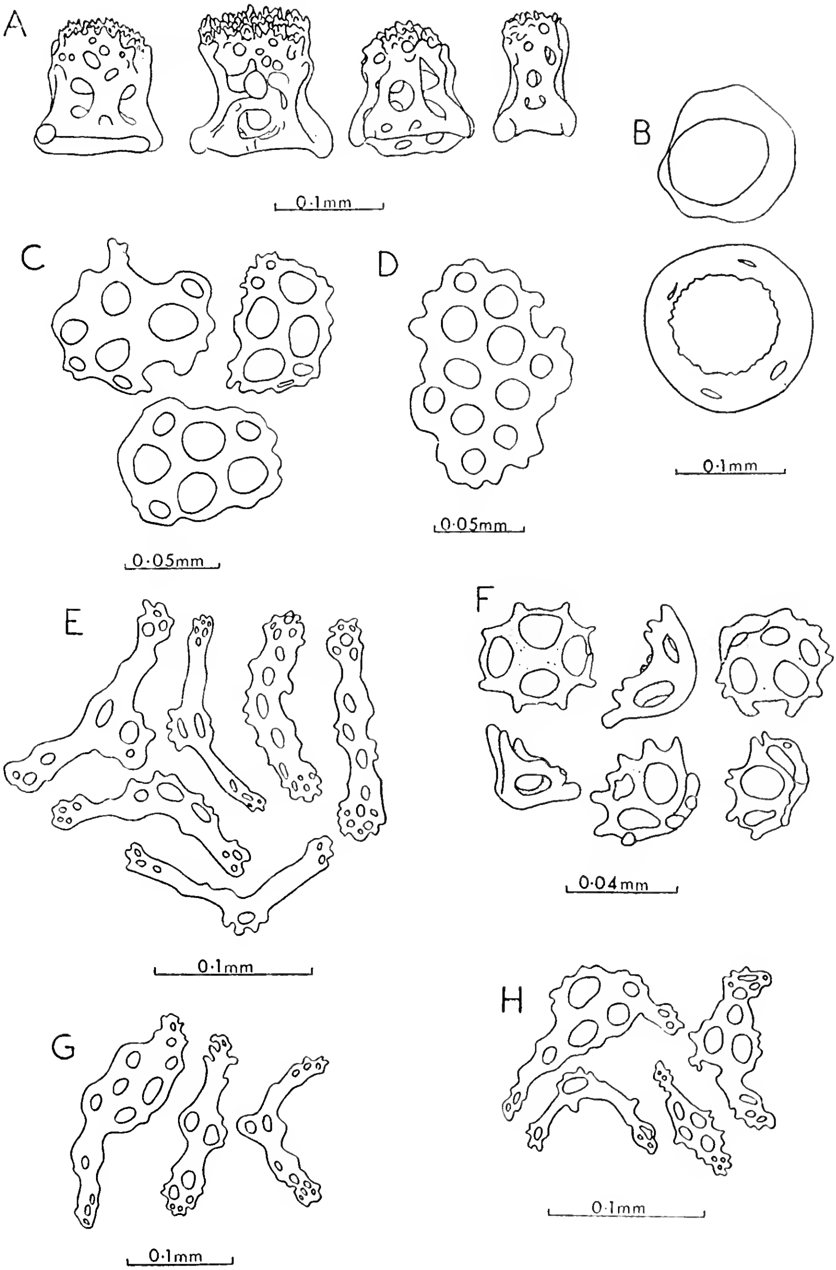

FIGURE 4.—*Lissothuria mortenseni*, new species: A, towers from dorsal body wall; B, basal view of towers (partly diagrammatic); C, rare plates from dorsal body wall; D, rare plate from sole; E, deposits from tube feet; F, cups from sole; G, larger deposits from tentacle; H, smaller deposits from tentacle.

Small plates (fig. 4C) sparingly scattered among towers. No hourglass-shaped deposits; no cups. Sole with numerous shallow cups, typically with 4 perforations (fig. 4F). Small plates (fig. 4D) occur rarely among cups. Ventral tube feet with well-developed end plates and supporting deposits in form of curved rods and plates 0.11 to 0.15 mm in length (fig. 4E). Tentacles with larger curved or straight rods and plates 0.130 to 0.225 mm in length (fig. 4G) and smaller rods and plates 0.08 to 0.13 mm in length (fig. 4H). No rosettes in tentacles.

HOLOTYPE.—Complete specimen, total length 12.5 mm, greatest breadth 9.8 mm. Located at Universitetets Zoologiske Museum, Copenhagen, Denmark.

TYPE-LOCALITY.—San Jose Island, Gulf of Panama, 25 fathoms, collected Jan. 27, 1916, by Th. Mortensen.

PARATYPES.—Thirteen specimens, total length 8–14.5 mm. Locality and depository as above.

REMARKS.—This species is named in honor of the late Dr. Th. Mortensen, whose Pacific Expedition of 1914–1916 contributed so much to our knowledge of echinoderms.

Lissothuria mortenseni is known from near the type-locality of *L. ornata* Verrill but differs from that species in lacking rosettes from the tentacles and hourglass-shaped deposits from the dorsal surface of the body.

***Lissothuria deichmannae*, new species**

FIGURE 5

DIAGNOSIS.—Dorsal scale covering complete. Deposits of dorsal surface are hourglass-shaped deposits and flat plates; no towers. Deposits of sole are larger heavily knobbed plates, which tend to become 2-layered, smaller plates with knobbed margins, and hourglass-shaped deposits. Tentacles lack rosettes.

DESCRIPTION.—Single specimen approximately half as broad as long. Tentacles expanded, oral and anal apertures dorsally placed, surrounded by numerous sharply pointed valves. Dorsal surface covered by scales overlaid by thick integument packed with calcareous deposits. Sole thin, with 2–3 rows of marginal tube feet. Midventral radius with 1–2 rows of tube feet throughout, more crowded anteriorly and posteriorly, but scattered at center of radius.

Dorsal deposits (apart from scales) are hourglass-shaped deposits and flat plates. No towers found. Hourglass-shaped deposits variable in shape and size (fig. 5A), length ranging from 0.05 to 0.1 mm. Some resemble cups with ventral projections; others are asymmetrical. Flat plates of 0.18 mm average greatest length, with larger perforations near center (fig. 5E); some plates may occur in dorsal tube feet.

Sole deposits are large plates with conspicuous knobs, which become multilayered with growth (fig. 5F); plates approximately circular, massive, of average diameter 0.14 mm. Smaller plates with indented, knobbed margins and occasionally small knobs elsewhere also present; plates with few large perforations, generally 4 central perforations larger. Average length of small plates 0.1 mm (fig. 5D). Overlying plates are small numbers of hourglass-shaped deposits similar to those of dorsal surface, but even more variable in shape.

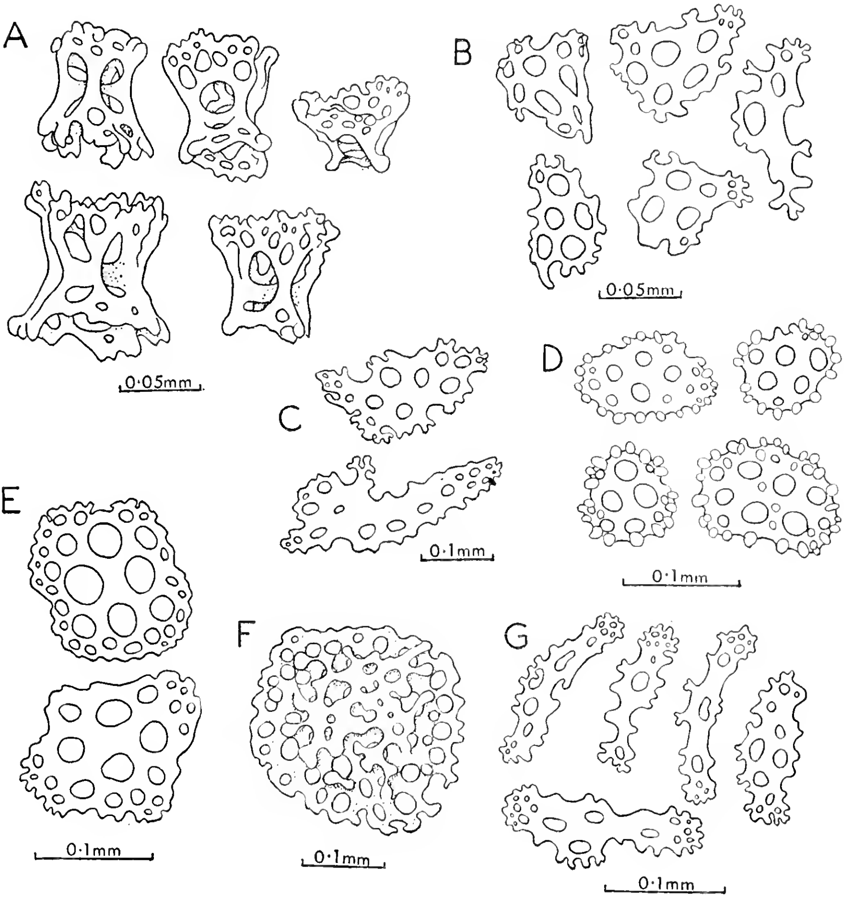

FIGURE 5.—*Lissothuria deichmannae*, new species: A, hourglass-shaped deposits from dorsal body wall; B, smaller rods and plates from tentacles; C, larger plates from tentacles; D, smaller knobbed plates from sole; E, plates from dorsal body wall; F, larger 2-layered knobbed plate from sole; G, deposits from ventral tube feet.

Tentacle stems and digits with larger plates up to 0.30 mm in length (fig. 5C) and smaller rods and plates up to 0.1 mm in length (fig. 5B). Ventral tube feet with well-developed end plate and curved, perforated supporting rods and plates of average length 0.14 mm (fig. 5G).

HOLOTYPE.—Complete specimen, total length 10.5 mm, greatest breadth 4.5 mm, height 3.0 mm. Located in the collection of the Allan Hancock Foundation, Los Angeles, AHF no. 325.1.

TYPE-LOCALITY.—Velero Sta. 1660–48, southwest shore of Smuggler's Cove, Santa Cruz Island, Calif., shore, collected Dec. 29,1948.

REMARKS.—It is a pleasure to name this species in honor of Dr. Elisabeth Deichmann of the Museum of Comparative Zoology, Harvard University. This species is unique in possessing large sole deposits that tend to become multilayered, and it is thus readily distinguishable from other *Lissothuria* species. Although *L. nutriens* (Clark) is known to occur in the area where this new species was collected, it is not likely that *L. deichmannae* is merely a variant of *L. nutriens*, for the sole deposits of the two species are completely different.

Lissothuria veleronis (Deichmann)

Thyonepsolus veleronis Deichmann, 1941, p. 140, pl. 26 (figs. 6–8), pl. 27 (figs. 8–9).

DIAGNOSIS.—Dorsal scale covering complete. Deposits of dorsal surface are hourglass-shaped deposits resembling cups; no towers. Deposits of sole are knobbed plates. Tentacles lack rosettes.

REMARKS.—This species has not been found since Deichmann (1941, p. 140) described the single specimen collected from Tagus Cove, Albemarle Island, Galapagos Islands. It may be distinguished readily from other Eastern Pacific species since no towers occur among the dorsal deposits. Deichmann (1941, p. 140) suggests that perhaps the lack of towers is accidental. If this is so, then the characteristic knobbed plates of the sole serve to distinguish this species from others in the genus.

Lissothuria hancocki (Deichmann)

Thyonepsolus hancocki Deichmann, 1941, p. 140, pl. 27 (figs. 1–7).

DIAGNOSIS.—Dorsal scale covering complete. Deposits of dorsal surface are hourglass-shaped deposits and towers. Deposits of sole are knobbed plates. Tentacles lack rosettes.

REMARKS.—As with the above species, no further material of *L. hancocki* has been reported in the literature. Deichmann (1941, p. 141) described this species on the basis of a series of 49 specimens collected in the Gulf of California and off the coast of Ecuador in depths of 5–165 fathoms.

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A NEW SPECIES OF VICTORELLA FROM SOUTHERN CALIFORNIA (BRYOZOA: CTENOSTOMATA)[1]

By WILLIAM C. BANTA[2]

A new species of ctenostome polyzoan, *Victorella argilla*, has been discovered in great abundance in seven southern California locations. It exists in two growth forms, similar to the growth forms of *Victorella pavida* Kent. In the younger stage (form A) the animal is nearly indistinguishable from certain species of *Arachnidium*, whereas the older stage (form B) shows closer affinities to *Nolella* and *Cryptopolyzoon*. In many respects, especially the budding of new zooids from the apertural papilla, the animal is a typical *Victorella*. In others, however, it is unique: it inhabits marine waters, not brackish ones as do other *Victorellas*, and it possesses peculiar filiform processes modified for the accumulation of sediment.

The colony consists of more than one-half inorganic matter tightly bound to the zoecia by an adhesive. The spreading zoaria appear early in the pattern of ecological succession of some environments and effectively crowd out many competitors. It is the most abundant animal species in certain areas.

This paper would not have been written without the patient efforts of Robert R. Given, to whom credit should be given not only for the

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discovery of *Victorella argilla* but also for much of the ground work necessary for its characterization. I especially wish to thank Patricia L. Cook of the British Museum (Natural History) for her helpful advice and criticism and for the loan of a number of specimens, John S. Bullivant for his invaluable suggestions, and John D. Soule for his kind encouragement and loan of specimens. G. Dallas Hanna, William Miller, D. W. Kelley, and J. S. Ryland were of great help in locating material; K. June Lindstedt and Kristian Fauchald deserve special mention for their help in illustrating, translating, and otherwise readying the manuscript for press. Many thanks also are due Russel L. Zimmer, Olga Hartman, John L. Mohr, Diane Robbins, Robert Woollacott, and Timothy Wyatt for their critical readings of the manuscript.

Victorella Kent, 1870

Victorella argilla, new species

Holotype.—United States National Museum, Washington, D.C., USNM no. 11918: fragment of form A colony fixed in Bouin's fluid and preserved in 70 percent alcohol.

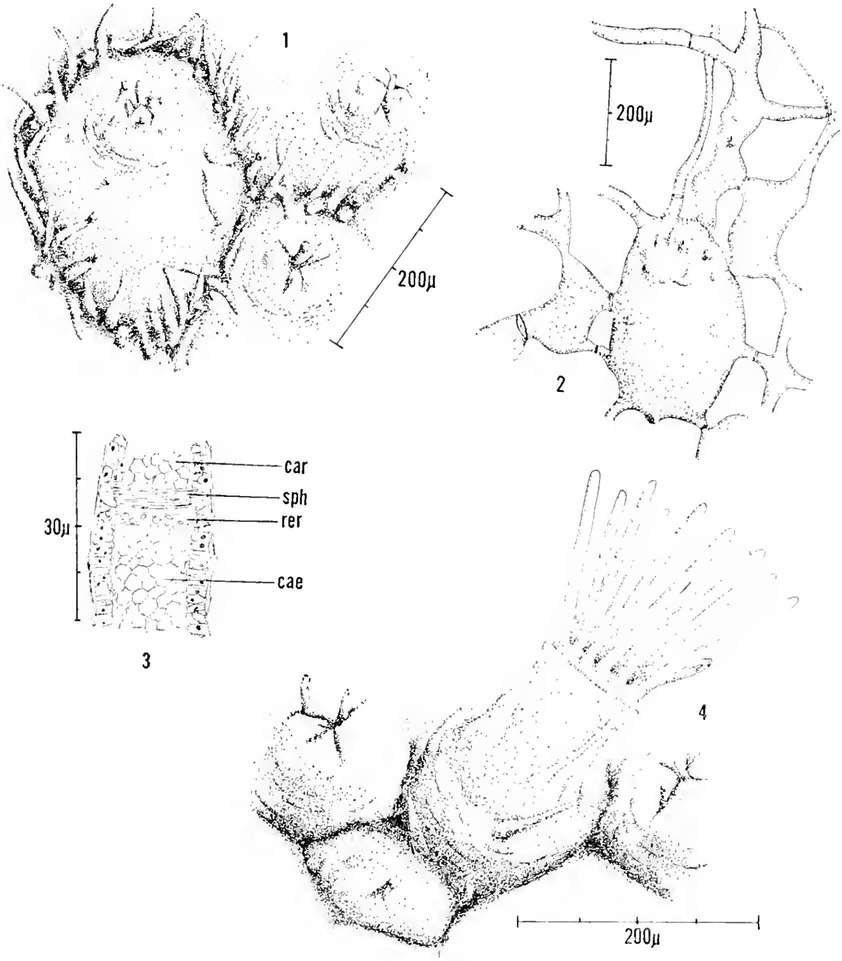
Paratypes.—USNM no. 11919: fragment of form B colony fixed in Bouin's fluid, preserved in alcohol. Allan Hancock Foundation, University of Southern California, Los Angeles; colonial fragments, form B. Some additional paratype material is retained in the author's collection. All material is from the type-locality (see p. 10).

Diagnosis.—Young colonies (form A) are composed of flattened zoecia connected by septate tubular evaginations of the body wall, which anastomose irregularly, producing an *Arachnidium*-like colony. Older zoecia (form B) are produced by a pronounced elongation of the apertural papilla, drawing the polypide away into the tubular portion of the zoecium.

The zoecia bear numerous filiform processes modified for the accumulation of foreign material, and old zoaria form thick, tough layers with a very high content of inorganic matter, especially silt. The polypide has 12 tentacles; an intertentacular organ is present in form B. There is no gizzard, a single funiculus; vestibular muscles are bilateral (form A) or radial (form B), and the aperture is not quadrangular.

FORM A

Zoarium.—In this growth form the species is a thin unilaminar mat of flattened zoecia resembling a small *Alcyonidium*. The zoecia, where clearly seen, are brownish to colorless, oval, and measure 0.3–0.4 mm long by 0.2–0.3 mm wide. In the center of the colony the zoecia stand in close quincunx (fig. 1), communicating with one another through very short tubules that originate from the basal-lateral wall of the zoecium. In the more peripheral portions of the colony the tubules are considerably longer and the zoecia are wider apart (fig. 2).



FIGURES 1–4.—*Victorella argilla:* 1, three zoecia from the center of a form A colony; 2, developing zooids and anastomosing tubules from the periphery of a form A colony; 3, tangential section at the junction of the cardium and caecum of a form A zooid (see fig. 7: sph.) (abbreviations: cae=caecum, car=cardium, rer=reinforced region, sph=sphincter); 4, surface of a form B colony, one polypide extruded.

Intercalary tubules are interrupted by a thick septum with a heavily reinforced annulus and a small central pore. There is only one septum per tubule; the tubules are therefore not kenozoecia and do not represent true stolons in the sense of Silén (1944, p. 29).

New zooids are formed at the periphery of the colony by the anastomosis of thin-walled tubules that originate as simple evaginations from the basal-lateral wall of young zoecia. The method is reminiscent of the budding pattern of *Arachnidium fibrosum* Hinks as described by Prenant and Bobin (1956, p. 228; see also p. 224 and fig. 99). It is unlike the budding of *Victorella pavida* Kent as described by Braem (1951, p. 10) or that of *Arachnidium irregulare* Harmer (1915, p. 49) in that the connecting tubules of these forms do not anastomose.

Filiform processes.—Early in development, even before the first traces of the polypide have begun to appear, elongate evaginations originate on the frontal surface of the zoecium (fig. 2). These processes are conspicuous, even at the early stage shown in figure 2, because a thick, dark coat of foreign material is already adherent to them. In section these processes can be seen to be composed of the following four layers: (1) an outermost layer of detritus and sediment; (2) a cuticle; (3) epidermis; (4) a peritoneum. The processes are clearly simple evaginations of the body wall. Septa are lacking.

Very similar, presumably homologous structures have been reported from a number of related ctenostome species. These include *Arachnidium fibrosum* Hinks (1880, p. 511), *Nolella sawayai* Marcus (1938, p. 52), *Nolella horridum* (O'Donoghue and O'Donoghue, 1926 p. 61), *Nolella spinifera* (O'Donoghue, 1942, p. 59), *Arachnoidea barentsia* Kluge (1962, p. 212), and *Cryptopolyzoon evelinae* Marcus (1942, p. 477). The structures have not been studied in detail and each author has coined his own terminology without reference to other species. As a result, the terminology has become cluttered by a number of different terms for structures that are apparently homologous. These include the "lateral processes" and "filiform processes" of Hinks (1880, p. 511), the "free encrusted appendages" of Marcus (1938, p. 52), and the "spinous processes" of O'Donoghue (1924, p. 59) and O'Donoghue and O'Donoghue (1926, p. 21). The "cuticular appendages" described by Prenant and Bobin (1956, p. 227) for *Arachnidium fibrosum* include broader basal lobations that adhere to the substrate, as well as erect, elongate processes. The structures of *Cryptopolyzoon evelinae* called "adhesive papillae" by Marcus (1942, p. 478) apparently include not only homologous elongations but some true kenozoecia as well. The term "filiform process" seems the most appropriate and is the name that will be used here for any filiform, aseptate evaginations of the body wall.

The filiform processes of *Victorella argilla* are modified for the accumulation of foreign material and secrete large quantities of an adhesive substance that stains a bright turquoise in Alcian Blue (suggesting an acid muco-polysaccharide). They are most abundantly developed on the marginal portion of the frontal surface or in the vicinity of the apertural papilla (fig. 1), but they may occur on the connecting tubules as well. In some cases, filiform processes are produced on the wall of the vestibule near the aperture so that, when the lophophore is withdrawn into the zoecium, the detritus accumulated on the neck of the extruded polypide is drawn directly into the vestibule. Vestibular filiform processes can be seen protruding from the apertures of the zoecia shown in figure 1.

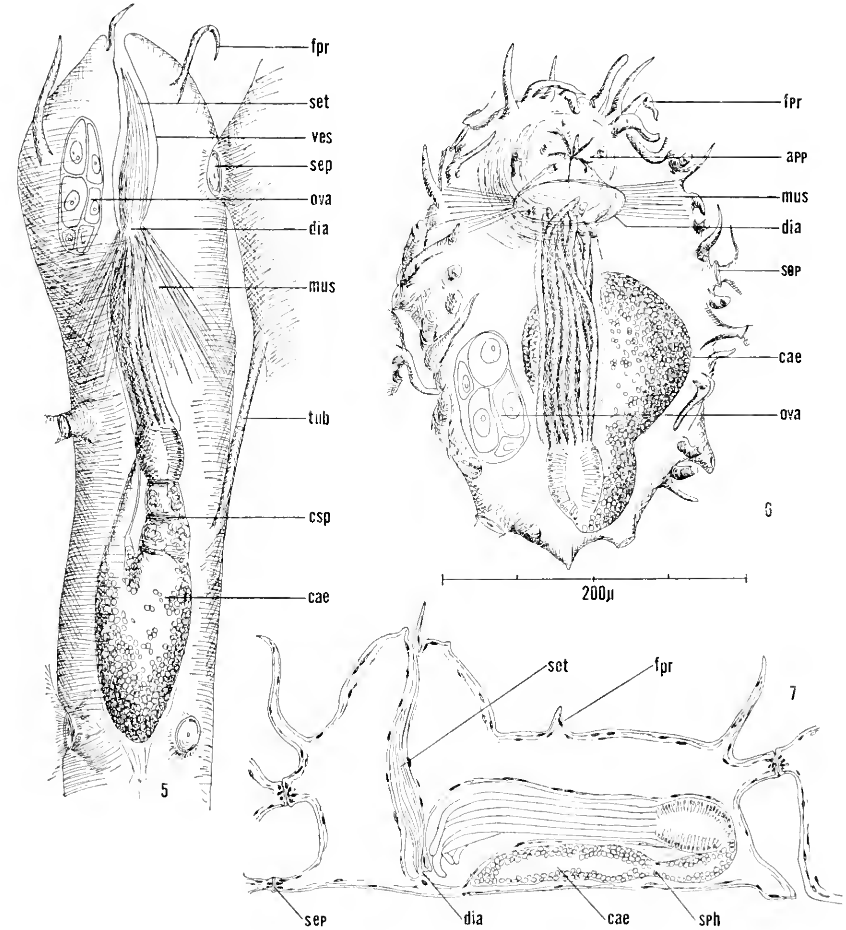
Digestive system.—The digestive system of form A is illustrated in figures 3, 5, 6, and 7. The lophophore, when retracted, is oriented parallel to the surface and at right angles to the vestibule, which is situated directly below the aperture (fig. 7). There are 11, 12, or 13 tentacles, 12 being the more common.

The short, ciliated pharyx passes into a spacious esophagus with very characteristic elongate, vacuolated cells. The esophageal cells pass insensibly into rounded eosinophilic cells of the cardiac stomach. Here the digestive tract is interrupted by a single discrete band of smooth muscle, the cardiac sphincter (fig. 3). The sphincter, without visible nuclei, is immediately followed by a short, ill-defined reinforced region. The caecum is broadly oval and distinctly flattened in the frontal plane (fig. 6 and 7). The rounded intestine leads distad and opens at the base of the setigerous collar.

Muscular system.—The vestibular musculature is strongly bilateral in form A, originating distolaterally below the vestibule (fig. 6) and inserting on the diaphragm. The arrangement is indistinguishable from that described for *Arachnidium fibrosum* by Marcus (1938, p. 51) and Prenant and Bobin (1956, pp. 227–228).

Reproductive system.—Testes in various stages of development have been repeatedly observed in specimens of form A collected in March 1965, but ovaries are uncommon. I have not seen an intertentacular organ in a zooid of form A, but one is present in many form B zooids.

The apertural papilla.—The term apertural papilla follows the usage of Silén (1944, p. 26) and is equivalent to the "peristome" of Ryland (1958, p. 317), the "tubular peristome" of Prenant and Bobin (1956, p. 233), and the "upright cylindrical structure" of O'Donoghue (1924, p. 59). In the typical form A zoecium, the apertural papilla is low, rounded, and occupies only about a third of the length of the zoecium (fig. 1). Transition from the A to the B form occurs through the exaggeration of the apertural papilla and the assumption of vertical budding of new zooids from the upright portion of the zoecial wall. Although they may be distinguished readily in their extreme forms, there is no clear line of demarcation between the A and B forms. Both forms occur on different regions of the same colony with a region of transition between them.



Figures 5–7.—*Victorella argilla*, schematic drawings (parietal muscles, retractor muscles, and testes omitted): 5, distal end of a form B zooid; 6, form A zooid, frontal view; 7, schematic median saggital section of a form A zooid. (Abbreviations: app=apertural papilla, cae=caecum, csp=central sphincter of three, dia=diaphragm, fpr=filiform process, mus=apertural muscles, ova=ovary, sep=septum, set=setigerous collar, sph=sphincter muscle of form A, tub=connecting tubule.)

Form B

Zoarium.—Foreign material in the form of siliceous sediment and detritus is extensively integrated into the mature colony of form B. The relative quantity of nonoxidizable inorganic material can be estimated by weighing portions before and after drying to constant weight (at 60° C) and again after digestion of the colony in boiling sodium hypochlorite. The results are as follows:

constituent	*percent by weight*
non-oxidizable material	49.1
water	45.4
dry organic matter	5.5
	100.0

The large quantity of foreign material frustrates interpretation of zoarial structure. Attempts to separate the animals physically from the sediment have met with failure. Perhaps the most satisfactory method, suggested by Patricia L. Cook of the British Museum (Natural History), is to shake the material in 10 percent trisodium phosphate.

Attempts to cultivate the animal in the presence and absence of suspended calcareous material (finely ground aragonite), have failed, due probably to starvation, although the animals were offered a variety of diatoms and dinoflagellates at varying concentrations while they were being maintained at different temperatures (10°, 15°, and 20° C).

Because of the difficulty in isolating *Victorella argilla* from its investment of foreign material, most of the conclusions about the zoarial structure of form B have been drawn from very thick paraffin sections, despite their poor technical quality. Only the examination of a great number of serial sections has made an accurate interpretation possible.

The zoecia of the mature form B are exceedingly elongate, without a basal dilation, and oriented perpendicular to the substrate. They are closely packed so that only the rounded tips of the apertural papillae and their filiform processes are visible at the surface (fig. 4). Mature zoecia are so variable in length and the sections are so distorted, it is impossible to estimate an average length, but the largest zoecia are very long and reach deeply into the thick zoarium. It is at least likely that some of the zoecia reach all the way to the substrate, suggesting that the zoecia must be among the largest of the Polyzoa—more than a centimeter in length. The polypides, however, are much shorter (0.3 mm) and are restricted to the most superficial parts of the colony. New zooids, which differ from adults only in length, are produced near the zoarial surface from the lateral wall of the mother zooid. In a few cases, they are produced, as in form A, by the dilation of connecting tubules, but the morphology is always that of form B. Form A zooids may give rise to form B zooids, but the converse apparently is not true.

The basal part of the zoarium is a poorly organized mass of zoecial tubes and degenerated "stolons." In some regions the zoecia are obviously dead, so that the basal parts of the thickest carpets are probably formed from collapsed and degenerating zoecia and connecting tubules held together by the adhesive substance secreted by the filiform processes. Septa are more resistant than the rest of the zoecium and are quite conspicuous in fuchsin-stained material as loose red discs with a central perforation. Brown bodies are distributed irregularly through the tubular zoecia, indicating that the animals grow by the successive death and replacement of several polypides in the same zoecium. The space between zoecia is filled with dense masses of detritus and sediment tightly cemented into the colony by the remains of filiform processes and probably also by an adhesive material produced on the cuticle itself. Filiform processes are represented more sparsely on the zoecial walls than on the exposed tips of the zoecia. It seems likely that they are formed at the growing tips and break down as the zoecium elongates distally (figs. 4, 5).

MUSCULAR SYSTEM.—Because the zoecia are tubular and because the polypides are confined to the most distal portion of the upright cystid, the tentacle sheath and vestibule are directly in line with one another and the strong bilateral symmetry of the apertural muscles seen in form A has been lost. The strong vestibular muscles probably are associated with the habit of drawing foreign material into the vestibule. Both the vestibular wall and the orificial collar are exceedingly sticky and large masses of foreign material, including sand grains nearly as large as the diameter of the zoecium, are introverted when the lophophore is retracted. As a result, the vestibules of all zoecia old enough to feed are packed solidly with foreign material. It has not been possible to ascertain how this material is eliminated when the polypides degenerate, but none has been observed incorporated into brown bodies.

The apertural muscles of form B arrange themselves radially around the vestibule and show none of the bilaterality of form A (see p. 5).

In some species (e.g., *Victorella pavida*), the disposition of the apertural muscles into four evenly spaced clusters imparts a quadrangular shape to the closed aperture. Even the apertures of tightly retracted zooids of *Victorella argilla* are puckered irregularly. It should be noted that all other species of *Victorella* so far described possess quadrate apertures (Braem, 1951).

DIGESTIVE SYSTEM.—Braem (1951, p. 23) attaches considerable taxonomic importance to the location of the sphincter muscle of the cardiac stomach. One of the principal reasons he gives for separating the genus *Tanganella* from *Victorella* is that the sphincter muscle of the latter is placed near the middle of the cardiac stomach while, in the former, it is at the junction of the cardium and the caecum. Unfortunately, it is difficult to delimit the cardiac stomach in *Victorella argilla* because a cardiac valve is lacking in this species. Nevertheless, it is clear that the greater part of the distal digestive tract proximal to the vacuolated cells of the esophagus is invested in very fine concentric muscles that may become elaborated into well-defined sphincter muscles at three possible sites. Figure 5 shows a polyp with all three sphincters developed though, as a rule, only one or two bands are present at a time. There is no trace of a gizzard or other chitinous reinforcement of the distal digestive tract.

REPRODUCTIVE SYSTEM.—Both form A and form B individuals have been found to contain ripe testes and ovaries. Both gonads occur in the distal region of the zoecium of form B, but they are located more proximally in form A. An intertentacular organ is present in most of the form B individuals examined, but I have not observed any in form A.

One of Braem's (1951, p. 33) reasons for separating *Tanganella* from *Victorella* was the possession of an intertentacular organ by the latter (*Victorella*) but not by the former (*Tanganella*). Sexually mature *Tanganella* extrude their eggs through a supraneural pore (Braem, 1951, p. 27; see also his discussion of *T. mulleri* on p. 6).

Unfortunately, none of the material at my disposal contains embryos and there is no sign of a modification of the vestibular wall to indicate that brooding takes place there as it does in *Tanganella mulleri* (Braem, 1951, p. 27). The extensive mass of foreign material filling the vestibule indicates that if indeed eggs are brooded in this species, the brooding must almost certainly take place elsewhere—in the tentacle sheath, for example.

ECOLOGY

The mature colony of form B is typically a thick, sandy or argillaceous carpet growing in sheets or knobs over hard substrate. The well-developed colony is by no means easily recognized as a polyzoan because of the massive accumulation of detritus and sediment between the zoecia. When the lophophores are retracted, foreign material effectively obscures the apertures, so that, even under high magnification, the colony is easily disregarded as inorganic. Teasing apart the zoarium fails to yield any information because the zoecia and connecting tubules form a tightly integrated mass, and zoecia tend to tear open rather than separate, with the result that the fragile polypides are lost against a background of sediment.

Victorella argilla, nevertheless, is quite abundant. It has been recorded from seven localities from Tomales Bay to Imperial Beach

Calif.; at each place it is present in great abundance. At the type-locality (Hermosa Beach, Calif.), for instance, virtually every exposed surface of the rocky environment is covered with a dense mat of *Victorella argilla* several centimeters thick.

Turner, Ebert, and Given (in ms.) have described the ecology of artificial reef environments and have recorded the impact of *Victorella argilla* on biological succession. These authors found that hard surfaces exposed to waters containing large amounts of suspended sediment were colonized by *V. argilla* at an early stage in the successional pattern. The animal becomes a thick, rapidly spreading mat that smothers and kills other sessile animals and inhibits the settling of competitors by the dense, muddy surface it presents. At length, the colony thickens, rising up into smooth knobs and clumps. These thick masses break away easily and apparently the surfaces thereby exposed are among the few places other animals may become attached. These authors report that the colony had been noticed but not recognized as organic until late in the study. It was referred to as a sediment layer or a muddy mucous layer until its animal nature was discovered by Given.

The following is a list of the Polyzoa from the type-locality:

Victorella argilla, new species	abundant
Pherusella, undescribed species	present
Tubulipora tuba Gabb and Horn, 1862	present
Diaperoecia californica (d'Orbigny, 1852)	abundant
Diaperoecia floridana Osburn, 1940	common
Crisia occidentalis Trask, 1857	common
Membranipora villosa Hinks, 1880	on algae
Antropora tincta (Hastings, 1930)	on *Kelettia*
Scrupocellaria bertholetti Robertson, 1905	common
Microporella californica Robertson, 1908	present
Fenestrulina malusi (Audouin, 1826)	present
Holoporella brunnea (Hinks, 1884)	present

DISTRIBUTION

TYPE-LOCALITY.—California Wildlife Conservation Board, cement block artificial reef, Hermosa Beach, Calif., 60 feet. Type material collected by the author June 10, 1965.

Mr. Robert Given informs me he has observed the animal at the following locations: Malibu artificial reef, Malibu, Calif., 60 feet (May 8, 1961); Standard-Humble oil tower "Hilda," Santa Barbara, Calif., from 10 to more than 110 feet (1961); artificial reef at Torrey Pines, near La Jolla, Calif., 65 feet (Oct. 19, 1964); docks and piers at the University of California at La Jolla; artificial reef at Imperial Beach, Calif., 15–20 feet (Oct. 20, 1965); artificial reef at Huntington Beach, Calif., 65 feet (Oct. 22, 1964).

I have examined specimens of the animal identified as *Alcyonidium parasiticum* (Fleming, 1828) by Soule (1953, p. 729). The specimens are almost certainly identical with form A of *Victorella argilla*, which extends the range of the species to Tomales Bay, Calif., 30 feet; Dr. Raymond C. Osburn, collector.

Discussion

The genus *Victorella* has been reviewed in detail by a number of zoologists (Annandale, 1911; Braem, 1951; Brattström, 1954; Marcus, 1925, 1940; Soule, 1957; and Valkanov, 1943). The most complete summary is that of Brattström (1954), wherein he reviews the tangled and controversial taxonomy of the genus but finally is able to conclude, with Valkanov (1943, p. 4), only that "we are a long way from a correct view of the genus *Victorella*."

Most of the taxonomic trouble stems from a long-standing controversy over whether or not *Victorella mülleri* Kraepelin, 1897, and *Victorella pavida* Kent, 1870, are the same species. As Brattström (1954, p. 8) points out, *V. mülleri* has never been taken from waters in which *V. pavida* does not occur. Some authors, led by Valkanov (1943), Marcus (1940), and Soule (1957), are of the opinion that *V. mülleri* is only a "growth phase encountered in the younger colonies of *V. pavida*" (Soule, 1957, p. 25) and point to the wide variability of the characters used to separate them. Braem (1951, p. 22), on the other hand, not only is of the opinion that they are distinct species, but also maintains that the differences are so fundamental that the species must be relegated to separate genera. After perhaps the most exhaustive recent study on the genus, Braem (1951, p. 33) concurs with previous authors that such characters as the relative length of the upright portion of the zoecium and the number of folds in the setigerous collar are of only superficial value in separating species or genera. He concludes, nevertheless, that *V. pavida* and *V. mülleri* may be distinguished on the basis of the following characters: (1) the cardiac sphincter in *V. pavida* is developed at the center of the cardiac stomach, whereas it is at the proximal end in *V. mülleri*; (2) an intertentacular organ is present in *V. pavida* but is replaced in *V. mülleri* by a supraneural pore at a corresponding position; (3) the embryos are brooded in the vestibule of *V. mülleri*, but the reproductive habits of *V. pavida* are not fully known (Braem, 1951, p. 33). Soule (pers. comm.) has pointed out that he misquotes Braem in his (Soule's) 1957 paper (p. 25). He states that entirely different characters were used in the generic description of *Tanganella* by Braem (1951, p. 33).

Other characteristics, such as the length of the apertural papilla and the pattern of budding, are useful, but wide variability makes them unreliable. The danger of employing these superficial characters is multiplied further by the existence of animals essentially indistinguishable from *V. pavida* but closely approaching *V. mülleri* in some respects. Braem (1951, p. 45) has erected a new species and genus, *Bulbella abscondita*, to include them. The species occurs only where both *V. pavida* and *V. mülleri* are common.

With regard to item 1 above, Braem (1951, p. 23) himself points out that the position of the "sitzenden Sphinkter" [fixed sphincter] is the most "wesentlich und konstant" [fundamental and constant] feature distinguishing *Victorella* from *Tanganella*, yet he states: "Die Lage des sitzenden Sphinkter ist nicht immer ganz gleich, da die benachbarten Darmteile einigermasser gegeneinander verschiebar sind" [The position of the fixed sphincter is not always entirely the same since the neighboring parts of the gut are somewhat displaceable against one another] (loc. cit.). A glance at his figures (plate II: fig. 9 and plate V: fig. 5C) is enough to convince a reader that the overlap is considerable. The situation in *V. argilla*, with its diffuse system of muscle bands around the entire distal portion of the gut, appears to cast doubt on the validity of this character among ctenostomes; nevertheless, if characters of this nature should prove reliable, then the position of the sphincter in form A of *V. argilla* would seem to ally it more to *V. pavida* (and *Bulbella abscondita?*) than to *V.* (=*Tanganella*) *mülleri*.

As regards items 2 and 3 above, *V. argilla* further resembles *V. pavida* in the possession of an intertentacular organ (lacking in *V. mülleri*). Unfortunately, little is known of the reproductive habits of *V. argilla* (see p. 9).

It is obvious that the systematics of *Victorella* and its relatives is unstable and that much of the confusion has arisen from an uncertainty as to what characters are of importance. Since it is not at all clear what the limits of the genera (or even of the species) should be, I am exceedingly hesitant to further confound the already perplexing taxonomy by inserting yet another genus into the literature. Therefore, even though the differences between *V. argilla* and other *Victorella* are greater than those between most other genera in its family (between *Victorella* and *Sundanella* or *Bulbella* and *Tanganella*, e.g.), I place it in the genus *Victorella* as defined by Prenant and Bobin (1956, p. 139). It should be distinguished from all other members of the genus by the following characters: (1) the possession of filiform processes that secrete an adhesive that causes them to be invested in a coat of foreign material; (2) the disposition of the apertural muscles into a radial or bilaterally paired configuration (the aperature of the retracted zooid is therefore not quadrangular); (3) the marine habitat of *V. argilla*. All other described forms are known only from brackish waters. The marine species *V. sibogae* Harmer (1915) has been removed by Braem (1939, p. 178) to a new genus, *Sundanella,* on anatomical grounds; Marcus (1941) agrees. The other morphological characters of specific value depend on whether or not the animal is in the A or B form.

A number of explanations have been given for the great variations of zoecial form in *Victorella.* In general, those authors who consider *V. mülleri* synonymous with *V. pavida* have offered two explanations for variation in zoecial length: the age of the zoecium and crowding of the colony. Most of these authors (Ulrich, 1926; Annandale, 1912; Borg, 1930; Braem, 1911; Soule, 1957; and Carrada and Sacchi, 1964) are of the opinion the *V. mülleri* is a juvenile form of *V. pavida.* The best presentation is that of Ulrich (1926). Valkanov (1943, p. 5), on the other hand, seems convinced that zoecial crowding caused by local irregularities of the substrate induces a lengthening of the zoecium, presumably by restricting growth laterally. More recently Brattström (1954, p. 11) stated: "It is possible that the two species here treated (if really separate) are capable of great seasonal variations as well as of variations resulting from environmental influences (temperature, density of colonies, etc.) and thus, though anatomically different, being able to appear in different growth forms which are more or less alike in the two species."

In the case of *V. argilla,* the elongate B zooids are produced in two possible ways: (1) by the elongation of the apertural papilla vertically from the substrate and the degeneration of several successive polypides, as described on page 8 (in this case, it is true that variability is age-induced and that A colonies invariably produce B colonies, but it should be noted that the zoecial wall of the B form represents the apertural papilla of the A form); (2) by the budding of B zooids. As mentioned before (p. 7), new buds may be formed as evaginations of the body wall of the upright portion of the zoecium; such buds produce only B zooids. Conversely, however, only A zooids are ever produced by the "stolonal" budding of another A zooid (see p. 7). This peculiar state of affairs may represent some biochemical difference in the two kinds of buds but it could as easily be due to some more direct physical influences. The zoecia may be so crowded, for instance, that only vertical growth is possible, or perhaps the volume of B zooids is too great for the quantity of foodstuffs that can be transmitted to the bud from feeding autozoecia through the connecting tubules. In this case, perhaps only the efforts of several generations of polypides within the same zoecium is enough to provide the nourishment necessary to produce the large B zooids. It should be recalled that some of these zooids may approach a centimeter in length (see p. 7).

The variations encountered in the two growth forms of *V. argilla* are far more fundamental, however, than mere changes in the shape and form of the zoecium. There are extensive changes, for instance, in the morphology of the digestive tract, muscular system, and reproductive system. Many of these changes are related to, if not a direct consequence of, the differences in zoecial shape. The basal-frontal flattening of the stomach in form A is almost certainly a consequence of the flattened shape of the zoecium to which it is confined. The same is probably also true of the differences in arrangement of the apertural muscles; the shape of the form A zoecium makes a bilateral arrangement of the muscles around the vestibule a virtual necessity (fig. 6). Other morphological changes are explained less readily. It is difficult to see a relationship, for instance, between the disposition of sphincter muscles around the cardinal stomach, on the one hand, and the degree of flattening of the stomach or the relative length of the zoecium, on the other. There is clearly a need for more exhaustive research before it will be possible even to propose a reasonable theory of the causes of variability.

Whereas the closest affinities of *V. argilla* appear to be with the other members of its genus, there are clear indications of relationships to other genera. Form A of *V. argilla* is almost indistinguishable from the not uncommon temperate ctenostome *Arachnidium fibrosum* Hinks 1880. They are alike in the possession, distribution, and function of filiform processes, the manner of growth (i.e., by the extension, dilation, and anastomosis of tubules), the structure of the apertural muscles, the absence of a gizzard, and the size and shape of the zoecium. In short, a specialist would be hard put to distinguish the two animals were it not for the somewhat denser manner of growth of *V. argilla* and its gradual extension into the B form. It should be noted, however, that *A. fibrosum* differs from other members of its genus in a number of respects. It possesses filiform processes and the pattern of budding differs somewhat from that of other species of *Arachnidium* (Prenant and Bobin, 1956, pp. 223–228).

Arachnidium fibrosum (and form A of *V. argilla*) might be mistaken easily for certain species of the genus *Nolella*, particularly *N. sawayai* Marcus (1938, p. 52), a peculiar species possessing filiform processes but having a long apertural papilla. The close relationship between *Nolella* and *Arachnidium* has been noted by Rogick (1949, p. 165), Harmer (1915, p. 58), Ryland (1958, p. 31), and others. Rogick, for example, only hesitantly refers her new species *N. blakei* to the genus *Nolella*, noting (1949, p. 165) that some individuals with very short apertures are better ascribed to *Arachnidium*. Other zoecia are clearly transitional.

Nolella, moreover, shows clear relationships to *Victorella*. Some authors (Prenant and Bobin, 1956, p. 239; Soule, 1957, p. 28) have commented on the similarities between the genera. In fact, there seem to be only two criteria for distinguishing them: (1) the fresh or brackish water environment of *Victorella* (except *V. argilla*); (2) the occurrence of zoecial budding from the apertural papilla in *Victorella* but not in *Nolella*. As Braem (1951, 11) has pointed out, however, young colonies of *V. pavida* do not show budding of this sort. The close relationship between *Nolella* and *Victorella* was emphasized by Soule (1957, p. 28), who places *Victorella* in the Nolellidae. This classification will be followed here, but it should be noted that this scheme does not indicate the close relationship between the Nolellidae and the Arachnidiidae. The family Nolellidae was placed in the Division Stolonifera by Soule (1957, p. 27–28) on the basis of the order of development of the apertural, parietal, and retractor muscles. As hinted by Ryland (1958, p. 317), this makes the family the only member of the Stolonifera to lack true stolons as defined by Silén (1944, p. 28). *Nolella* apparently lacks true stolons (Soule, 1953, p. 737; Rogick, 1949, p. 159) and *Victorella* almost certainly does (Braem, 1951, pp. 10–12).

In addition, *V. argilla* shows some links to *Cryptopolyzoon evelinae* Marcus, 1942. Both are similarly committed to the incorporation of foreign material, and both possess filiform processes, especially near the aperture (Marcus, 1942, p. 478). *Cryptopolyzoon* differs, however, in the possession of a true gizzard (Dendy, 1888, pp. 6–7, pl. II: fig. 8), a quadrangular aperture, the erect, dichotomously branching growth habit, and other aspects.

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A STUDY OF THREE SPECIES OF SARSIELLA (OSTRACODA: MYODOCOPA)

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The family Sarsiellidae is represented in the world's oceans between latitudes of 53°N to 47°S (Poulsen, 1965, p. 468). Specimens have been obtained from depths of 2333 m but are more numerous in shallower coastal waters. Members of the family seem better adapted to the shallow inshore environment than other Myodocopa; e.g., sarsiellids were the only myodocopids found in Texas bays and lagoons by Kornicker and Wise (1962) and in San Francisco Bay by Jones (1958a), and only sarsiellids and one other group of myodocopids were reported in the Woods Hole area, Mass., by Cushman (1906). Sarsiellids are benthonic; they swim near the bottom and burrow in sediment. Present evidence indicates that they are carnivores, feeding upon small crustaceans and worms.

The present study has three objectives: (1) to establish more firmly the relationship between *Sarsiella zostericola* Cushman, 1906, *Sarsiella americana* Cushman, 1906, and *Sarsiella tricostata* Jones, 1958; (2) to redescribe *Sarsiella capsula*, the type-species of the genus, which is the type-genus of the family; (3) to determine whether parasitism is the cause of the unusual asymmetry of valves of *Sarsiella disparalis* Darby, 1965, and to ascertain if asymmetry of valves is reflected in appendages.

Abbreviations used in the figures are as follows: ant.=antenna, 1st or 2nd as indicated; bas.=basale; cox.=coxale; e.=edges of valve; end.=endite; exop.=exopodite; i. m.=inner margin of inner lamella; l. p.=lamellar prolongation of selvage; Mn.=mandible; Mx.=maxilla; s.=sensory bristle; 5th=5th limb; 6th=6th limb; numerals=number of each joint in limb; small letter=specific type bristle.

I wish to thank Mr. J. S. Nagle for specimens of *S. zostericola* from Hadley Harbor, Mass., Dr. M. L. Jones for specimens of *S. tricostata* from San Francisco Bay, Calif., Dr. John Day and Miss Mary E. Potts of the Duke University Marine Laboratory for specimens of *S. disparalis* from the Atlantic Shelf off North Carolina, Dr. J. P. Harding and Miss P. D. Lofthouse for assistance in obtaining for examination specimens in the Norman Collection at the British Museum (Natural History), and Dr. Harbans S. Puri for assistance in obtaining for examination specimens collected by G. W. Müller in the Gulf of Naples, which were on loan to Dr. Puri from the Zoological Museum of Greifswald. I also wish to thank Mrs. June M. Gilby for making camera lucida drawings of appendages of *S. capsula* from specimens at the British Museum and Dr. F. M. Swain, who made the arrangements. I also wish to thank Mrs. Carolyne Bartlett Gast and Mr. Leon Connelly for final preparation of plates and figures 9–19, and of figures 3–8, respectively. Criticisms of all or parts of the manuscript by Drs. T. E. Bowman, H. H. Hobbs, Rosalie F. Maddocks, R. B. Manning, and I. G. Sohn are deeply appreciated. Finally I wish to thank Dr. Robert V. Kesling for the opportunity to examine the holotype (UMMP 48819) and a paratype (UMMP 48818) of *S. disparalis* Darby.

Family Sarsiellidae Brady and Norman, 1896

When Poulsen (1965, p. 44) revised the family Sarsiellidae, he recognized the following genera: *Sarsiella* Norman, 1869; *Chelicopia* Kornicker, 1959; *Eusarsiella* Poulsen, 1965; *Scottiella* Poulsen, 1965; *Muelleriella* Poulsen, 1965; *Parasarsiella* Poulsen, 1965.

He also (1965, p. 74) included the following species in *Sarsiella: S. capsula* Norman, 1869; *S. rugosa* Poulsen, 1965; *S. carinata* Scott, 1905, sensu Kornicker, 1959 (male only).

In his "Key to Genera of Sarsiella," Poulsen (1965, p. 55) separated *Sarsiella* from *Scottiella, Muelleriella, Chelicopia*, and *Parasarsiella* on the basis of characters common to both sexes, but he separated *Sarsiella* from *Eusarsiella* on the basis of a male character:

Endopodite of male 2nd antenna an unjointed bulge . . . . **Sarsiella**
Endopodite of male 2nd antenna 3-jointed, prehensile . . . . **Eusarsiella**

Among the species included in *Sarsiella* sensu Poulsen, the female is known only for *S. capsula* Norman. The lengths of claws and bristles of the mandible, and the relative lengths of parts of the mandible to shell length of the female *S. capsula* are compared to females of other sarsiellids by Poulsen (1965, pp. 76, 147, table 4). Although the relative lengths of claws, bristles, and joints of the mandible of *S. capsula* are somewhat different from other sarsiellids, the value of these characters for distinguishing *Sarsiella* from other genera is diminished because the variability of the measured characters among females of *Sarsiella* is unknown.

In his diagnosis of *Sarsiella,* Poulsen stated (1965, p. 76) that the distal bulge of the ventral margin of the coxale of the mandible of the female does not have a fringe of hairs. This observation must have been based on the description and illustration of the mandible of *S. capsula* by Müller (1894) because neither Norman (1869) nor Brady and Norman (1896) described the coxale and the specimen of *S. capsula* illustrated by Sars (1888, pl. X: fig. 4) has a fringe of hairs along the ventral margin of the mandibular coxale. I examined the mandible of a specimen from the Gulf of Naples that had been identified by Müller as *S. capsula* Norman and found that, contrary to Müller's description, the ventral margin of the mandibular coxale is fringed with hair. Lack of hairs on the coxale would have been a useful criterion for separating the female *Sarsiella* from *Eusarsiella,* which does have hairs.

I have been unable to find satisfactory morphological characters for separating females of *Sarsiella* from *Eusarsiella.* Males of the Sarsiellidae are relatively sparse compared to females and are unknown for many species. I believe, therefore, that it is premature to separate *Eusarsiella* from *Sarsiella* until it is possible to do so on the basis of females or until males of more species become known.

Only Müller (1894) identified and described males of *S. capsula.* It was, therefore, on the basis of Müller's specimens that Poulsen (1965) retained the generic name *Sarsiella* for species with an unjointed bulge forming the endopodite of the male 2nd antenna and referred to *Eusarsiella* the remaining species with a 3-jointed endopodite. As discussed on page 33, Müller erred in his identification of *S. capsula,* and the endopodite of the male 2nd antenna of *S. capsula* Norman is actually 3-jointed. According to this criterion, the type-species of *Sarsiella* would belong in the genus *Eusarsiella. Eusarsiella,* therefore, should be considered a synonym of *Sarsiella.*

Sarsiella Norman, 1869

Sarsiella Norman, 1869, p. 293.
Nematohamma Brady and Norman, 1896, p. 680.
Eusarsiella Poulsen, 1965, p. 79.

Type-species by monotypy: *S. capsula* Norman, 1869.

Diagnosis.—Sarsiellid having furca without secondary claws and with 5 (rarely 6) main claws of which only claw no. 1 is united with lamella. Sixth limb with only 1 endite. Male mandible with exopodite. Endopodite of 2nd antenna of male with 1 or, more usually, 3 joints. Inner margin of "clasper" of male copulatory limb either smooth or serrated. Shell of adult male with rostrum and shallow sinus; shell of female generally without rostrum or sinus.

Sarsiella zostericola **Cushman, 1906**

FIGURES 1–15; PLATES 1, 2

Sarsiella zostericola Cushman, 1906, pp. 364–366, pl. 28 (figs. 7–18).—Blake, 1933, p. 230 [listed].—Kornicker and Wise, 1962, p. 61, figs. 2 A–G, 4 A–C.

Sarsiella americana Cushman, 1906, pp. 363, 364, pl. 27 (figs. 1–6).

Sarsiella tricostata Jones, 1958a, pp. 48–52, figs. 1, 2; 1958b, figs. 1–3; 1961, pp. 261, 262, figs. 20, 28, table 19 [listed].

Eusarsiella zostericola Cushman-Poulsen, 1965, p. 83 [in key].

Eusarsiella americana Cushman-Poulsen, 1965, p. 83 [in key].

Lectotype: USNM 113357, male whole specimen preserved dry. Cushman (1906) did not designate a holotype; however, one slide in his collection is marked "type." The specimen on this slide is herein designated lectotype.

Paralectotypes: USNM 113358, 1 male and 2 juveniles, whole specimens preserved dry. These specimens are in a slide in the Cushman Collection marked "co-types." These specimens are designated paralectotypes herein.

Sarsiella zostericola was established by Cushman (1906, p. 364) to receive numerous specimens collected from the "Gulf of Canso," a channel near Woods Hole, Mass. In the same paper, Cushman based a second species, *S. americana,* on a single specimen collected in the western part of Vineyard Sound, Mass. Blake (1933) extended the range of *S. zostericola* to the Mount Desert region of Maine, but neither illustrated nor described the specimens. Jones (1958a) collected from San Francisco Bay, Calif., ostracods that closely resembled *S. zostericola* but differed sufficiently from the description of *S. zostericola* to warrant his establishing the new species *S. tricostata.* Kornicker and Wise (1962) extended the range of *S. zostericola* to southwest Texas, where the species was collected in bays and lagoons along the coast bordering the Gulf of Mexico. After examining the carapace of the specimen of *S. americana* described by Cushman (1906), Kornicker and Wise (1962) reported it identical to that of *S. zostericola,* and concluded that apparent differences are due to the carapace of *S. americana* having been distorted after death of the animal. They also concluded that "differences in appendages [of *S. zostericola* and *S. americana*] reported by Cushman (1906) may partly be the result of individual variation, or possibly the result of comparing animals not of the same age," and, therefore, they considered *S. americana* to be a junior synonym of *S. zostericola*. Because some of the differences between *S. zostericola* and *S. tricostata* disappear when *S. zostericola* and *S. americana* are considered to be conspecific and because some of Cushman's observations are obviously in error, Kornicker and Wise (1962) considered *S. tricostata* also to be a junior synonym of *S. zostericola*.

The present study of the ontogeny of *S. zostericola* shows that the pre-adult female bears 2 ventral bristles on the 4th joint of the 1st antenna, compared to 3 on the adult, and has the caudal process of the carapace more posteriorly located than on the adult. The female *S. zostericola* described by Cushman (1906, p. 365, pl. 28: figs. 15, 16) bears only 2 bristles on the 4th joint of the 1st antenna, and the caudal process is posterior, indicating that it is a pre-adult female.

Since appendages of the holotype of *S. americana* are not available, it is necessary to rely on the original description of the species in which Cushman (1906) illustrated the 1st antenna (pl. 27: fig. 3), the exopodite of the 2nd antenna (pl. 27: fig. 4), the caudal lamellae (pl. 27: fig. 6), and the mandible (pl. 27: fig. 5). Cushman reported only 5 bristles on the end joints of the 1st antenna. As other sarsiellids have 9 bristles on the end joints (5th–8th), it seems likely that some bristles were overlooked by Cushman. Cushman reported only 1 seta on the ventral margin of the basale of the mandible of *S. americana*, whereas *S. zostericola* has 5. The caudal lamellae and the exopodites of the 2nd antenna of *S. americana* and *S. zostericola* are similar.

Except for a possible difference in the number of bristles on the ventral margin of the mandibular basale, *S. zostericola* and *S. americana* seem identical and, therefore, I concur with Kornicker and Wise (1962) in considering *S. americana* a synonym of *S. zostericola*.

I have compared the shells and appendages of adult specimens from Massachusetts (*S. zostericola*) and California (*S. tricostata*) and I find that the 2 populations cannot be distinguished, which confirms the conclusion of Kornicker and Wise (1962) that *S. tricostata* and *S. zostericola* are conspecific. Specimens of *S. zostericola* from Texas could not be distinguished from those from Massachusetts and California, and I can find no evidence of subspeciation in this ostracod.

Because of the presence of instars in the collection from California, it has been possible to study the ontogenetic development of the species and to describe instars as well as the adults.

Material.—The number, source, and collection data for the specimens examined during this study are as follows:

USNM	*number of specimens*	*locality*	*date collected*	*remarks*
113357	1 adult ♂ dried	Gulf of Canso, Woods Hole, Mass.	Aug. 3, 1905	lectotype
113358	1 adult ♂ 2 juveniles, all dried	Gulf of Canso, Woods Hole, Mass.	Aug. 3, 1905	paralectotypes
113356	1 adult ♀ consisting of dried left and right valves	Vineyard Sound, Mass. Fish Hawk Sta. 7723		identified as *Sarsiella americana* Cushman by J. S. Cushman; slide is marked "Type"
100903	1 adult ♀ in alcohol	Pt. Richmond, San Francisco Bay, Calif.	July 14, 1957	holotype of *Sarsiella tricostata* Jones
107847	1 adult ♂ consisting of dried left and right valves	Redfish Bay, Tex.	1958	specimen illustrated by Kornicker and Wise (1962, figs. 2A–B)
107848	1 adult ♀ dried	Port Isabel, Tex.	1958	
113461	11 adult ♀♀ 1 adult ♂ 1 juvenile in alcohol	Port Isabel, Tex.	1958–1960	
113462	6 adult ♀♀ 5 adult ♂♂ 17 juveniles in alcohol	Pt. Richmond, San Francisco Bay, Calif.	1955–1956	
113463	84 adult ♀♀ in alcohol	Hadley Harbor, Mass. Sta. P. 1907	1965	
113508	2 juveniles	Hadley Harbor, Mass. Sta. P. 242	1965	
113509	1 adult ♂ 4 juveniles in alcohol	Hadley Harbor, Mass. Sta. P. 264.25	1965	
113510	2 juveniles in alcohol	Hadley Harbor, Mass. Sta. P. 264.50	1965	

When the lengths of shells of females in the collection are plotted as a function of shell height, the points form 4 discrete clusters representing 4 developmental stages (fig. 1). As seen in figure 1, considerable space exists between the smallest instar and embryos obtained from the brood chamber of a gravid female. The space is interpreted as showing that 1 or more of the younger female instars are missing from the collection. By using Przibram's growth factor of 1.26, which predicts the theoretical difference of a linear dimension in 2 consecutive molts (Przibram, 1931, p. 21), it is possible to conclude that instars I and II are missing from the collection. The conclusion, however, must be considered tentative because of the many factors that cause the growth rate to deviate from the theoretical (Teissier, 1960, p. 541). Males of instars I and II are also missing from the collection. Lateral outlines of shells at stages of development present in the collection are illustrated in figure 2. Average dimensions at each growth and calculated growth factors of females from California are tabulated as follows:

growth stage	*average length (mm)*	*growth factor*	*average height (mm)*	*growth factor*
adult	1.24		1.11	
		1.34		1.41
V	0.92		0.79	
		1.33		1.33
IV	0.69		0.59	
		1.23		1.29
III	0.56		0.46	
		1.26[a]		1.26[a]
II (missing)	0.44[b]		0.36[b]	
		1.26[a]		1.26[a]
I (missing)	0.35[b]		0.29[b]	
embryo (from Mass.)	0.32		0.26	

[a] Przibram's theoretical growth factor for a linear dimension.

[b] Calculated dimensions estimated by dividing Przibram's factor (1.26) into dimension of succeeding growth stage.

In several collections off Point Richmond, Calif., Jones (1961, figs. 20d–g) obtained a total of about 240 adult females and 36 adult males; adult females outnumbered adult males by 6 or 7 to 1. In the present study juveniles were picked at random from available collections from Point Richmond. The numbers are too few to determine accurate ratios; however, females outnumbered males in all molt stages:

developmental stage	*no. of females*	*no. of males*
III	4	1
IV	5	1
V	4	2

Description of adult female.—Shell (figs. 3*a*, *b*; 4; 5*a–d*; pl. 1): dorsal view with broadly rounded posterior and acuminate anterior (fig. 3*b*); oval in lateral view except for posteroventral caudal process (figs. 3*a*, 4*a*). Surface ornamented with punctae and 3 raised ribs radiating from hub slightly forward of center of valve; posterior rib terminating in knob with 2 small lateral pits; velate ridge parallel to edge of valves; shell broadest at hub of radial ribs or at pitted knob of posterior ridge; valve surface with scattered hairs; valve margins with rows of long hairs faintly annulated proximally (figs. 4*a*, *b*).

Adductor muscle scars consisting of clusters of ovate scars near junction of radial ribs (fig. 4*e*); several ovate dorsal muscle scars occurring below anterior termination of hinge; false radial canals numerous, each with long bristle (fig. 4*b*); normal pore canals sparsely distributed over valve surface.

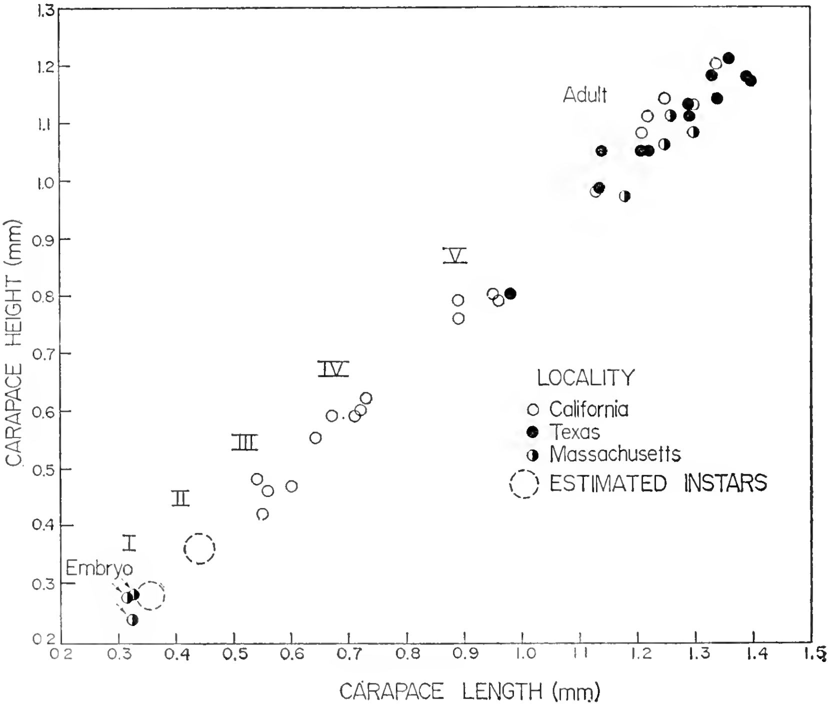

FIGURE 1.—*Sarsiella zostericola* Cushman: relationship between shell length and height of female.

Duplicature broad except dorsally; 1 or 2 small bare medial bristles along anterior part (figs. 4*a–e*), 1 long and 2–6 short bristles medially on caudal process, long bristle posterior to shorter bristles, all bristles bare (figs. 4*f–j*; 5*a–d*); 2–3 small bare bristles near inner margin of duplicature dorsal to caudal process followed by 2 long hirsute bristles near outer margin (figs. 4*g*; 5*c*); 1–3 short bare bristles near inner margin of duplicature anterior to caudal process and posterior to a cluster of 3 bare bristles (figs. 4*g*; 5*c*). Selvage narrow with transverse striations and extending outward in unstriated lamellar prolongation with fine marginal fringe along anterior and posterior parts on some specimens (figs. 4*c*, *g*). Hinge simple, occupying posterior two-thirds of dorsal margins (fig. 4*a*) and connected by ligament (pl. 1*a*, *b*).

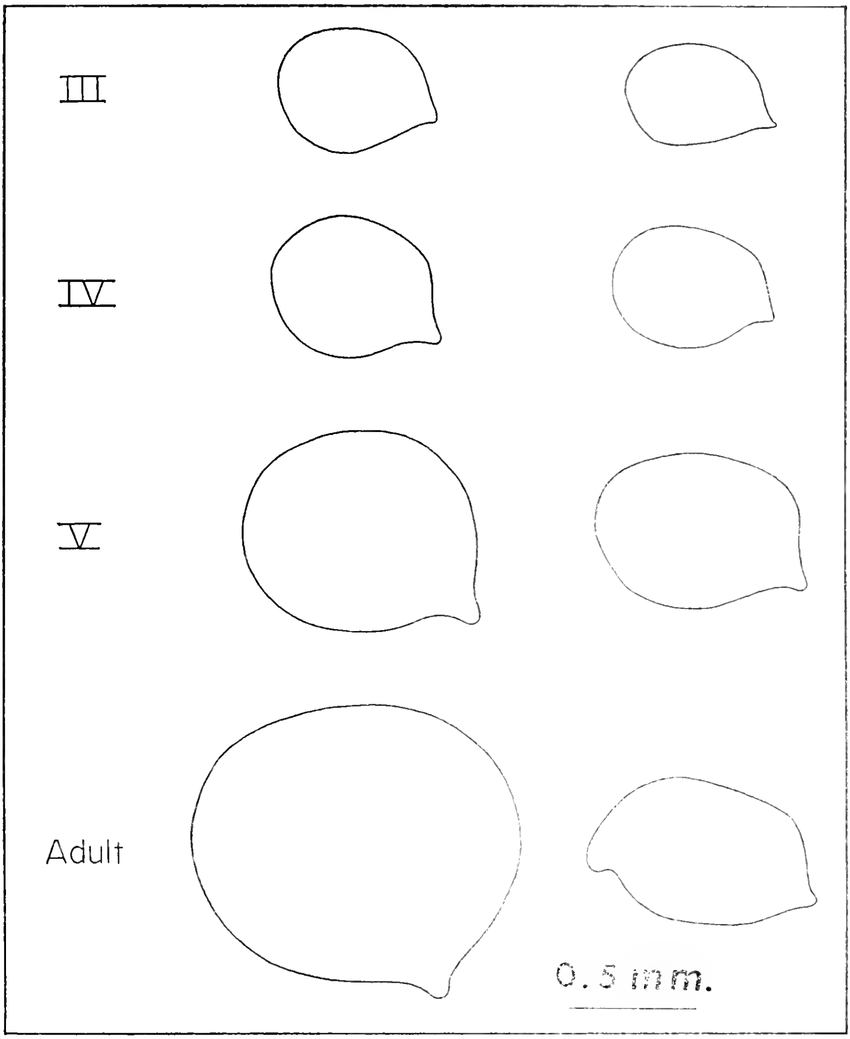

FIGURE 2.—*Sarsiella zostericola* Cushman: comparison of lateral outlines of instars III–V and adults (females on left, males on right).

Outer lamella of valve laminated (pl. 1*c–f*); duplicature in x-section appearing as fold in inner part of outer lamella (pl. 1*d*); marginal ridge (pl. 1*d*) and medial ridge (pl. 1*e*) in x-section appearing as fold in outer part of outer lamella. Clusters of dorsally oriented spines occupying middle ventral area within inner margin of inner lamella (fig. 4*d*).

The carapace of *S. americana* illustrated by Cushman (1906, pl. 27: fig. 1) is labeled: "Shell of female seen from the side." This illustration shows the left valve. It has been interpreted as the right valve by Poulsen (1965), who, in his "Key to the Species of the Genus *Eusarsiella*," distinguishes *americana* from *zostericola* by the former having a few irregular teeth along the anteroventral margin of the shell.

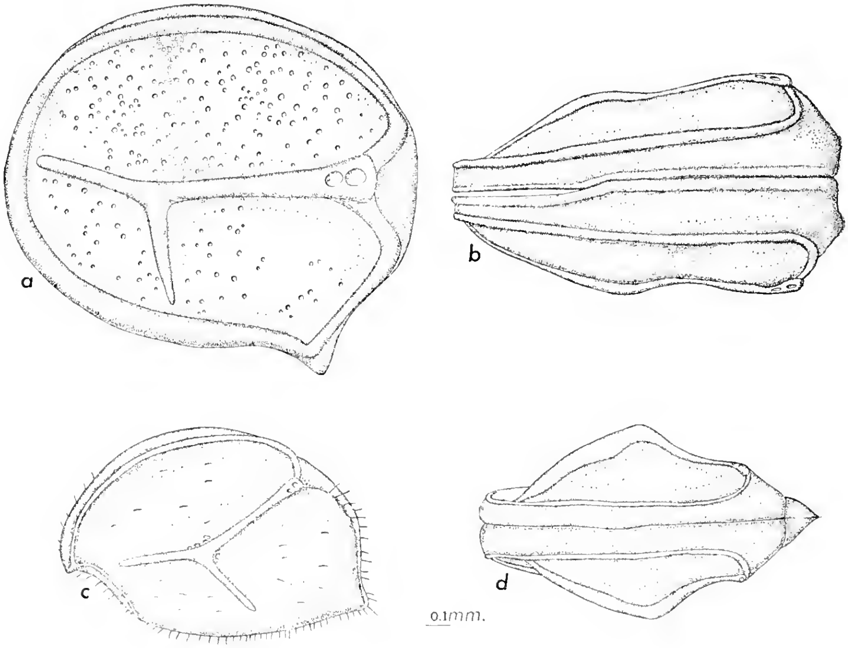

FIGURE 3.—*Sarsiella zostericola* Cushman, Hadley Harbor, Mass., adult ♀, sta. P. 1907, 1.25 mm: *a*, left lateral view; *b*, dorsal view, anterior to left. Adult ♂, sta. P. 264.25, 1.01 mm: *c*, left lateral view; *d*, dorsal view, anterior to left.

The "teeth" described as spines by Cushman (1906, p. 363) are actually along the posterodorsal margin. The illustration of Cushman (pl. 27: fig. 1) does, in fact, look more like a right than left valve because the valve is higher than it is long. This indicates that the drawing is of a distorted valve because Cushman (1906, p. 363) states that the length of the shell is very slightly greater than the height.

Mean lengths of selected adult females from San Francisco, Calif., Hadley Harbor, Mass., and Port Isabel, Tex., are 1.23 mm (N=17), 1.24 mm (N=8) and 1.28 (N=11), respectively. These means do not

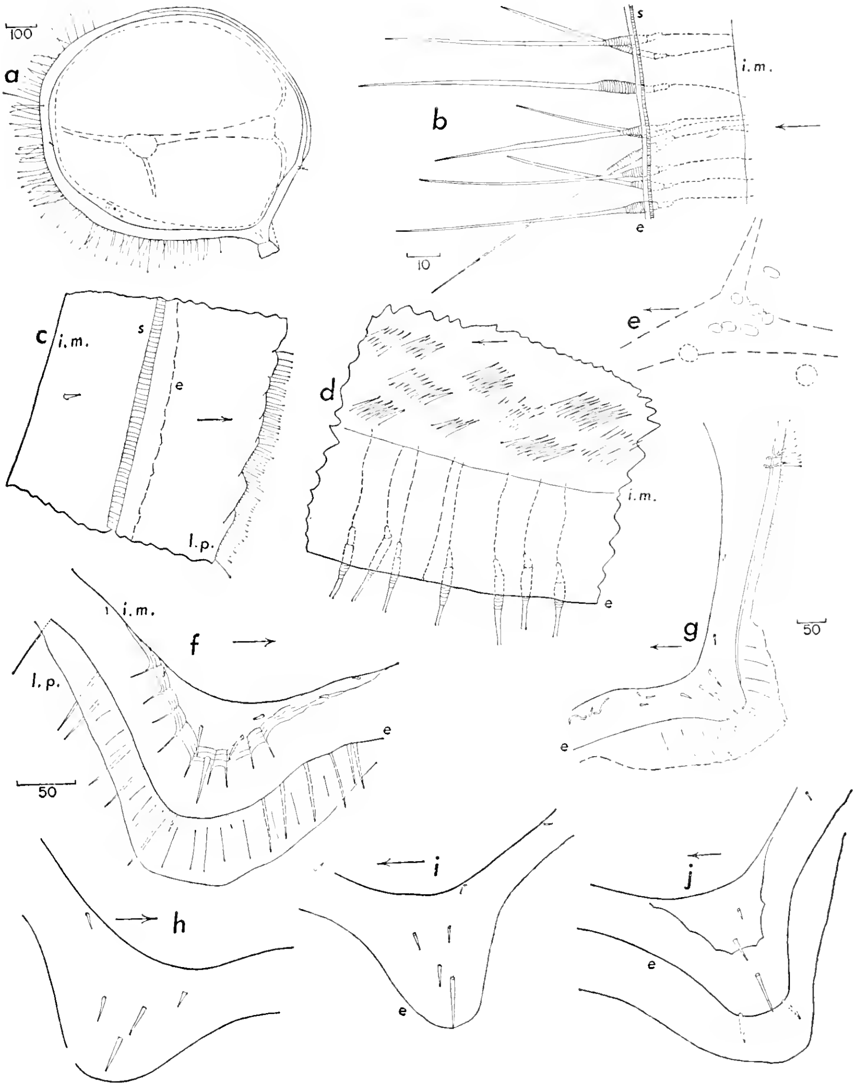

FIGURE 4.—*Sarsiella zostericola* Cushman, Hadley Harbor, Mass., ♀, 1.26 mm: *a*, medial view right valve (broken circle encloses muscle scars); *b*, anterior part of right valve showing small bristle on inner lamella and marginal bristles; *c*, anterior part of left valve; *d*, ventral part of right valve showing clusters of spines; *e*, muscle scar area of left valve; *f*, caudal process of left valve; *g*, caudal process and posterior margin of right valve. Female, 1.30 mm: *h*, caudal process of left valve. Female, 1.25 mm: *i*, caudal process of right valve. Female, 1.30 mm: *j*, caudal process of right valve. (Lamellar prolongation not shown in *b, h, i;* same scale in microns: *a; b–d; e, g; f, h–j.*)

differ significantly at the 95 percent level of probability. Dimensions of representative specimens are as follows:

locality	*midlength (mm)*	*midheight (mm) (excluding caudal process)*	*remarks*
San Francisco, Calif.	1.30	1.13	11 eggs in brood chamber
" "	1.34	1.20	10 " " " "
" "	1.25	1.14	well-developed eggs
" "	1.22	1.11	6 well-developed eggs within body
" "	1.21	1.08	no eggs in brood chamber
" "	1.13	0.98	eggs in brood chamber
Port Isabel, Tex.	1.13	0.98	5 eggs in brood chamber
"	1.14	1.05	6 " " " "
"	1.39	1.18	no " " " "
"	1.34	1.14	" " " " "
"	1.22	1.05	" " " " "
"	1.36	1.21	14 " " " "
"	1.21	1.05	5 " " " "
"	1.40	1.17	5 " " " "
"	1.29	1.11	no " " " "
"	1.33	1.18	7 " " " "
"	1.29	1.13	7 " " " "
Hadley Harbor, Mass.	1.26	1.11	eggs in brood chamber
" "	1.25	1.06	" " " "
" "	1.30	1.08	" " " "
" "	1.18	0.97	8 embryos in brood chamber

The number of medial bristles on the caudal process were found to vary considerably among specimens from the same locality and, indeed, on opposite valves of the same specimen. In general, the Atlantic and Pacific specimens are similar, each having a long posterior and several smaller anterior bristles.

First antenna (figs. 5*e, f*): 1st joint bare; 2nd joint with 1 spinous dorsal bristle and 2 groups of short spines along dorsal margin; 3rd joint with 1 dorsal bristle and without suture separating it from 4th joint; 4th joint with 1 spinous dorsal bristle, 1 short and 2 long ventral bristles, and 2 groups of short spines along ventral margin; 5th joint with stout sensory bristle; 6th joint with short spinous, medial bristle; 7th joint with medium a- and b-bristles and long c-bristle; 8th joint with d-, e-, f-, and g-bristles about same length as sensory bristle on 5th joint.

The 1st antenna of *S. zostericola* is described by Cushman (1906, pl. 28: fig. 16) as having only 1 long and 1 short ventral bristle on the 4th joint because Cushman described a juvenile specimen. Cushman's description of the 1st antenna of *S. americana* (1906, p. 363, pl. 27: fig. 3) shows it to be similar to adult specimens of *S. zostericola*.

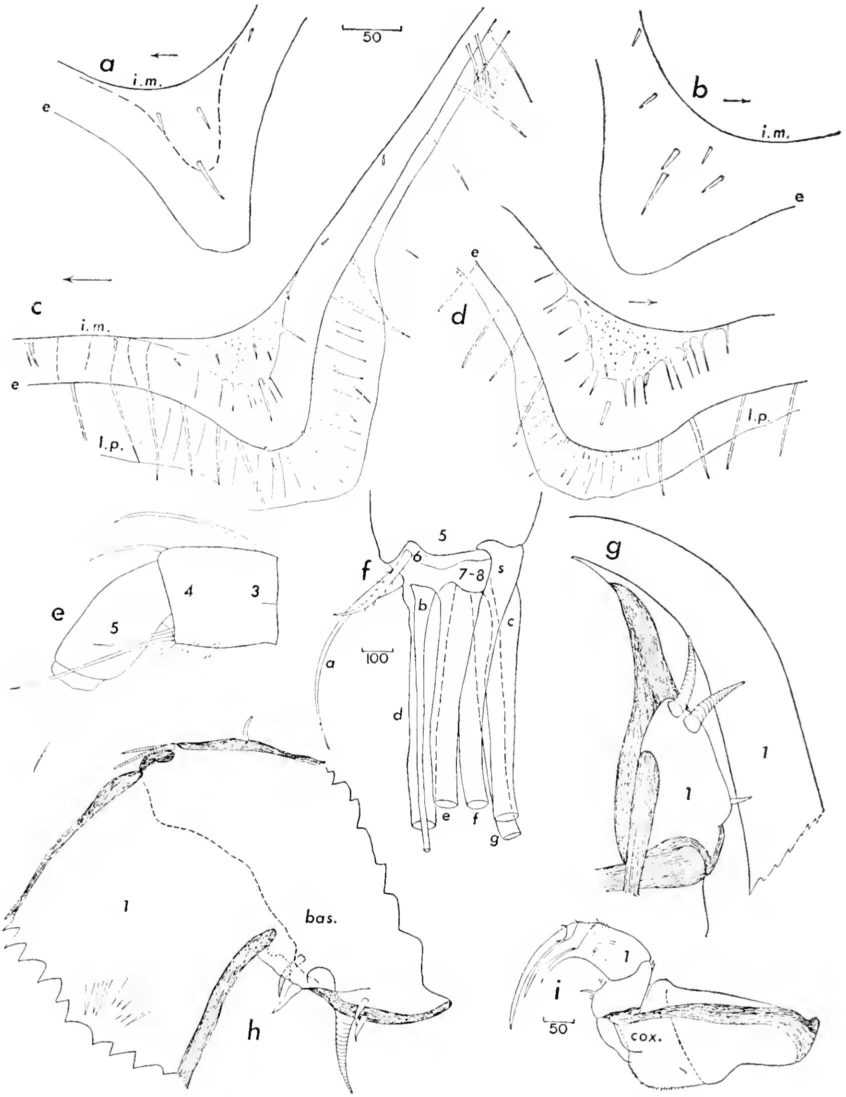

FIGURE 5.—*Sarsiella zostericola* Cushman, ♀, 1.30 mm, Texas, medial view caudal process, lamellar prolongation not shown: *a*, right valve; *b*, left valve. Female, 1.30 mm, California: *c*, caudal process and posterior of right valve; *d*, caudal process of left valve. Female, 1.26 mm, Hadley Harbor, Mass.: *e*, 1st antenna, 3rd to end joints, bristles shown only on 3rd and 4th joints; *f*, 1st antenna medial view of distal part of 5th–8th joints; *g*, 2nd antenna, endopodite and proximal part of 1st joint of exopodite; *h*, mandible, medial view, part of basale and 1st joint of exopodite; *i*, mandible complete appendage. (Same scale in microns: *a–e*; *f–h*; *i*.)

Sarsiella tricostata Jones (1958a, p. 49, fig. 1B) has 3 medium length ventral bristles on the 4th joint; only the outer 2 are annulated. On each of 3 adult females from California that I examined, the inner bristle is always shorter than the outer bristles and, although the annulations on the inner bristle are fainter than on the outer bristles, it is always annulated.

Second antenna: exopodite with 9 joints decreasing in width distally; 2nd–8th joints each with 1 long stout bristle with marginal hairs; 9th joint with 1 medium and 1 long bristle, each with marginal hairs; 7th and 8th joints each with comb of short spines along distal margins; endopodite 1-jointed with 1 short terminal spine and 2 proximal bristles dorsally (fig. 5*g*).

Cushman (1906, p. 365) described the endopodite of *S. zostericola:* "The secondary branch of the antenna of the female (pl. 28, fig. 17) is reduced to a single joint having at the tip a stout curved claw and just back from it a small pointed spine." The "stout curved claw" is actually part of the sclerotized framework connecting the endopodite to the protopodite, and the "small pointed spine" observed by Cushman is one of the proximal bristles.

Mandible (figs. 5*h*, *i*): coxale with rows of short spines along ventral margin and proximally 1 short ringed medial bristle; dorsal margin of basale with spine near midde and 2 short ringed subterminal bristles; ventral margin with 5 subequal bristles; endopodite has 1st joint with 1 short terminal dorsal spine and stout curved ventral claw, medial surface with short spines; 2nd joint with short terminal dorsal spine and stout curved ventral claw; 3rd joint with 1 short dorsal spine, 1 short ventral spine, and 1 long terminal claw.

Cushman (1906, pl. 28: fig. 18) did not illustrate the spines and bristles on the coxale of *S. zostericola*. He apparently overlooked the small spines at the bases of the 3 claws on the endopodite and medial spines on the 1st endopodite joint. On the other hand, I did not observe on 3 specimens I studied the 2 short spines proximal to the 5 dorsal bristles on the basale shown in Cushman's illustration. Cushman (1906, p. 363, pl. 27: fig. 4) described the basale of the mandible of *S. americana* as having a single bristle. He may have overlooked the smaller spines. Jones (1958a, p. 49, fig. 1D) did not describe the coxale of *S. tricostata* and did not report the medial spines on the 1st endopodite joint or the dorsal spine near the middle of the basale.

Maxilla (fig. 6*a*): protopodite with fringe of long hairs and 1 short anterior bristle; exopodite with 1 long and 2 short bristles. Basale with bristle close to exopodite; endopodite has 1st joint with terminal spinous alpha and beta bristles and 1 short subterminal spine on anterior margin; 2nd joint with 2 slender a-bristles, 1 short c-bristle and 5 stout terminal b- and d-bristles with marginal denticulations and spines; three endites, each with about 4–5 bristles.

FIGURE 6.—*Sarsiella zostericola* Cushman, ♀, Hadley Harbor, Mass., 1.26 mm: *a*, maxilla, lateral view; *b*, distal part of 5th limb, lateral view; *c*, 6th limb, medial view; *d*, 7th limb; *e*, terminus of 7th limb; *f*, furca and genitalia; *g*, frontal organ and medial eye (stippled); *h*, lateral eye. (Same scale in microns: *a–d*, *g*, *h*; *e*; *f*.)

Fifth limb (fig. 6*b*): single endite with 1 short bare bristle; exopodite has 1st joint with 2 bristles; 2nd–5th joint hirsute, not separated by distinct sutures; 2nd joint with 3 bristles; 3rd–5th joints with total of 4 bristles; surface of 2nd–5th joints with fine hairs; epipodial appendage with about 33 hirsute bristles.

Sixth limb (fig. 6*c*): single endite with 3 spinose bristles; end joint with 10 spinose bristles forming 2 rows separated by space from 2 long hirsute posterior bristles and with long hairs on posterior margin and medial surface.

Seventh limb (figs. 6*d, e*): terminal end with comb of about 6 teeth opposite smaller comb with 4–5 teeth; 6 bristles in distal group, 3 on each side; 4–6 bristles in proximal group; all bristles with 2–5 distal bells.

Seventh limbs from 3 Pacific and 3 Atlantic specimens were examined. All had 6 terminal bristles. The Pacific specimens and 2 of the Atlantic specimens had 4 bristles in the proximal group. The 3rd Atlantic specimen had 5 bristles on one appendage and 6 on the other. The number of bells on proximal bristles varied, with some specimens having 3–4, and others with as many as 5 or as few as 2.

Furca (fig. 6*f*): each lamella with 5 curved claws decreasing in length posteriorly; claw no. 1 joined to lamella; with lateral and medial spines in row along concave margin; 5th claw with minute spines along concave margin; margin of each lamella posterior to 5th claw with clusters of fine hairs; anterior margin of each lamella above base of 1st claw with 2 minute spines; surface above lamellae with numerous spines.

Cushman (1906, p. 363, 365, pl. 27: fig. 6) apparently overlooked the clusters of fine hairs on the margin of each lamella posterior to the 5th claw.

Genitalia (fig. 6*f*): two large vaginal openings present anterior to 5 small ringed bristles.

Frontal organ (fig. 6*g*): with short proximal joint and elongate terminal joint with rounded tip.

Eyes: medial eye large pigmented (fig. 6*g*); lateral eyes similar in size to medial eye and with 6–7 ommatidia (fig. 6*h*).

Eggs: Each gravid female has to 5–16 ovate eggs in the brood pouch, with most specimens having 10–11 eggs. All eggs in the brood pouch of a single specimen are about the same size but occasionally 1–2 are smaller than the average. Some specimens contain unextruded eggs in addition to eggs in the brood pouch. These are smaller than those in the brood pouch. Each egg appears mottled and is enclosed in an individual transparent sheath. Only 1 specimen contained larvae.

Description of adult male.—Shell (figs. 3*c, d*; 7*a-c*): symmetrical in dorsal view with acuminate caudal process; suboval in lateral view except for rostrum, shallow anterior sinus and truncate posterior (fig. 3*c*); surface ornamented with punctae and 3 raised ribs radiating

FIGURE 7.—*Sarsiella zostericola* Cushman, adult ♂, valves, medial view: *a*, rostrum and sinus of right; *b*, caudal process and posterior of left; *c*, caudal process of right; *d*, 1st antenna, 6th and 7th joints, medial view. 2nd antenna: *e*, endopodite; *f*, endopodite and 1st and 2nd joints of exopodite. 1st antenna: *g*, 3rd to 5th joints and part of 6th joint, filaments of sensory bristle not illustrated. Mandible: *h*, medial view, medial spines not illustrated; *i*, distal part of endopodite. (Figs. *a–d*, *g* from Point Richmond, Calif., 1.06 mm; figs. *e–f*, *h–i* from Hadley Harbor, Mass., 1.01 mm. Same scale in microns: *a–c*, *d*, *e*, *g*, *i*; *f*, *h*.)

from hub slightly forward and below center of valve; posterior ribs terminating in knob with 2 small lateral pits; anterior and ventral ribs not reaching outer margin of valves; shell broadest at hub of radial ribs, highest near middle; valve surface with scattered short hairs; valve margins with rows of long hairs faintly annulated proximally; long hairs in row between ventral edge of valve and ventral flange; false radial pore canals numerous, true radial pore canals sparse; normal canals sparsely distributed over valve surface.

Duplicature with 1 small bare bristle below rostrum (fig. 7*a*); 3 small bare bristles and 2 hirsute bristles dorsal to caudal process (fig. 7*b*); 1 short bare bristle and cluster of 3 bare bristles anterior to caudal process (fig. 7*c*), and 2–3 medial bristles on caudal process; lamellar prolongation extending outward from selvage in area of caudal process (fig. 7*c*).

Dimensions of adult males are as follows:

Locality	*Maximum length (mm)*	*Midlength (mm)*	*Maximum height (mm)*	*Maximum width (mm)*
Massachusetts	1.01	0.97	0.60	0.55
California	1.06	1.01	0.72	–
"	1.01	0.97	0.69	–
"	0.93	0.89	0.55	–
"	0.96	0.91	0.62	–
"	1.02	0.98	0.65	–

First antenna: first joint bare; 2nd joint with 1 spinous dorsal bristle and 2 groups of spines along dorsal margin; 3rd joint with 1 dorsal bristle and without suture separating it from 4th joint (fig. 7*g*); 4th joint with 1 dorsal bristle with a few marginal hairs and 2 short ventral bristles; 5th joint triangular, inserted ventrally between 4th and 6th joints; sensory bristle of 5th joint with about 6 filaments distally and numerous filaments fringing "cup" at base; 6th joint with 1 short medial bristle with marginal spines (fig. 7*d*); 7th joint with short bare a-bristle, medium length b-bristle with a few distal filaments, and long c-bristle with distal filaments; 8th joint with long slender, bare d- and e-bristles and long stout f- and g-bristles, each with a few filaments distally; d- and e-bristles about the same length as f-bristle. The 2 ventral bristles of the 4th joint were not observed on all appendages examined. Some variation occurs in the spinosity of the bristles on the 2nd–6th joints.

Second antenna: exopodite with 9 joints decreasing in width distally; 1st joint with short, recurved medial bristle on terminal margin; 2nd–9th joints each with 1 long, stout bristle with marginal hairs; 9th joint with 1 medium and 1 long bristle, each with marginal hairs; 2nd–5th joints with comb of short spines along terminal margin. Endopodite 3-jointed (figs. 7*e*, *f*); 1st joint with 2 annulate spinous bristles at base; 2nd joint with 3 annulate stout spinous bristles near middle; 3rd joint elongate, recurved, with 2 short, slender terminal bristles and tip with ridges.

Cushman (1906, pl. 28: fig. 11) erred in illustrating an endopodite with 4 joints. Jones (1958a, p. 52) used the 4-jointed endopodite of *S. zostericola* as one of the criteria for distinguishing that species from *S. tricostata,* which has a 3-jointed endopodite.

Mandible: coxale bare without endite; basale with 5 bristles ventrally and 3 dorsally (figs. 7*h*; 8*b*); endopodite has 1st and 2nd joints each with stout ventral claw with marginal spines and medial surface with short spines (figs. 7*i*; 8*a*); 3rd joint with long stout terminal b-claw with spines in 2 rows along proximal two-thirds and short a-, c-, and d-bristles, c-bristles considerably shorter than a- and d-bristles.

The mandible of *S. zostericola* illustrated by Cushman (1906, pl. 28: fig. 12) differs from the above in having 3 medium ventral bristles and 5 dorsal bristles on the basale. The distribution of bristles on the basale of the mandible of *S. tricostata* illustrated by Jones (1958a, fig. 1–L) is similar to that in the above description.

Maxilla (fig. 8*c*): protopodite with fringe of long hairs on margin and 1 short bristle near middle; endite of protopodite with about 4 bristles; exopodite with 3 bristles; endopodite indistinctly segmented with about 9 bristles.

Fifth limb (fig. 8*d*): single endite with 1 spinose bristle; exopodite has 1st joint with 2 spinose bristles; 2nd-5th joints not separated by distinct sutures, with total of 7 bristles; epipodial appendage with about 32 plumose bristles (only base of distal 3 bristles shown in figure).

Sixth limb (fig. 8*e*): single endite with 3 short bristles; end joint with about 10 hirsute bristles forming 2 rows separated by space from 2 long hirsute posterior bristles, and with long hairs on posterior margin and lateral and medial surfaces.

Seventh limb not observed. Males of sarsiellids usually have at least a short bare stump for a 7th limb. The absence of a 7th limb, however, was reported previously for the male of *Sarsiella georgiana* Darby, 1965 (Darby, 1965).

Furca: each lamella with 5 curved claws; claw no. 1 joined to lamella; all claws with lateral and medial spines in row along each side of concave margin; margin of left lamella posterior to 5th claw with about 10 small spines, right lamella with about 4 small spines; anterior margin of each lamella above base of 1st claw with 2–3 minute spines.

Frontal organ (fig. 8*f*): elongate with rounded tip and 2 segments.

Copulatory limb (fig. 8*h*): each limb consisting of a proximal and distal lobe; proximal lobe with 2 short slender terminal bristles; distal lobe consisting of large smooth curved tooth with a short stout secondary tooth and 3–4 bristles at its base (2 short bristles were observed near upper part of each proximal lobe, but whether or not they originated on the lobe could not be ascertained).

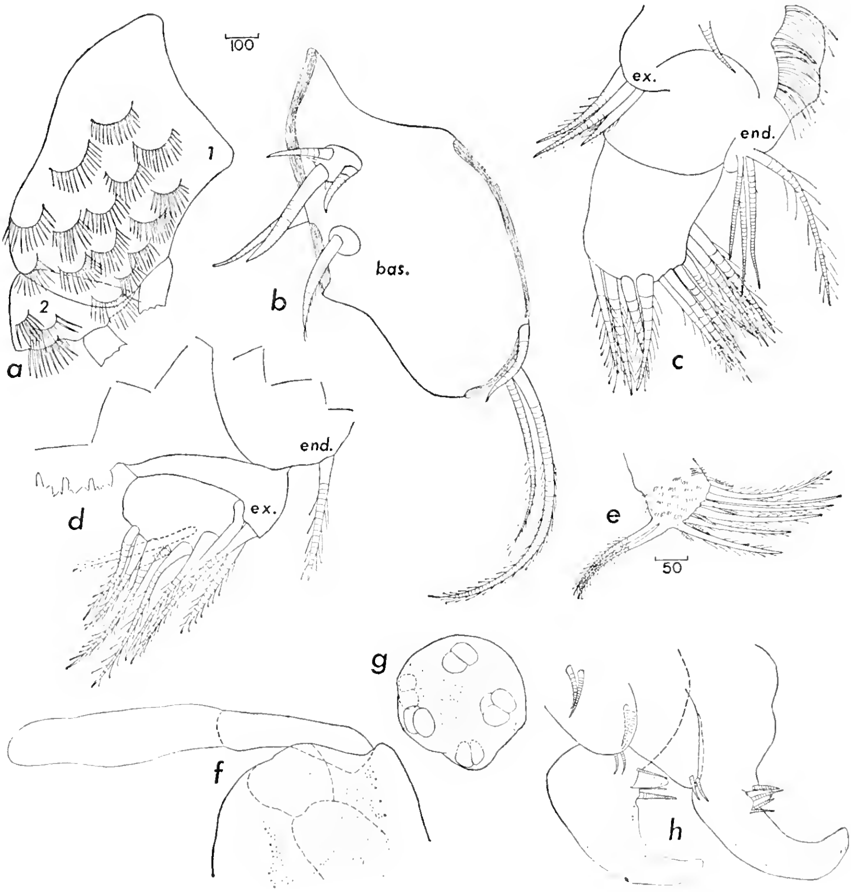

FIGURE 8.—*Sarsiella zostericola* Cushman, adult ♀: *a*, mandible, medial spines on 1st and 2nd endopodite joints; *b*, mandible, basale, medial view; *c*, maxilla; *d*, 5th limb, *e*, 6th limb; *f*, frontal organ and medial eye (stippled); *g*, lateral eye; *h*, copulatory organ. (Figs. *c-g* from Point Richmond, Calif., 1.06 mm; figs. *a-b*, *h* from Hadley Harbor, Mass., 1.01 mm. Same scale in microns: *a-d*, *f-h*; *e*.)

Cushman (1906, p. 365) described the copulatory limb as having 2 short setae at the upper end. These setae are probably equivalent to the 2 terminal bristles of the proximal lobe described above. No differences could be observed on the copulatory organs of the specimens of *S. tricostata* and *S. zostericola* I examined.

Eyes: medial eye large pigmented (fig. 8*f*); lateral eyes smaller with about 6 ommatidia (fig. 8*g*).

DESCRIPTION OF EMBRYO.—Shell: in lateral view oval without ornamental ridges; uncalcified; surface and margins with long bristles (fig. 9*b*); rostrum absent, posteroventral process small (fig. 9*a*)

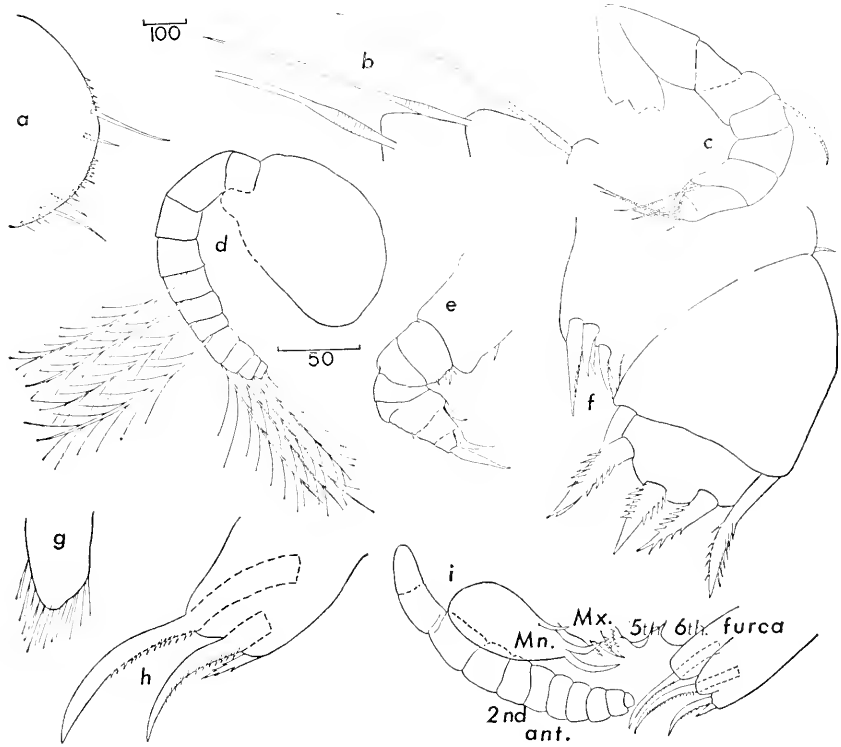

FIGURE 9.—*Sarsiella zostericola* Cushman, embryo, Hadley Harbor, Mass., 0.323 mm: *a*, posterior process of left valve, lateral view; *b*, bristles along anterodorsal margin of valve; *c*, 1st antenna; *d*, 2nd antenna; *e*, mandible; *f*, maxilla; *g*, 6th limb; *h*, left furcal lamella; *i*, ventral part of whole embryo showing right 2nd antenna, mandible ,maxilla, 5th and 6th limbs and lamellae of furca, all in place. Same scale in microns: *a*, *b*, *f-h*; *c-e*, *i*.

Dimensions of 4 embryos from *S. zostericola* (specimen from Hadley Harbor, Mass.) are as follows:

greatest length (mm)	*greatest height (mm)*	*greatest width (mm)*
0.315	0.276	–
0.323	0.235	–
0.314	–	0.216
0.328	0.280	–

First antenna (fig. 9*c*): divided by sutures into about 8 joints; long annulate bristle dorsally near middle, 6–7 bristles terminally.

Second antenna (figs. 9*d*, *i*): exopodite with 11 joints; joints 1–3 without bristles; joints 4–10 each with 1 hirsute bristle; joint 11 with 1 short and 1 long bristle; endopodite consists of small mode without bristles.

It is interesting to note that the 2nd antennae on embryos of *Gigantocypris agassizi* Müller, 1895, examined by Poulsen (1965, p. 37) also had more joints than on the adult. Hairs on bristles of the exopodite on the embryo are longer than on the adult, suggesting that the larvae after hatching are capable of swimming. Joints 1–3 of the exopodite on embryo are equivalent to the 1st joint on the adult.

Mandible (figs. 9*e*, *i*): coxale with short bristle proximally; basale with 4 or 5 subequal bristles ventrally; endopodite 3-jointed; each joint with weakly sclerotized claw.

Maxilla (figs. 9*f*, *i*): protopodite with short anterior bristle; endopodite has 1st joint with spinous alpha and beta bristles; 2nd joint with 3 denticulate b- and d-bristles; 3(?) endites, each with bristles, some bristles with marginal spines.

Fifth limb (fig. 9*i*) and 6th limb (figs. 9*g*, *i*): leaflike hirsute.

Furca (figs. 9*h*, *i*): each lamella with 3 claws; all claws with marginal spines; anterior margin of right lamella above claw no. 1 with clusters of hairs (not shown in figure).

Frontal organ: minute, transparent, 1-jointed.

Eyes: not observed.

Description of female instar III (fig. 10).—Shell: lateral view oval, without rostrum; posterior truncate, with caudal process. Measurements of selected specimens are as follows:

locality	*midlength* (*mm*)	*midheight* (*mm*)
California	0.54	0.48
"	0.56	0.46
"	0.60	0.47
"	0.55	0.42

First antenna (fig. 10*a*): fourth joint without ventral bristles, otherwise similar to adult female.

Second antenna (fig. 10*b*): endopodite 1-jointed, with small terminal bristle and 1 short dorsal bristle; exopodite 9-jointed, similar to adult female; joints 2–6 with terminal comb of short spines; bristles of 2nd, 3rd, 9th joints with short spines proximally along outer margins.

Mandible, maxilla: similar to adult female.

Fifth limb: similar to adult female except for having only 2 bristles on 2nd joint of exopodite.

Sixth limb (fig. 10*c*): leaflike with hirsute margin and 1 terminal bristle.

Seventh limb (fig. 10*d*): short stump without terminal comb or bristles.

Furca: similar to adult female except for fewer teeth on 4th and 5th claws.

Frontal organ: 1-jointed with rounded tip.

Eyes: medial eye large, pigmented; lateral eyes about same size as medial eye, with about 4 divided ommatidia.

Genitalia: undeveloped.

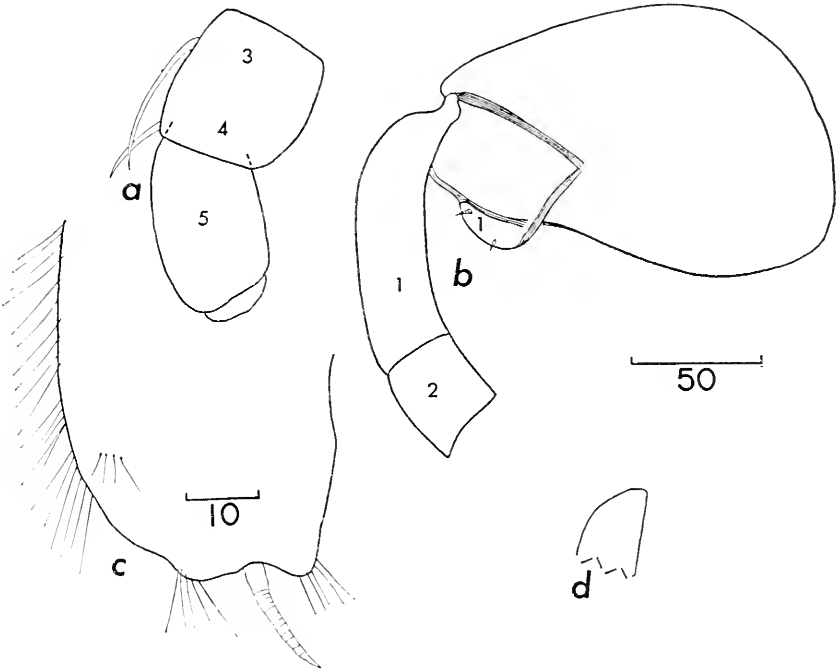

FIGURE 10.—*Sarsiella zostericola* Cushman, stage III ♀ from California: *a*, 1st antenna, 3rd to end joints, bristles shown only on 3rd and 4th joints; *b*, 2nd antenna, protopodite, endopodite, 1st and 2nd joints of exopodite; *c*, 6th limb; *d*, 7th limb. (Same scale, in microns: *a*, *b*, *d*; *c*.)

DESCRIPTION OF FEMALE INSTAR IV (fig. 11).—Shell: lateral view, oval, similar to female instar III, but more rounded. Dimensions of selected specimens are as follows:

locality	*midlength (mm)*	*midheight (mm)*
California	0.71	0.59
"	0.73	0.62
"	0.72	0.60
"	0.67	0.59
"	0.64	0.55

First antenna (fig. 11*a*): fourth joint with 1 ventral bristle; otherwise similar to adult female.

Second antenna: endopodite 1-jointed with short terminal spine and 1–2 short annulate dorsal bristles (fig. 11*b*); exopodite similar to adult female; bristles on 2nd and 3rd joints and 9th joint with short spines proximally along outer margin.

Mandible, maxilla, 5th limb, furca: similar to adult female.

Sixth limb: endite with 2 subequal bristles; end joint with 8 bristles, otherwise similar to adult female.

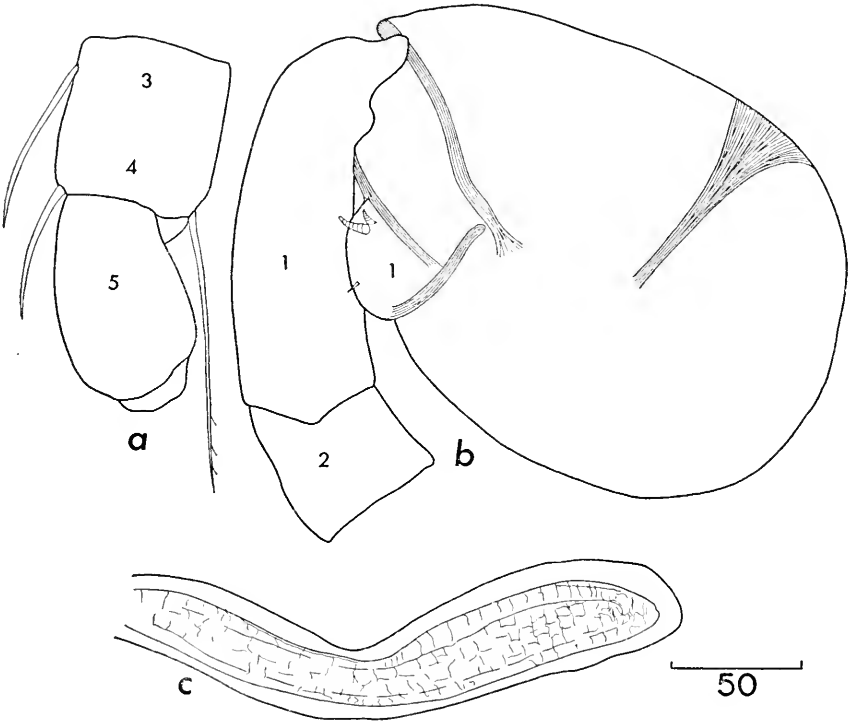

FIGURE 11.—*Sarsiella zostericola* Cushman, stage IV ♀ from California: *a*, 1st antenna, 3rd to end joints, bristles shown only on 3rd and 4th joints; *b*, 2nd antenna, protopodite, endopodite, 1st and 2nd joints of exopodite; *c*, 7th limb. (Scale in microns.)

Seventh limb (fig. 11*c*): elongate without bristles or terminal comb.

Eyes: medial eye large, pigmented; lateral eyes about same size as medial eye.

Frontal organ: 1-jointed with rounded tip.

Genitalia: undeveloped.

DESCRIPTION OF FEMALE INSTAR V (fig. 12; pl. 2).—Shell: oval in lateral view; posterior more truncate than adult female. Dimensions of selected specimens are as follows:

locality	*midlength (mm)*	*midheight (mm)*	*remarks*
California	0.89	0.79	eggs in ovaries
"	0.95	0.80	–
"	0.96	0.79	–
"	0.89	0.76	–

First antenna (fig. 12*a*; pl. 2*a*): 4th joint with 1 long and 1 medium ventral bristle, otherwise similar to adult female.

Second antenna, mandible, maxilla, 5th limb, 6th limb, furca (pl. 2*b*): similar to adult female.

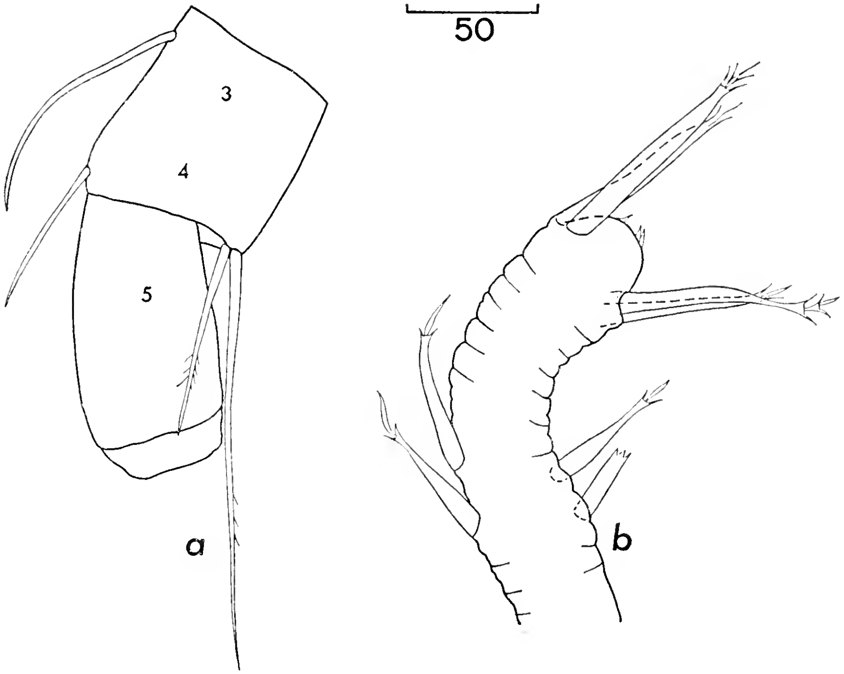

FIGURE 12.—*Sarsiella zostericola* Cushman, stage V ♀ from California: *a*, 1st antenna, 3rd to end joints, bristles shown only on 3rd and 4th joints; *b*, 7th limb (one of lateral bristles broken). (Scale in microns.)

Seventh limb (fig. 12*b*): terminal end with 4 small teeth near tip; 4 bristles in distal group, 2 on each side; 4 bristles in proximal group, 2 on each side; all bristles with 1–2 bells distally.

Frontal organ (pl. 2*a*): 2-jointed with rounded tip.

Eyes (pl. 2*a*): medial eye large, pigmented; lateral eyes about same size as medial eye, with 4 or 5 divided ommatidia.

Genitalia (pl. 2*b*, *c*): undeveloped.

Eggs (pl. 2*d*): about 5 eggs in ovary of 1 specimen. Absence of developed genitalia in instar V indicates that eggs, when present at this stage, are not fertilized.

Description of male instar III (fig. 13).—Shell: more elongate and slightly smaller than female instar III. Dimensions of a selected specimen are as follows:

locality	*midlength (mm)*	*midheight (mm)*
California	0.53	0.40

First antenna (fig. 13*a*), 5th, 6th, 7th limbs (fig. 13*c*), furca, eyes, frontal organ: similar to female instar III.

Second antenna: endopodite 2-jointed (fig. 13*b*); 1st joint with 1 dorsal bristle; 2nd joint with 1 small terminal bristle; exopodite 9-jointed, similar to mature female; bristles on 2nd to 4th joints and 9th joint with short marginal spines proximally.

Mandible, maxilla: similar to adult female.

Copulatory limb: undeveloped.

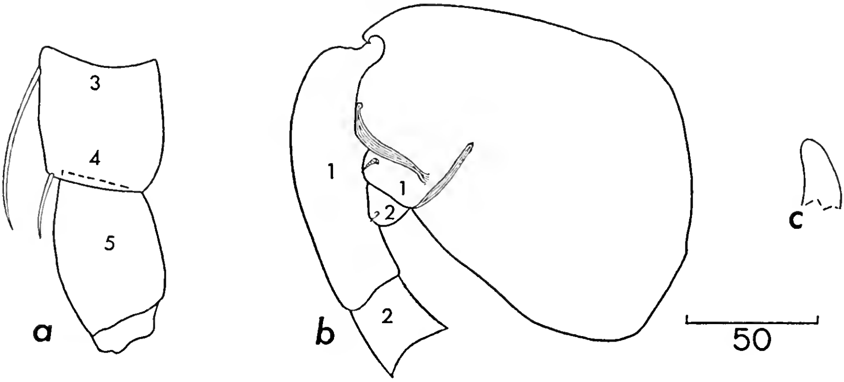

Figure 13.—*Sarsiella zostericola* Cushman, stage III ♂ from California: *a*, 1st antenna, 3rd to end joints, bristles shown only on 3rd and 4th joints; *b*, 2nd antenna, protopodite, endopodite, 1st and 2nd joints of exopodite; *c*, 7th limb. (Scale in microns.)

Description of male instar IV (fig. 14).—Shell: slightly more elongate and smaller than female instar IV. Dimensions of a selected specimen are as follows:

locality	*midlength (mm)*	*midheight (mm)*
California	0.59	0.50

First antenna (fig. 14*a*), 6th limb, frontal organ, eyes: similar to female instar IV.

Second antenna: endopodite 2-jointed (fig. 14*b*); 1st joint with 1–2 short annulate bristles; 2nd joint with 2 subequal bristles near middle and 1 short stubby bristle terminally; exopodite similar to adult female; bristles on 3rd and 4th joints with short spines proximally along outer margin.

Mandible, maxilla, 5th limb: similar to adult female.

Seventh limb (fig. 14*c*): short stump.

Copulatory limb: consists of 2–3 lobes, hook not developed.

DESCRIPTION OF MALE INSTAR V (fig. 15; pl. 2*e*–*o*).—Shell: More elongate and slightly smaller than female instar V. Dimensions of selected specimens are as follows:

locality	*midlength (mm)*	*midheight (mm)*
California	0.81	0.63
"	0.84	0.68

First antenna (fig. 15*a*; pl. 2*e*, *f*), eyes, and frontal organ (pl. 2*o*): similar to female instar V.

Second antenna (fig. 15*b*; pl. 2*e*, *g*, *h*): endopodite 3-jointed (fig. 15*b*): 1st, 2nd, and 3rd joints each with 2 short bristles; bristles on 3rd joint terminal; exopodite similar to adult female.

Mandible (pl. 2*e*, *i*), maxilla (pl. 2*j*, *k*), 5th limb (pl. 2*l*), 6th limb (pl. 2*m*), furca (pl. 2*n*): similar to adult female.

Seventh limb (fig. 15*d*): short stump.

Copulatory limb (fig. 15*c*): consisting of hooklike "clasping organ" and large transparent lobe having medially a smaller lobe with small bristle.

SUMMARY OF DEVELOPMENT.—Shell (fig. 2): Bristles on the outer side of the shell seem already fully developed in the embryo. Also present in the embryo are 2 hirsute bristles on the posterodorsal part of the inner lamella. The inner side of the caudal process of the embryo was not observed, but the distribution of bristles on the outer side of the caudal process is similar to that of the adult. All instars have truncate posteriors somewhat similar to the adult male. In lateral view, the posterior is more rounded in the adult female than in the instar, and the caudal process is on the ventral margin of the shell. In dorsal view, the shell is broadest in instar stages near the middle of the shell, where the radial ridges intersect. In the adult female the posterior of the shell is relatively broader than in instars, and in many the posterior is the broadest part of the shell.

Shells of male instars are similar to equivalent stages of the female but are slightly smaller and more elongate. The adult male is about the same height as the shell of instar V but is longer. It has a prominant rostrum, and the posterior is truncate as in the shells of juveniles. The shell of the adult male is much smaller than the adult female.

First antenna: In the embryo the 1st antenna is divided into about 8 joints by sutures. One long annulate bristle is located dorsally near the middle and about 7 bristles are terminal. In instar III, the 1st antenna has essentially the same form as the adult female but has no ventral bristles on the 4th joint. The number of ventral bristles on the 4th joint increases with each instar: 1 in instar IV, 2 in instar V, and 3 in the adult. The outer bristle is formed first and each succeeding bristle is added on the inside.

In the adult male the 6th joint is elongate; the 5th joint consists of a small triangle wedged ventrally between the 4th and 6th joints, and the sensory bristle has at its base a small cuplike process bearing numerous thin filaments.

Second antenna: In the embryo the exopodite of the 2nd antenna is divided into 11 joints: each joint from 4 to 10 bears a long hirsute bristle; joint 11 bears 1 long hirsute bristle and 1 short bristle. Marginal hairs on the bristles of the exopodite are relatively longer on the embryo than on older stages. Except for small variations in distribuition of marginal spines on bristles, the exopodite of the 2nd antenna is essentially the same from instar III to the adult. The endopodite of the embryo consists of a node without bristles. The endopodite on the female is 1-jointed and has 1 terminal bristle on all stages from instar III through the adult, but the number of dorsal bristles varies: 1 on instar III, 1–2 on instar IV, 2 on instar V and the adult.

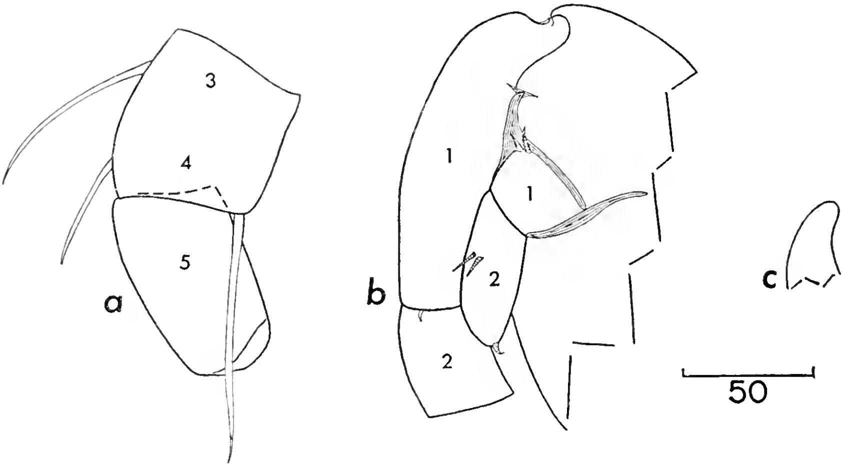

FIGURE 14.—*Sarsiella zostericola* Cushman, stage IV ♂ from California: *a*, 1st antenna, 3rd to end joints, bristles shown only on 3rd and 4th joints; *b*, 2nd antenna, endopodite, 1st and 2nd joints of exopodite; *c*, 7th limb. (Scale in microns.)

In instar III of the male the endopodite is 2-jointed with 1 dorsal bristle on the 1st joint and a small terminal bristle on the 2nd; in instar IV the 1st joint has 1–2 dorsal bristles, and the 2nd joint has 2 subequal bristles near the middle and 1 short stubby bristle terminally; instar V is 3-jointed: the 1st joint has 2 bristles near the base;

the 2nd joint has 2 short bristles near the middle; the 3rd joint has 2 short terminal bristles. A 3rd bristle is present on the 2nd joint of the adult.

Mandible: In the embryo the claws of the endopodite are only weakly sclerotized. The mandible of instars III–IV and the adult female are similar. The adult male differs in having longer dorsal bristles on the basale and in having the claw of the 1st endopodite joint situated more proximally on the ventral margin.

Maxilla: In the embryo the 2nd joint of the endopodite has only 3 b- and d-bristles. The maxilla of instars III–V and the adult female are similar. The maxilla of the adult male differs from the female in being smaller, having 1 instead of 3 endites, and in having bristles of the end joints distributed differently.

Fifth limb: In the embryo the 5th limb is poorly developed and minute. In instar III it is similar to the adult female except for having 2 instead of 3 bristles on the 2nd exopodite joint. Instars IV and V are similar to the adult female. The 5th limb of the adult male differs from the female in being considerably smaller and also in the distribution of marginal hairs on bristles.

Sixth limb: In the embryo the 6th limb is minute and foliaceous with marginal hairs. In instar III the 6th limb has 1 terminal bristle. In instar IV the 6th limb is similar to the adult female with the exceptions of having 2 instead of 3 bristles on the endite and 8 instead of 10 bristles on the end joint. Instar V is similar to the adult female. The 6th limb of the adult male is somewhat smaller than on the female.

Seventh limb: In the embryo the 7th limb was not observed and is probably absent. In the female in instar III the 7th limb is a short stump, in instar IV the 7th limb is elongate but bare; in instar V the 7th limb has 4 small teeth near the tip, 4 distal bristles and 4 proximal bristles; in the adult the 7th limb has a terminal comb of about 6 teeth opposite a smaller comb with 4–5 teeth, 6 distal bristles, and 4–6 proximal bristles. In the male the 7th limb consists of a short stump on instars and is absent or negligible in adult.

Furca: In the embryo the furca has only 3 claws. In instars III–V the furca is essentially the same as in the adult except for variations in the distribution of marginal teeth on proximal claws.

Copulatory organs: In the female instars III–V the genitalia are poorly developed; in the adult the genitalia contains 2 large vaginal openings. In the male genitalia are undeveloped on instars III and IV; on instar V the copulatory limb is bilobate and has a hooklike "clasping organ"; in the adult the hooklike organ is strongly developed and complicated, and each lobe bears 2–4 bristles.

Frontal organ: In the embryo and instars III and IV the frontal organ is elongate and 1-jointed with a rounded tip. In instar V and in the adult the frontal organ is 2-jointed but the presence or absence of a suture dividing the organ into 2 joints is difficult to establish with certainty because of folds and creases that develop in the appendage.

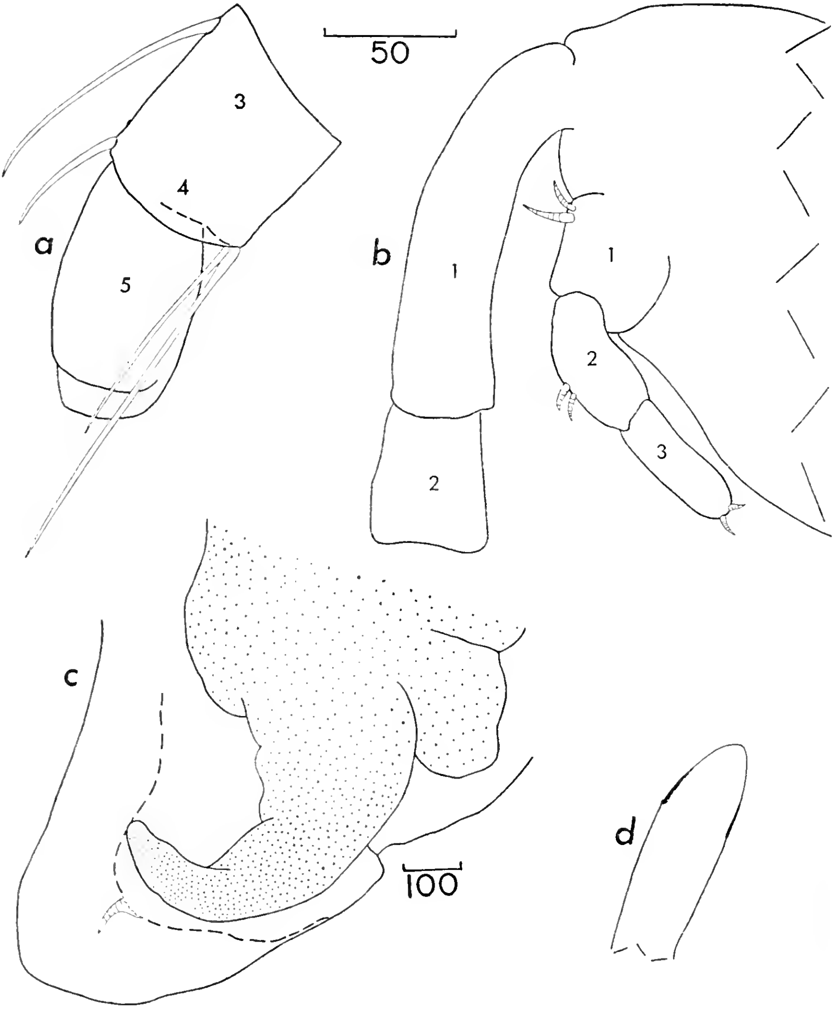

FIGURE 15.—*Sarsiella zostericola* Cushman, stage V ♂ from California: *a*, 1st antenna, 3rd to end joints, bristles shown only on 3rd and 4th joints; *b*, 2nd antenna, endopodite, 1st and 2nd joints of exopodite; *c*, copulatory organ; *d*, 7th limb. (Same scale in microns: *a*, *b*, *d*; *c*.)

Eyes: Lateral eyes were not observed in embryo but are present along with a medial eye in instars III–V and in adults. The lateral eye of the adult male may be smaller than on the female.

Reproduction.—Eggs were observed in the ovary of 1 pre-adult (stage V) female. Since the genitalia of the stage V females were not completely developed, however, we can conclude that eggs are probably not fertilized at this stage. Apparently eggs remain in the ovary of the pre-adult until the adult stage when the posterior of the adult shell broadens to accommodate the eggs.

Most gravid adult females in the collection have 10–11 eggs in the brood chamber but the observed range is 5–16. Some specimens have eggs both in the ovaries and brood chamber. Embryos with well-developed appendages were observed in only one specimen. Jones (1961, figs. 20d–f) reported that at least 55 percent of adult females in collections made throughout the year off Point Richmond, Calif., contain either eggs or embryos.

Prior to molting it is often possible to observe the new appendages and valves inside the old. About 20 adult females with eggs in the brood chamber were examined but no indication of post-adult molting was observed.

Ecology.—Water depth: Specimens of *S. zostericola* were collected in the Hadley Harbor area at depths of not more than 6 m. Blake (1933, p. 230) collected *S. zostericola* from along the coast of Maine at depths of 1–22 m, but specimens were sparse at 22 m. Specimens of *S. zostericola* from the Texas coast were collected in 1–2 m of water (Kornicker and Wise, 1962). In the Point Richmond area, Calif., *S. zostericola* was collected at depths of 2–11 m (Jones, 1954.) The tabulation below from data in Jones (1954) shows that ostracod abundance decreases markedly at depths below about 6 m (20 ft).

The distribution of *S. zostericola* at various depths in the vicinity of Point Richmond, Calif., is as follows (Jones, 1954):

water depth (feet)	*number of samples with ostracods*	*percent of samples with ostracods*	*number of ostracods in samples*	
			average per sample	*range per sample*
1–10	27	81.5	8	1–36
11–20	15	73.3	11	1–54
21–40	12	50.0	4	1–9

Temperature and salinity: In the Point Richmond area, Calif., *S. zostericola* was collected at temperatures from 17.2°C to 18.8°C and salinities from 22 to 30‰ (see tabulation on p. 32). Along the coast of Texas specimens were collected at temperatures from 16.2°C to 25°C and salinities from 20 to 36‰ (Kornicker and Wise, 1962).

Substrate: Specimens of *S. zostericola* were collected in Hadley Harbor in sediment with a median diameter of 60 microns and sorting index (SO) of 2.5 (Nagle, in litt., 1965). In the Point Richmond area, Calif., *S. zostericola* was collected from grey to black muds composed of more than 64 percent of particles in the fine sand to clay range (see tabulation below). In the Texas area specimens were collected from mud, sand, and shell (Kornicker and Wise, 1962). In the "Gulf of Canso," Cushman (1906, p. 366) found specimens of both sexes clinging to eel grass and hydroids (*Pennaria tiarella*).

Food: A complete harpacticoid copepod (identified by T. E. Bowman) was in the stomach of a juvenile female from the Point Richmond area, Calif. The copepod contained some internal organs indicating that it was swallowed alive. The relatively large size of the copepod suggests that *S. zostericola* is capable of stretching its esophagus to several times its relaxed diameter while ingesting prey.

Behavior: Kornicker and Wise (1960) showed experimentally that *S. zostericola* burrows more rapidly in silty sand than in oolitic sand. Jones (1961, p. 290, table 2) reported that off Point Richmond, Calif., 92 percent of specimens of *S. zostericola* were collected in cores of sediment at depths within the cores of 0-20 mm, 8 percent at 20–40 mm, and none below 40 mm. Jones (1961, p. 262) stated that specimens in the core deeper than 20 mm were probably pushed to that depth by the coring tube.

The California Department of Public Health (1954) gives the environmental data from the vicinity of Point Richmond, Calif., as follows:

	total range	*range at stations containing ostracods* [a]	*total number of samples*	*date of collecting*
water [b]				
dissolved oxygen ppm	6.6–9.0	6.6–8.6	50 [c]	Oct. 5, 1953
temperature °C	17.2–19.8	17.2–18.8	50 [c]	" " "
chlorides ppm	12,000–17,800	12,000–16,900	50 [c]	" " "
sediment				
sulphide ppm	17–647	79–647	25	Sept. 14, 15, 1953
volatile solids %				
wet basis	0.5–4.8	0.5–4.8	24	" " " "
dry basis	0.7–16.0	0.7–11.4	24	" " " "
particles smaller than 0.104 mm %	64.7–98.5	64.7–97.0	65	" " " "
water depth (feet)	5–37+	6–37+	56	" " " "

[a] Ostracods were collected on Sept. 14, 15, 1953, using an Eckman grab sampler. Ostracods were collected from sediment samples, not water samples.

[b] Water samples were taken 3–4 feet below the surface with a Kemmerer water sampler.

[c] Number represents 25 samples at low tide and 25 at high tide from same stations.

Sarsiella capsula **Norman, 1869**

FIGURE 16; PLATE 3

Sarsiella capsula Norman, 1869, p. 293.—Brady and Norman, 1896, p. 677, pl. LX (figs. 1–4, 18).

Sarsiella levis Müller, 1894, p. 216, pl. 4 (figs. 11, 19, 20, 23, 24, 26, 32, 36, 45–47), pl. 8 (figs. 2, 3).

Nematohamma obliqua Brady and Norman, 1896, pp. 680–682, pl. LII (figs. 1, 2), pl. LIII (figs. 12–15).

Not *Sarsiella capsula,* Sars, 1888, p. 229, pl. III (figs. 5–7), pl. X [probably *Sarsiella,* new species].—Müller, 1894, p. 214, pl. 4 (figs. 4–6, 8–10, 22, 25, 27–29, 31, 33–35, 37, 48), pl. 8 (figs. 6, 7) [probably *Sarsiella,* new species].—Brady, 1911, p. 395 [listed, probably *Sarsiella,* new species].—Rome, 1942, p. 8 [listed, probably same species as Müller, 1894]; 1964, p. 4 [listed].

Holotype: *S. capsula* Norman, 1869, unique, female.

Norman (1869, p. 293) described *S. capsula* from a single specimen collected in the vicinity of the Shetland Islands. His description included only the external features of the carapace and was not illustrated. Brady and Norman (1869, p. 677, pl. LX: figs. 1–4, 18) emended the description and illustrated the carapace and the maxilla. In addition to the Shetland Island specimen, they had available specimens collected by Norman from Valentia, Ireland, and the Gulf of Naples, Italy. They state (1896, p. 678) that the male is unknown.

A Shetland Island specimen and 3 specimens from Valentia are together on a dry slide (1911. 11. 8, M 3985) in the Norman Collection at the British Museum (Natural History). It is not possible to establish which of the specimens is from the Shetland Islands. Fortunately, Brady and Norman (1896) correctly identified the Valentia specimens so that all 4 specimens on the slide may be used to characterize the species. The slide contains 2 adult females and 2 juveniles (pl. 3*a–d*).

Specific locality data on the back of the slide (10 miles off Balta, Shetland, 73 fath.) does not agree with that given in Norman's 1869 publication (St. Magnus Bay, Shetland, 30-60 fath.); therefore, it is possible that the specimen on the slide is not the holotype. I am inclined to believe, however, that wrong locality data was published. Otherwise, I think that another specimen from the Shetland Islands would have been in the Norman Collection at the British Museum. If the holotype is lost, however, the specimen on the slide is at least a specimen from the same general locality and identified by the same author and therefore the best specimen available on which to base the species.

Comparison of the carapaces of the specimens of *S. capsula* from the Shetland Islands and Valentia with specimens identified as *S. capsula* by Müller (1894), Brady (1911), and Rome (1942) and with the description of *S. capsula* by Sars (1888) revealed that they are not conspecific. *Sarsiella capsula* Norman has in the posterodorsal region a flat-topped, crestlike prominence, whereas the other species have 2 conical projections and probably belong in 1 or more new species.

On the other hand, when the carapaces of specimens identified by Müller as *Sarsiella levis* Müller, 1894, were compared with *S.*

capsula Norman, they were found to be identical and, therefore, *S. levis* has been placed in synonymy with *S. capsula*.

Misidentifications of Sars (1888) and Müller (1894) are understandable considering the unillustrated description of Norman (1869), which could include many extant sarsiellids. Actually Müller (1894) prefaced his *S. capsula* identification with a "?" but this was omitted in his synoptic work in 1912. Both males and females of *S. capsula* and *S. levis* were described and illustrated by Müller (1894).

Brady and Norman (1896) established the genus *Nematohamma* to receive their new species *N. obliqua*, which was based on males collected off Valentia and Birterbuy Bay, Ireland. *Nematohamma obliqua* was placed in synonomy with *S. levis* Müller by Müller (1912). As previously stated, *S. levis* is a synonym of *S. capsula* Norman; therefore, *N. obliqua* is also a synonym of *S. capsula* Norman. I have compared carapaces of of *S. capsula* Norman from the Shetland Islands and Valentia with the carapace of a specimen of *N. obliqua* from Valentia (Norman Collection, British Museum) and find that they are indeed conspecific. A carapace of *N. obliqua* from off Valentia (from slide 1911.11.8, M3989, British Museum) is illustrated in plate 3*e*.

MATERIAL.—Information concerning specimens examined is as follows:

	contents of label (location of material)	*remarks*
1.	1911.11.8, M3986; *Sarsiella capsula* Norman, Madeira, off Praia Bay, 50 fathoms, A.M.N. 1897 [British Museum]	A dry slide containing a left and right valve. Absence of a posterodorsal prominence indicates it is not conspecific with *S. capsula* Norman but is probably a new species. Occurrence of the species off Madeira was reported in Brady (1911).
2.	1911.11.8, M3985; *Sarsiella capsula* Norman, Types, Shetland 1863 & Valentia 1870 [British Museum]	Specimens in this dry slide are illustrated in figures 16*a-d*. The back of the slide contains these notations: "a, 10 miles off Balta, Shetland 73 fathoms; b. off Valentia, 112 fathoms." These data do not agree with locality and depth information for Shetland given in Norman (1869, p. 293). The date (1863) does not agree with the date of 1869 given by Brady and Norman (1896).
3.	1911.11.8, 37013; *Sarsiella capsula* Norman, Birterbuy Bay, Ireland. 1874 [British Museum]	A vial containing a whole specimen preserved in preservative.

contents of label (location of material)	*remarks*
4. 1900–3–6–456; *Sarsiella capsula*, off Capri, Bay of Naples, April, 1887 [British Museum]	A dry slide containing a dry whole mount, a female.
5. 1900–3–6–457; *Sarsiella capsula*, off Valentia, Ireland, 1870 [British Museum]	A slide containing mounted appendages of an adult female.
6. 1900–3–6–458; *Sarsiella capsula*, off Valentia, Ireland, 1870 [British Museum]	A slide containing mounted appendages of an adult female. Illustrations of appendages in this paper are from appendages on this slide.
7. 1911.11.8, M3987; *Nematohamma obliqua* Bra[dy] and Nor[man], Type, Valentia Ireland, 1870 [British Museum]	A slide containing appendages of a dissected specimen. Specimen was reported in Brady and Norman (1896).
8. 1911.11.8, M3988; *Nematohamma obliqua* Bra[dy] and Nor[man], Type, Birterbuy Bay, Ireland, 1874 [British Museum]	A slide containing appendages of a dissected specimen. Specimen was reported in Brady and Norman (1896).
9. 1911.11.8, M3989: *Nematohamma obliqua* Bra[dy] and Nor[man], Type, off Valentia, 112 fath. 1870 [British Museum]	A dry slide containing a whole specimen in good condition. Specimen was reported in Brady and Norman (1896). The bottom of the slide contains the pencilled notation: "Philomedes Folinii, off Valentia, 112 fath. 1870." This specimen is illustrated in figure 16*c*.
10. Acc. Cat. No. 25019; *Sarsiella capsula* Norman [Zoological Institute of Greifswald]	Vial containing about 15 specimens including 1 adult male. These specimens were collected by G. W. Müller from the Gulf of Naples and reported in Müller (1894).
11. Acc. Cat. No. 25020; *Sarsiella levis* Müller [Zoological Institute of Greifswald]	Vial containing about 6 specimens including 1 adult male. These specimens were collected by G. W. Müller in the Gulf of Naples and reported in Müller (1894).
12. *Sarsiella capsula* Norman, 20–30 M, 19/21/39, Station 07722, Rocquerbrane ♂ [Zoological Station of Naples]	A slide containing a whole specimen mounted in balsam. It is a juvenile of a species similar to *S. capsula* of Müller, not Norman. Collected by Dom. R. Rome.

Description of adult female.—Shell (pl. 3*a*, *b*): Oval in lateral view with posteroventral caudal process; posterodorsal part of shell inflated, median part depressed. Ornamentation: prominent ridge within and parallel to dorsal and ventral margins of shell becoming faint or disappearing anteriorly and posteriorly but forming crest along dorsal margin of posterodorsal inflation; 7 radial ridges within anterior and ventral submarginal regions; 3 anterior, 3 ventral, and 1 extending onto caudal process. Surface punctate.

Typical of sarsiellids, the caudal process of *S. capsula* is more anteriorly located on adults than on juveniles (pl. 3*c*, *d*). The shell of *S. capsula* illustrated by Brady and Norman (1896, pl. LX: figs. 1–4) has the caudal process posterior, suggesting that it is a juvenile. The lateral outline of the carapace is similar to that of the specimen illustrated in plate 3*c* of this paper.

Both adult females and juveniles have 3 prominent radial ridges anteriorly. Three ventral radial ridges on juveniles may be present on adults also; however, it is not possible to be certain of the ridges on the adults because the ventral margins of both adult shells on the type slide are considerably distorted. Juveniles, adult females, and males (*N. obliqua*) (pl. 3*e*) have the flat-topped, crestlike prominence on the posterodorsal part of the shell.

Measurements: Because adult specimens on slide no. 1911.118, M3985 (British Museum) are somewhat distorted, the dimensions given below must be considered as approximate (the letters used to designate specimens refer to specimens illustrated in plate 3):

specimen	*length (mm)*	*height (mm)*	*developmental stage*
a	1.2	09.	adult ♀
b	1.2	0.9	adult ♀
c	0.7	0.6	juvenile
d	0.5	0.4	juvenile
e	1.2	0.7	adult ♂

Norman (1869, p. 293) recorded the length of the carapace of *S. capsula* as about $\frac{1}{15}$ inch [about 1.7 mm]. Brady and Norman (1896, p. 678) recorded the length of *S. capsula* as 1.2 mm and height as 1 mm. The dimensions given by the latter authors are close to my measurements of female adults.

First antenna (fig. 16*a*): 1st joint bare; 2nd joint with 1 dorsal bristle; 3rd joint with 1 dorsal and 1 ventral bristle and without suture separating it from 4th joint; 4th joint with 1 dorsal bristle and 2 long and 1 short ventral bristles; 5th joint with stout terminal ventral bristle; 6th-8th joints apparently with normal number of bristles, but difficult to discern because of poor condition of slide.

Brady and Norman (1896, p. 678) reported only 2 ventral bristles on the 4th joint.

Second antenna (fig. 16*b*): exopodite with 9 joints decreasing in width distally; 2nd–8th joints each with 1 long stout bristle; 9th joint with 1 short and 1 long bristle; bristles on 2nd–9th joints without hairs or marginal spines; endopodite 1-jointed with 2 short ringed proximal bristles.

Brady and Norman (1896, p. 678) described the endopodite as a "secondary branch rudimentary, consisting only of a little nodulous process carrying one short seta." A second spine is clearly discernable on British Museum slide no. 1900–3–6–458.

Mandible (fig. 16*c*): Each joint of endopodite with long curved claw ventrally. The mandible on each slide is in poor condition permitting discrimination of only gross features. A faint row of short spines borders the ventral margin of the coxale of a mandible mounted

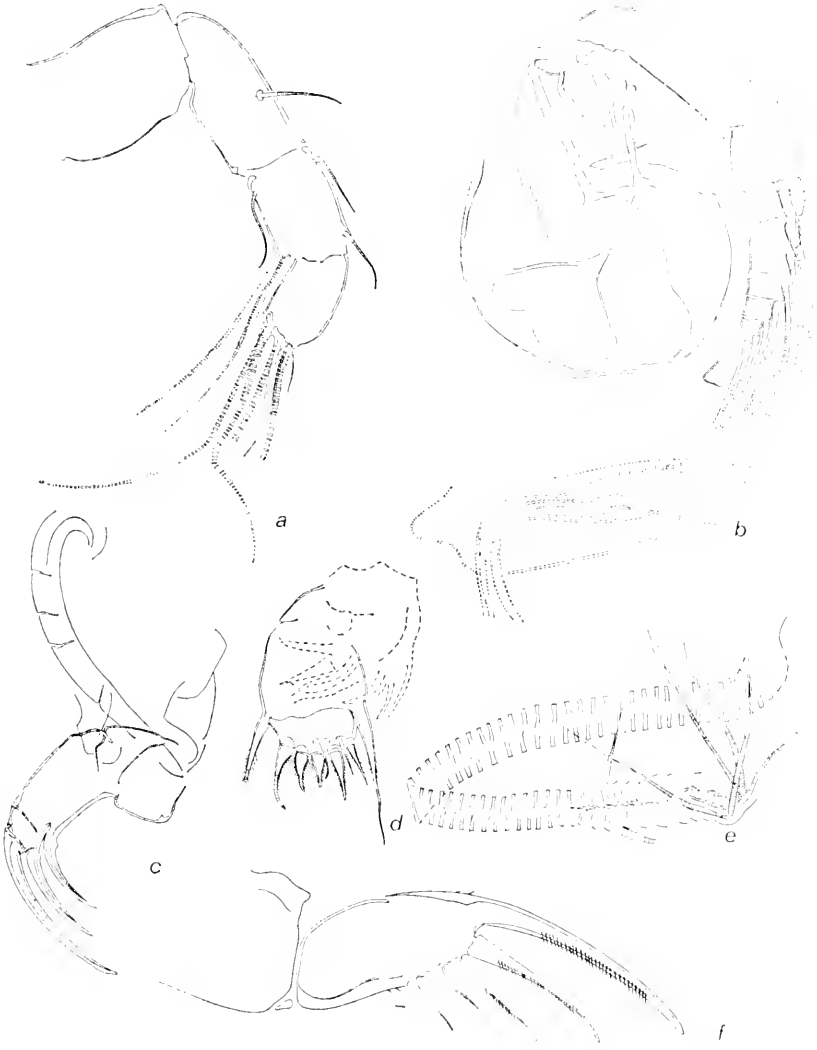

FIGURE 16.—*Sarsiella capsula* Norman (slide 1900–3–6–458, British Museum): *a*, 1st antenna; *b*, 2nd antenna; *c*, mandible; *d*, maxilla; *e*, 7th limb; *f*, furca.

on slide no. 1900–3–6–457 (British Museum) but not on mandibles on slide no. 1900–3–6–458 (British Museum).

Maxilla (fig. 16*d*): 2nd joint of endopodite with 2 slender bristles on outer side, 1 short bristle on inner side, and 5 stout terminal bristles with marginal spines.

The maxilla was the only appendage illustrated by Brady and Norman (1896, pl. 9: fig. 18). It is essentially the same as the maxilla on slide no. 1900–3–6–458 (British Museum) illustrated in this paper (fig. 16*d*).

Seventh limb (fig. 16*e*): 6 bristles in terminal group; 2 bristles in proximal group; all bristles with 2–4 distal bells.

The distal tip of the 7th appendage can not be observed clearly on British Museum slides (1900–3–6–457; 1900–3–6–458). This limb was not described by Brady and Norman (1896).

Furca (fig. 16*f*): each lamella with 5 curved claws decreasing in length posteriorly; claw no. 1 joined to lamella; claws 1–3 with lateral and medial spines in row along concave margin.

Brady and Norman (1896, p. 678) described the furca as having 6 claws. In both British Museum slides (1900–3–6–457; 1900–3–6–458) the furca is compressed, making the claws difficult to distinguish; however, only 5 claws can be observed on each lamella.

Sarsiella disparalis **Darby**

FIGURES 17–19; PLATE 4

Sarsiella disparalis Darby, 1965, p. 40, pls. 30, 31.

Holotype: Museum of Paleontology, University of Michigan, 48819, female.

Darby (1965, p. 40) described *S. disparalis* based on 5 females collected off Sapelo Island, Ga. The shells of his specimens varied considerably in ornamentation, some weakly and others strongly ornamented, or the right valve ornamented and the left valve almost plain. I received 2 mature females of this unusual species, both with asymmetrical shells, in a collection from the Atlantic shelf off Beaufort, N.C. To determine whether the asymmetry and variability of the shells might be caused by parasitism, both specimens were examined for parasites, but none were found. Left and right appendages were compared to determine if asymmetry in valves was reflected in them, but differences were found to be minor. Examination of a slide (UMMP 48818, no. 86) of a paratype prepared by Darby revealed the presence of a parasitic copepod of the family Choniostomatidae, but it is not considered likely that it is the cause of shell asymmetry in *S. disparalis* because the specimen containing the copepod is fairly symmetrical. Both the holotype and the above-mentioned paratype were examined.

MATERIAL.—Collection data on the specimens is as follows:

USNM number	sta. no.	no. of specimens	latitude-longitude	date collected	depth (m)	type bottom	sediment temp. (° C)	sampler type
113470	92	1	34°34.5′ N–76°25.5′ W	June 24, 1964	19	fine sand and shell	23.0	0.2 m van Veen
113471	158	1	34°22.8′ N–75°52.7′ W	Sept. 30, 1965	200	sandy mud	21.0	15 min. dredge

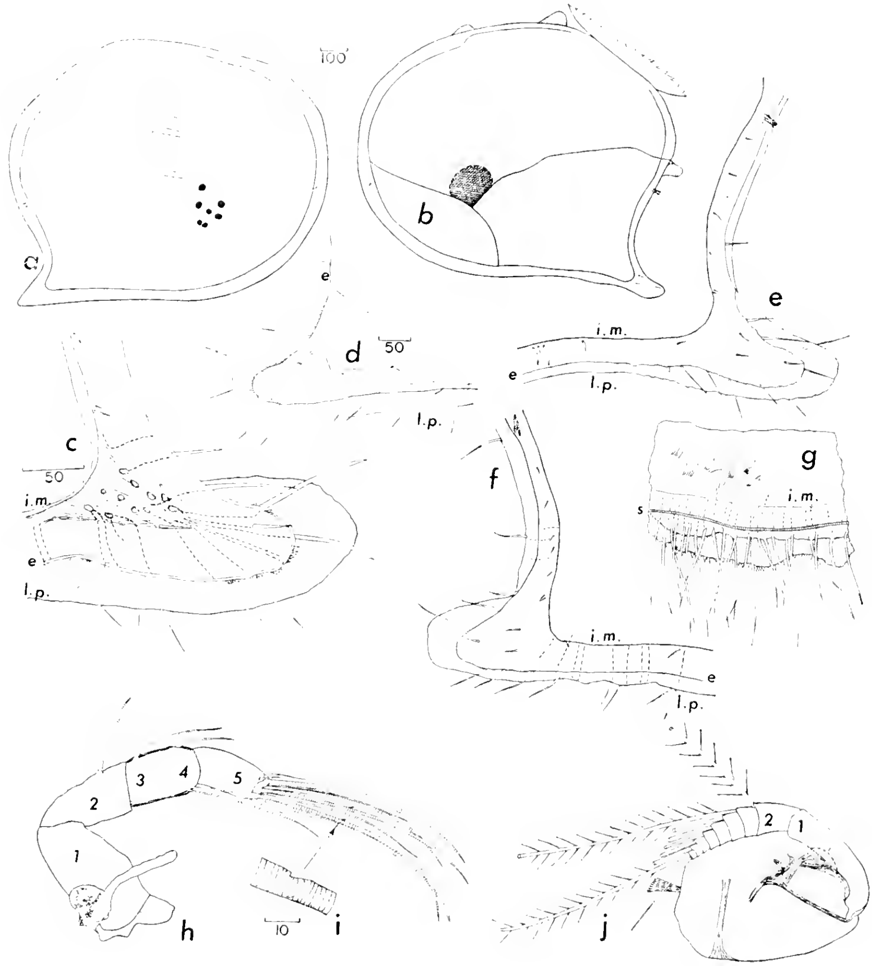

FIGURE 17.—*Sarsiella disparalis* Darby, sta. 92, ♀, 1.50 mm: *a*, medial view left valve; *b*, medial view right valve (cross-hatching indicates area of adductor muscle attachments). Caudal process right valve: *c*, medial view; *d*, lateral view. Medial view of posterior and caudal process of valves: *e*, right valve; *f*, left valve. Other parts: *g*, margin of right valve showing clusters of spines, medial view; *h*, 1st antenna, frontal organ and medial eye; *i*, enlargement of spine on bristle of 1st antenna; *j*, left 1st antenna. (Same scale in microns: *a*, *b*; *c*; *d-h*, *j*; *i*.)

Description of females in collection.—Shell (figs. 17*a-g*; pl. 4): Right valve ornamented, left relatively plain (pl. 4); caudal process directed posteriorly (figs. 17*a*, *b*), with spines and bristles on lateral surface (fig. 17*d*); selvage narrow striated, (fig. 17*g*); lamellar prolongation of selvage with denticulate margin in some areas, becoming wider around caudal process; adductor muscle scars obscure, consisting of several ovoid scars anteriorly and ventrally to midvalve; marginal flange narrow, becoming wider along ventral and posterior margins, with numerous bristles and toothlike spines; false radial pore canals numerous, normal pore canals sparse.

Inner lamella with small bristle anteriorly (figs. 17*a*, *b*), 3 bristles on caudal process (figs. 17*c*, *e*, *f*), 5 bristles near inner margin anterior to caudal process, and, dorsally to caudal process, 6–7 bare bristles followed by 2 hirsute bristles (figs. 17*e*, *f*).

Dimensions of specimens in collection are as follows:

USNM	*maximum length (mm)*	*height (mm) excluding caudal process*	*remarks*
113470	1.50	1.2	♀, 8 eggs in brood chamber
113471	1.43	1.15	♀, 6 " " " "

First antenna (figs. 17*h*, *i*; 19*k*): 1st joint bare; 2nd joint with 1 dorsal bristle and 2 dorsal spines; 3rd joint with 1 dorsal bristle; no suture between 3rd and 4th joints; 4th joint with 1 dorsal and 2 ventral bristles distally; 5th joint with 1 long ventral bristle distally; 6th joint with 1 short medial bristle distally; 7th–8th joints with 1 short and 7 long bristles.

Second antenna (figs. 17*j*, 18*a–c*): exopodite with 9 joints; 1st joint with short, curved terminal spine medially; 2nd–8th joints each with 1 bristle with natatory hairs; 9th joint with 1 long and 1 short bristle, both, or only longer bristle, with natatory hairs; distal lateral margins of 3rd–8th joints may have 2 or more small spines; endopodite 1-jointed, with 2 proximal bristles and 1 short, unringed ventral bristle.

The endopodite of the right 2nd antenna of USNM 113471 differs from the left and also from USNM 113470 in having only 1 proximal bristle. The 8th and 9th joints on the exopodite of the right 2nd antenna on USNM 113470 are abnormal in being fused and in having the long bristle on each joined together, forming a single forked bristle (fig. 18*c*). The short bristle on the 9th joint of each exopodite on USNM 113471 is shorter than the equivalent bristle on USNM 113470.

Mandible (figs. 18*d–i*): coxale with ventral fringe of short spines and short ringed medial spine (spine not observed on right mandible of specimen 113470); basale with 3 spinelike bristles dorsally and 1 lateral and 4–5 medial bristles ventrally; endopodite 3-jointed; 1st

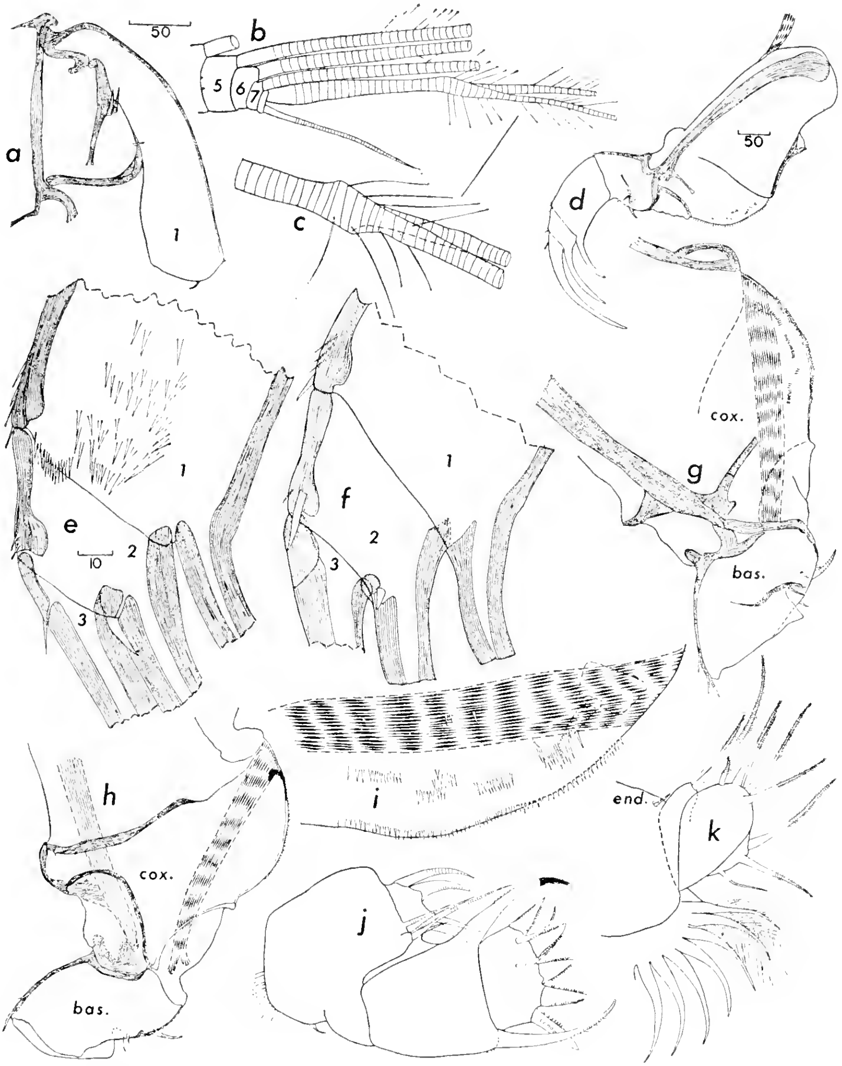

FIGURE 18.—*Sarsiella disparalis* Darby, sta. 92, ♀, 1.50 mm: *a*, left 2nd antenna, endopodite and 1st joint of exopodite; *b*, right 2nd antenna, end joints of exopodite; *c*, right 2nd antenna, abnormal combined bristles of 8th and 9th joints. Mandible: *d*, left appendage; *e*, right endopodite; *f*, left endopodite; *g*, left coxale and basale; *h*, right coxale and basale; *i*, enlargement of ventral part of left coxale, lateral view. Other parts: *j*, left maxilla, lateral view; *k*, left 5th limb. (Same scale in microns: *a, b, g, h, j, k; d; c, e, f, i.*)

joint with large curved terminal claw, 3 dorsal spines, and numerous spines medially (fig. 18*e*), 2nd joint with large terminal claw and 1 long and 1 short spine dorsally, 3rd joint with large curved terminal claw and 1 short spine dorsally and 1 ventrally.

Maxilla (figs. 18*j*, 19*k*): protopodite with short bristle on anterior margin and fringe of marginal hairs; basale with bare bristle near exopodite; exopodite with 1 long and 2 short bristles; 1st endopodite joint with 2 stout curved bristles with marginal spines, bristles annulate distally; end joint with 5 stout pectinate bristles, 2 slender lateral bristles and 1 short medial bristle; 1st endite with about 6 bristles, 2nd endite with about 5 bristles, 3rd endite with 4 bristles.

Fifth limb (fig. 18*k*): endite with 1 bare bristle; exopodite: 1st joint with 2 bristles with short spines, 2nd–5th joints with marginal hairs and total of 7 bristles, 6 with marginal spines, 1 bare, joint sutures indistinct; epipodial appendage with about 36 bristles.

Sixth limb (fig. 19*a*): endite with 1 long and 2 short bristles, ventral margin of end joint with 10 spinous bristles followed by 2 hirsute posterior bristles.

Seventh limb (figs. 19*b*, *c*): cleaning bristles: 6 terminal, 4–5 proximal, each with 3–8 bells; terminal comb with 8–14 teeth on each side.

Furca (figs. 19*d–f*): each lamella with 5 curved and pointed claws; claw 1 joined to lamella, remaining claws separated from lamella by suture; claws decrease in length proximally on lamella; posterior margins of claws 1–4 with lateral and medial teeth in rows; distal end of anterior margin of 5th tooth on left lamella with small tooth or spine; ventral margin of lamella, posterior to 5th claw, with 2–3 spines on left lamella and 1 spine on right lamella; medial surface of left lamella, between claws 4 and 5, with small spine; margins of lamellae without hairs; anterior part of ostracod body, proximal to furca, spinous (figs. 19*d*, *g*).

Frontal organ (figs. 17*h*; 19*h*, *k*): 2-jointed with short 1st joint and elongate 2nd joint, with rounded tip.

Genitalia (fig. 19*j*): genitalia with 2 large vaginal openings beneath 5 minute ringed bristles.

Eyes: median eye large, pigmented (figs. 17*h;* 19*h*, *k*); lateral eyes small, pigmented, with about 6 ommatophores around edge (figs. 19*i*, *k*).

Upper lip (fig. 19*k*): triangular process present between upper lip and basis of 1st antenna.

Eggs (fig. 19*l*): each egg surrounded by transparent membrane and containing numerous small oil globules; 6–8 eggs occupying brood chamber between posterior lobes of valves.

ECOLOGY.—Depth: One specimen from the North Carolina shelf was collected from a depth of 19 m, the second from 200 m. Darby

(1965) collected specimens in water 12.5–18.6 m deep on the Georgia shelf; the known depth range, therefore, is 12.5–200 m.

Temperature and salinity: Temperature of the sediment on the North Carolina shelf was 23°C at 19 m and 21°C at 200 m (Day, in litt.). It is probable that the salinity was 35–36 parts per thousand at 200 m depth, where a specimen was collected on the North Carolina shelf. Darby (1965, p. 40) reported the salinity in the area he collected *S. disparalis* to be about 25 parts per thousand.

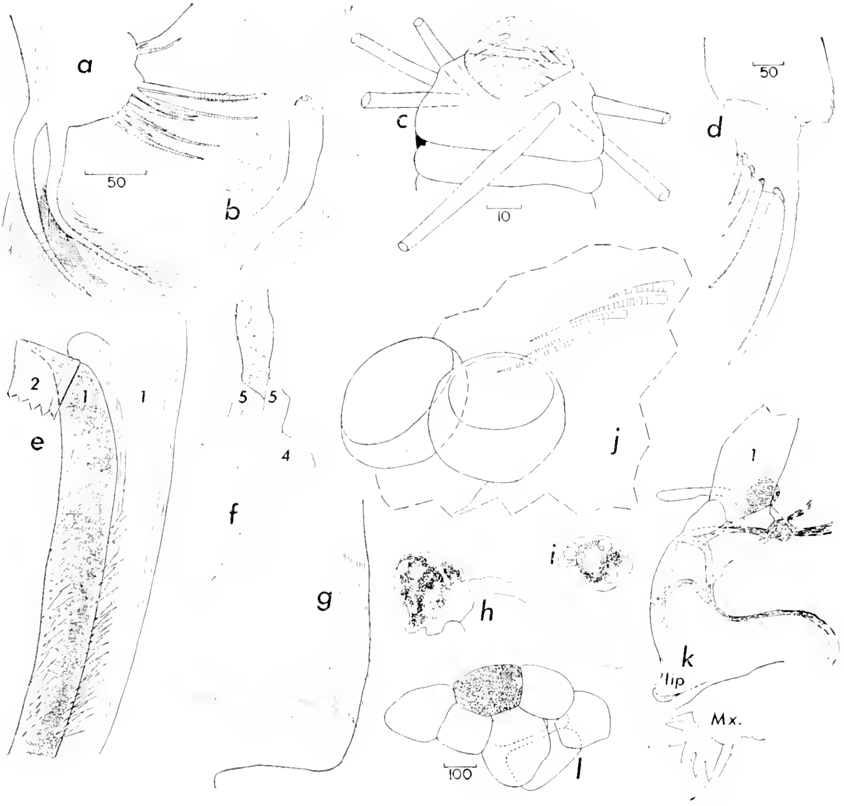

FIGURE 19.—*Sarsiella disparalis* Darby, ♀: *a*, right 6th limb, lateral view; *b*, 7th limb; *c*, enlargement of terminal process on 7th limb; *d*, furca, lateral view right lamella; *e*, furca, enlargement of claw no. 1 showing distribution of teeth (left lamella stippled); *f*, furca, enlargement of claws 4, 5 (left lamella stippled); *g*, enlargement of part of anterior surface above furcal attachment shown in *d* above; *h*, frontal organ and medial eye; *i*, lateral eye; *j*, genitalia; *k*, anterior of ostracod showing medial eye, frontal organ, 1st joint of 1st antenna, lateral eye, upper lip, maxilla; *l*, group of 8 eggs from brood chamber. (Figs. *a-i*, *k*, *l* from sta. 92, 1.50 mm; fig. *j* from sta. 158, 1.43 mm. Same scale in microns: *a*, *h*, *i*; *b*, *d*, *k*; *c*, *e-g*, *j*; *l*.)

Substrate: The specimen from 19 m on the North Carolina shelf was collected in a sediment consisting of fine sand and shell; the specimen from 200 m was collected in sandy mud.

Food: The specimen from 200 m depth on the North Carolina shelf contained in its stomach a large, whole harpacticoid copepod, several arthropod appendages, and a diatom. One of Darby's specimens (UMMP 48819) examined by me contains 2 free-living nematodes in the stomach: 1 appears to be partly digested, and the good condition of the other suggests that it had been ingested only prior to capture of the ostracod.

Parasites: No parasites were observed on the 2 specimens from the North Carolina shelf. One of Darby's specimens from off Georgia, however, contained in the brood chamber a parasitic female copepod of the family Choniostomatidae along with several clusters of copepod eggs. The slide (UMMP 48818, no. 86) containing the copepod and copepod eggs is labeled "Eggs" by Darby, who apparently thought them to be ostracod eggs. The shell of the specimen containing the parasite is quite symmetrical indicating that the parasitic copepod is not the cause of some specimens of *S. disparalis* having asymmetrical shells.

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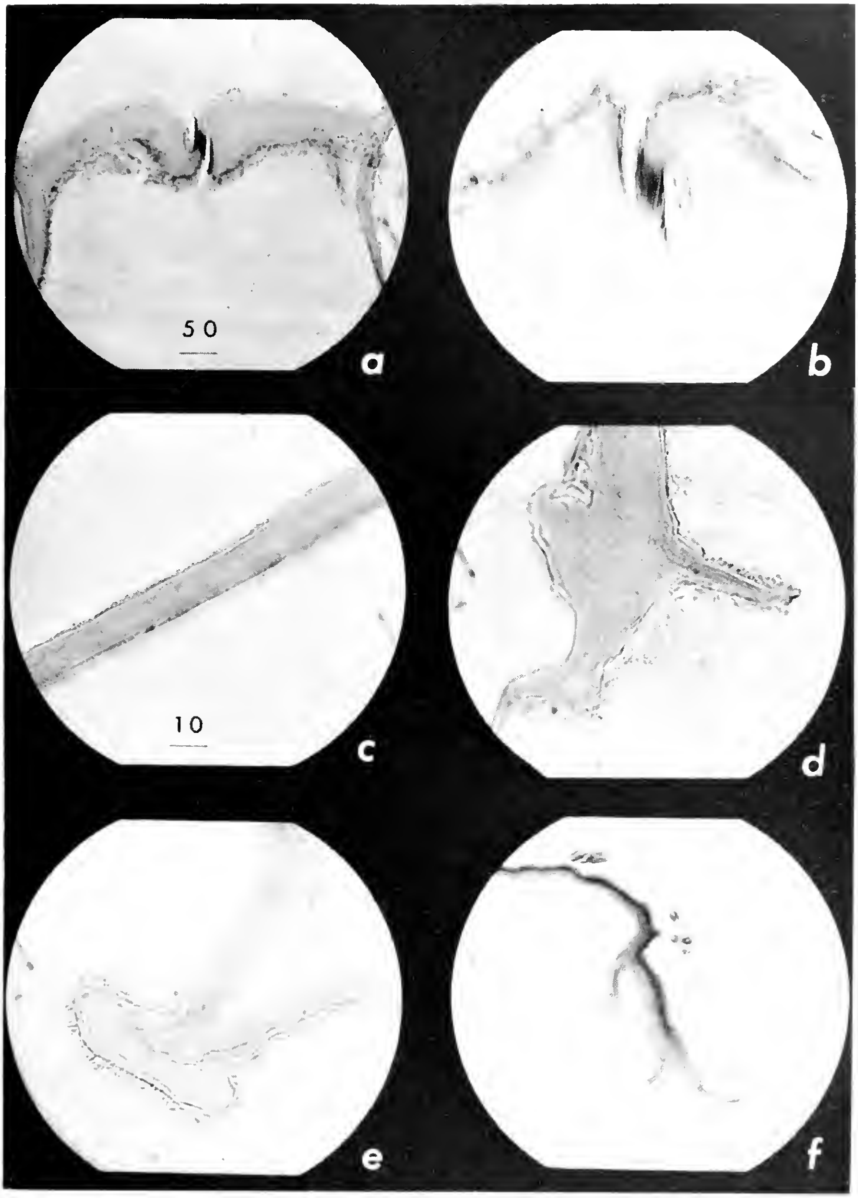
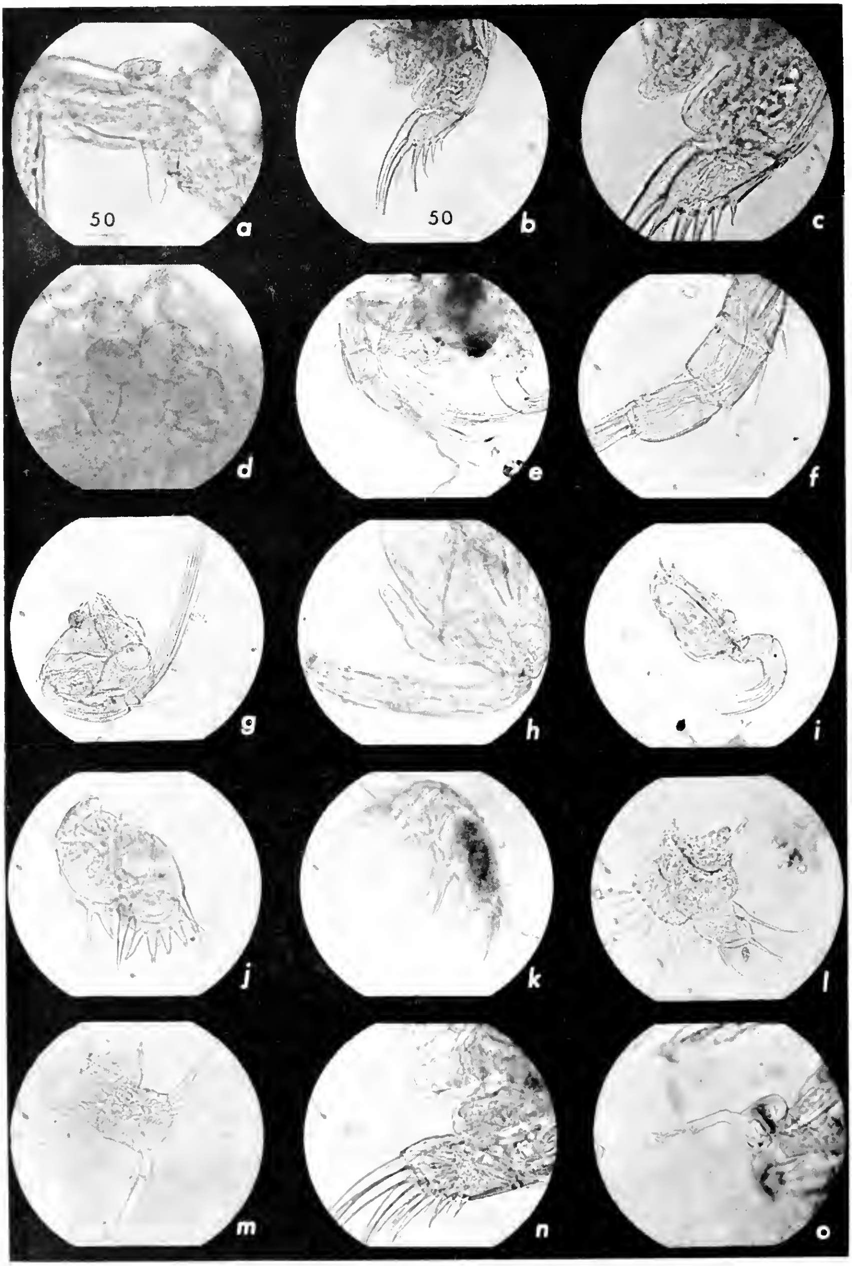
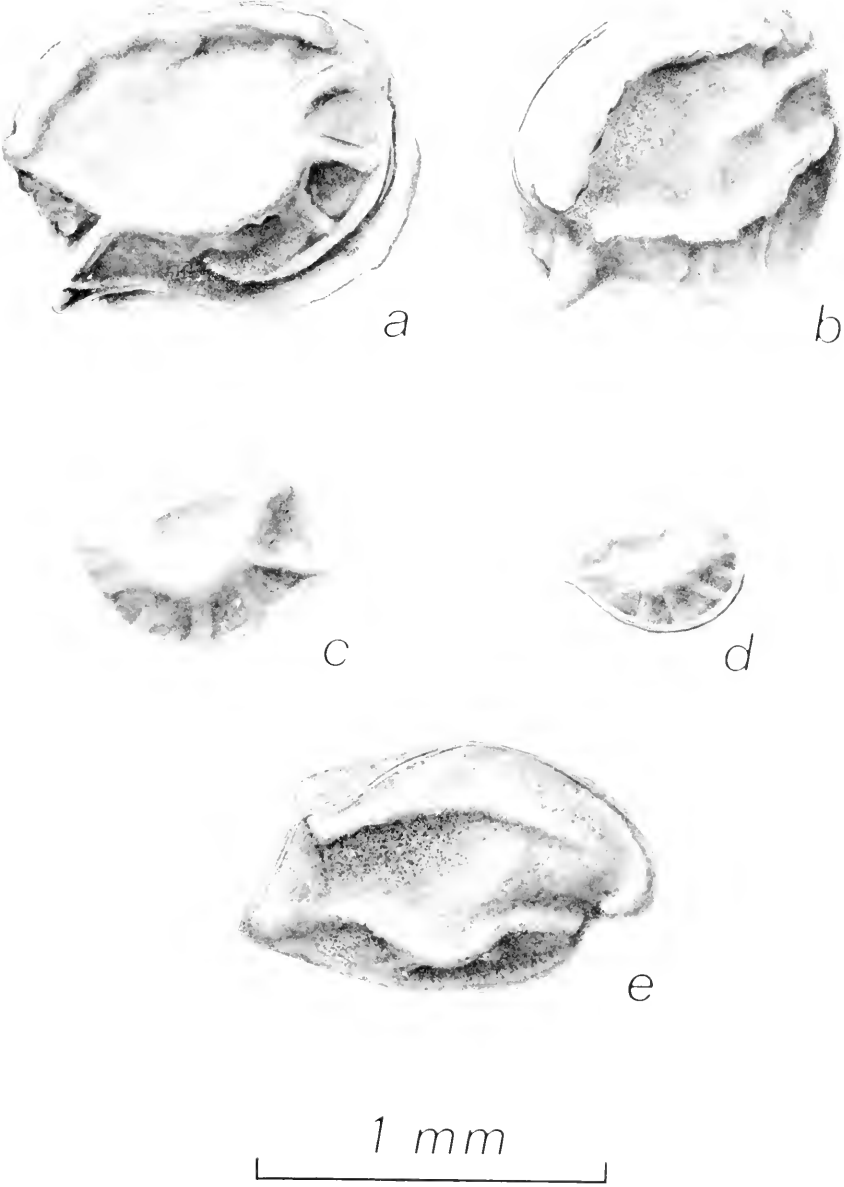
PLATES



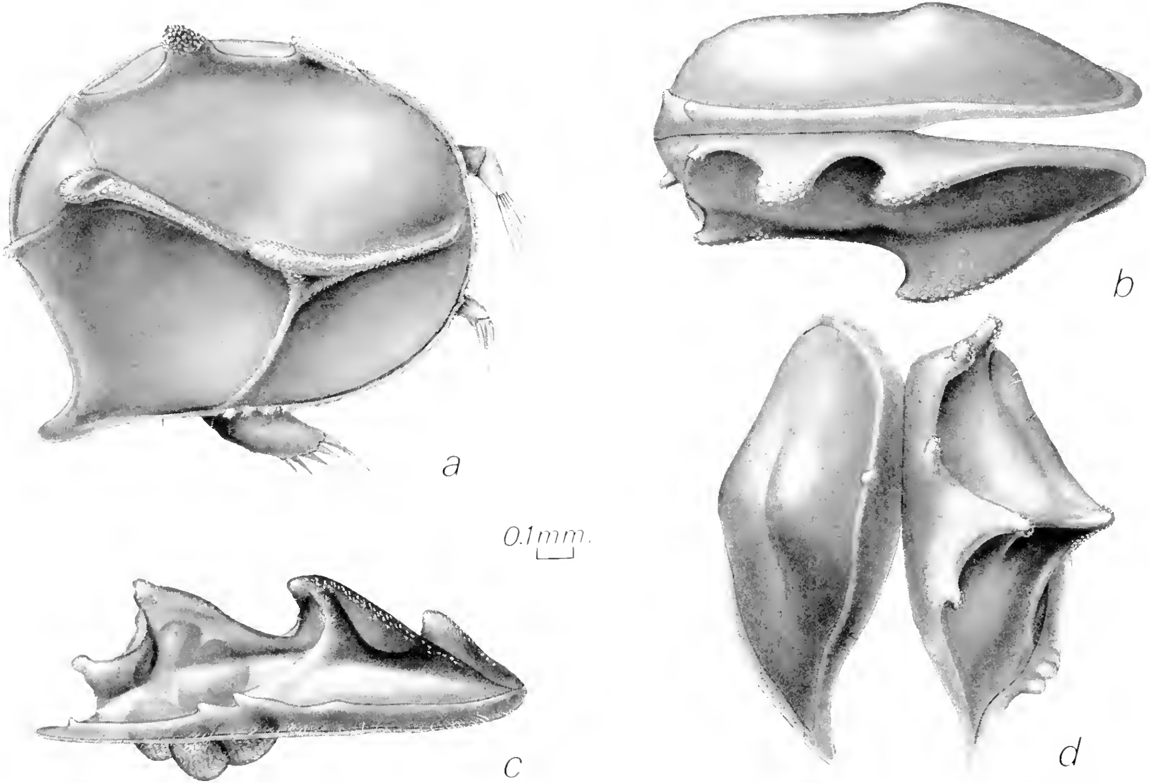
Sarsiella zostericola Cushman, transverse sections through shell: *a*, dorsal, through hinge and ligament; *b*, enlargement of ligament in *a; c*, outer lamella showing lineations, inner side of lamella is toward bottom of illustration; *d*, ventral margin, left valve; *e*, middle ridge; *f*, ventral margin right valve showing selvage, false marginal pore canal with bristle, marginal ridge. (Same scale in microns: *a, f; b–e.*)



Sarsiella zostericola Cushman, stage V ♀: *a*, proximal part of 1st antenna, frontal organ with medial eye, lateral eye; *b*, furca and genitalia; *c*, enlargement of genitalia in *b*; *d*, eggs in ovaries. Stage V ♂: *e*, 1st and 2nd antenna, mandible; *f*, 1st antenna, 2nd–8th joints; *g*, 2nd antenna; *h*, 2nd antenna, endopodite, and proximal part of exopodite; *i*, mandible; *j*, maxilla; *k*, maxilla, oblique view; *l*, 5th limb, distal part; *m*, 6th limb; *n*, furca and copulatory organ; *o*, frontal organ and medial eye. (Same scale in microns: *a*, *c*, *d*, *f*, *h*; *j*–*o*; *b*, *e*, *g*, *i*.)



Sarsiella capsula Norman, slide 1911.11.8, M 3985, British Museum: *a*, *b*, adult females *c*, *d*, juveniles. Slide 1911.11.8, M 3989, British Museum: *e*, adult male.



Sarsiella disparalis Darby, sta. 92, ♀, 1.50 mm: *a*, right lateral view; *b*, dorsal view, valves slightly open; *c*, ventral view, from slightly to rear, of right valve with eggs; *d*, posterior view, from slightly above, with valve partly open.

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Ecology and Social Organization In the Iguanid Lizard *Anolis lineatopus*

By A. Stanley Rand [1]

Introduction

This paper reports the findings of a 10-month (August 1961 to June 1962) field study of the ecology and behavior, particularly the social behavior, of *Anolis lineatopus,* in edificarian situations, in the vicinity of Kingston, Jamaica.

The geographical variation of this common Jamaican lizard has been discussed by Underwood and Williams (1959) and by Grant (1940) but, beyond brief notes in these papers and in Barbour (1910), its natural history has never been described.

There have been a number of detailed studies on free-living lizards, but most of them have dealt with temperate zone species in temperate environments. Few investigators have had the opportunity to conduct intensive and extensive studies on lizards in the tropics. The few exceptions include Evans (1951), Harris (1964), and Hirth (1963 a and b). No extended field study with an emphasis similar to this one has been published on any tropical *Anolis* though the shorter papers of Evans (1938a) and Oliver (1948) report relevant

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information for *A. sagrei*. Evans (1961) gives a quite complete bibliography of lizard natural history.

Throughout this study I have attempted to verify critical points with counts, censuses, or other objective measurements, and I have used these extensively here. They have the disadvantage of excluding all information which is not being measured and so present a limited picture and one which is sometimes difficult to comprehend by someone who is not familiar with anoline behavior. To offset this and provide a frame of reference, I have included frequent abstracts from my field notes [direct quotes and paraphrasing both are in smaller type—ed.] and have appended two short sections to provide a picture of the general behavior of this species, one reporting the behavior of an individual which was under observation for an entire day, and the other giving a composite and hypothetical account of the usual course of the life of an *A. lineatopus*.

I want to thank first Dr. Ernest E. Williams and my wife Patricia, the two people who contributed most to this study. Dr. Williams, principal investigator of the National Science Foundation grant under which the field work was done, helped organize the project, advised me during our time in the field, and criticized the manuscript at various stages of completion. My wife helped with the field work, did most of the editing and typing of the manuscript, and provided both moral and logistic support.

A number of other people contributed importantly to the work. My father, Dr. A. L. Rand, supplied very valuable criticism of both the ideas and form of the work. Prof. Garth Underwood discussed the problem with me and gave me the benefit of his years of experience with the Jamaican anoles. Dr. P. E. Vanzolini advised on the analysis of the data and criticized the manuscript. Discussion with Dr. W. J. Smith provided additional insight into certain aspects of the behavioral concepts. Drs. M. Moynihan, E. Willis, J. Eisenberg, and W. Milstead read and criticized the manuscript.

I am indebted to Prof. D. Steven, who allowed me to use the facilities of the Zoology Department of the University of the West Indies, and to the rest of the staff there, particularly Prof. Ivan Goodbody and Mr. William Page for their assistance. I wish to thank them and the visitors at the University, such as Mr. Malcolm Edmunds and Dr. Arthur Hughes, for listening to lengthy discourses on anoles and for criticizing them most helpfully.

I am also indebted to Mr. William Page and Mrs. L. Jones for their help in determining the insects found in lizard stomachs.

Finally, I must acknowledge the financial support for this project from National Science Foundation grant number 16066.

Material and Methods

Anolis lineatopus shows considerable geographic variation within Jamaica. Those from the vicinity of Kingston are medium-sized *Anolis*, the adult males about 50 to 70 mm in snout-vent length and reaching about 8 to 9½ grams in weight. The adult females are smaller, about 37 to 47 mm in snout-vent length and about 1¼ to 3 grams in weight. Both sexes are brown to gray brown in color. The adult males are marked with irregular black bars. The females are more variable and may be almost unicolor, or they may have a diamond- or rhomb-shaped pattern on the back or a light middorsal stripe. There is only limited color change, from light to dark. The feet have the usual *Anolis* form with moderately wide toe pads and an intermediate number of lamellae (29–34 under second and third phalanges on fourth toe). The dewlap or throat fan, large and light yellow with an orange central spot, is well developed only in the male. These are called *A. lineatopus lineatopus* by Underwood and Williams (1959).

Anolis are strictly diurnal and depend almost entirely on vision in their social behavior and in locating food. They may respond to sounds but seem to pay no attention to odors.

Jamaica, at 18° north latitude, lies well within the tropics and there is relatively little variation in temperature in the two wet and two dry seasons. The *Anolis* are active year round and neither fighting, courting, nor copulation seems seasonal. There does seem to be some seasonal variation in the production of young: more in the wet season. Whether this is due to variation in egg laying or in egg survival, I do not know.

In the dry lowlands on the south coast of Jamaica, *A. l. lineatopus* is widespread and abundant but much more abundant in some places than others. This is particularly striking when one is trying to collect samples at predetermined intervals along a transect. In some cases the differences in abundance are correlated with ecological differences, but in others I could see no difference in habitat.

The areas where this study was made were all much disturbed by man. Those on which I concentrated were highly artificial gardens, the campus of the University of the West Indies, and roadside hedges and fence rows. Relatively little time was spent in natural habitats and no detailed studies were made therein. Little undisturbed habitat is left in Jamaica and what remains is mangrove swamp, scrub on dogtooth limestone and mountain forest, and all difficult of access. Since the edificarian areas were easier to work in, closer at hand and, most important, usually supported denser populations of lizards, I concentrated on these areas.

Though I made repeated trips to the other parts of the island, the intensive observations reported here were made in two suburbs of Kingston, Barbican and Mona.

In studying social behavior, I concentrated on *A. lineatopus* living in small areas, marking them individually, mapping their positions, and describing their behavior. They were marked by clipping the terminal phalanx from one front and one hind toe, according to a code (removing one additional toe allowed higher numbers). The clipped toes did not regenerate but were not visible from any distance. A number was painted on the back of each lizard with white paint (a quick-drying amylacetate base airplane paint). This was visible at a distance but each *A. lineatopus* had to be recaptured and repainted after each shedding. Though inconvenient, this gave us an opportunity to remeasure these lizards at intervals. The clipping of the terminal phalanx removed the claw but not the pad and did not seem to affect the lizard's climbing or running ability. The white painted numbers interfered slightly with shedding and certainly made the lizard more conspicuous to me and presumably to other predators. The interference with shedding however, was temporary and the increased conspicuousness unavoidable.

The lizards were measured from the tip of the snout to the anterior margin of the vent by holding them along a ruler. The measurements were recorded to the nearest millimeter, and repeated measurements on the same individual during a short period frequently varied by one millimeter but seldom by more. Throughout the paper the anole sizes given are snout-vent lengths in millimeters.

Each lizard was marked in the field as soon as it was caught and released in less than five minutes in the area where it had been captured. Two methods were used in catching the lizards. Some were noosed during the day with a running noose of nylon filament on the end of a slender stick. Others were caught by hand at night while they were sleeping. The latter technique is very effective and is the one Cagle (1948) describes as being used by professional anole collectors in Louisiana.

The marking process disturbed the lizards, and, after being released, a lizard usually remained quiet for an hour or so before resuming its normal activities.

Though the lizards learned to avoid the noose, they soon came to ignore me completely, particularly if I were stitting quietly, even in plain view and only a few feet away. Those in the areas where I spent hours watching them became very tame and would approach me without hesitation to catch an insect. One female even took an insect from my fingers.

Once the lizards had been marked and the study area mapped, observations were usually made daily. Many lizards were not recorded every day, but some were and most were seen repeatedly. In addition to this census, I made general observations, sitting quietly watching one relatively small area and noting the interactions between lizards. Finally, there were continuous observations on individual lizards when we attempted to keep track of everything that an individual did. These were mostly on the order of an hour or half an hour, but in one case we watched a lizard from before sunrise to after sunset.

I supplemented observations on aggressive behavior with experiments with stake-outs. This technique, developed by Evans (1938a) and used by Ruibal (1961) in Cuba and by me in Puerto Rico, consists of tying a lizard to the end of a stick, then placing it in the vicinity of another and recording the reaction of the resident.

Throughout my time in Jamaica, even when I was not engaged directly in studying anoles, I was aware of them and watched what they were doing. Many of my conclusions originated as general impressions based on these casual observations.

Individual Ecological Requirements

The social behavior of *A. lineatopus* can be considered as one of the adaptations of the species to its environment. The form of its social behavior is as strongly influenced by its environment as is its morphology.

In order to understand the social behavior of *A. lineatopus,* it is necessary to consider the ecological demands of each individual and how these are satisfied.

Successful reproduction is a requirement of the population but it is not necessary for the continued life of the individual. Social behavior is so involved with reproductive behavior that discussion of reproductive requirements is postponed until social behavior is being described.

The demands of the individual are of two sorts: fundamental requirements and habitat requirements. The fundamental requirements are those that an animal must satisfy to live. For *A. lineatopus* these include food, water, suitable temperatures, and protection from predators.

The habitat requirements are those structures in the environment that an animal uses to satisfy its fundamental needs. They are usually not necessary for the life of an animal, for a caged individual lives without them, but they are frequently those things that must be present if a wild individual is to settle in an area. For *A. lineatopus* they include an observation and basking perch, cover near the ground, and a sleeping site.

Fundamental Requirements

FOOD.—As is true of almost all lizards of its size, *A. lineatopus* feed primarily on insects and other small arthropods, occasionally on very small vertebrates and snails.

Anolis lineatopus waits for its prey on a perch a few inches to several feet above the ground rather than foraging for it. This hunting technique is common in visually oriented insectivorous lizards and contrasts with the active searching technique that is typically used by olfactorily oriented lizards such as skinks and teiids as well as some visually oriented iguanids.

Some prey *A. lineatopus* can catch without having to move, but usually it must move and frequently to the ground or nearby foliage. Large individuals move farthest to catch something, sometimes going four or five feet. The approach is a quick run, often broken by one or more pauses, and usually a pause just as the prey is reached. During a pause *A. lineatopus* cocks its head and looks at the prey with one eye and then shifts back to binocular vision. The binocular vision presumably uses the temporal fovea and allows better judgement of distance and direction, the monocular vision probably uses the central fovea, which may give better definition (Underwood, 1951). Sometimes *A. lineatopus* leaps several inches to seize an insect. A small insect is frequently eaten where caught but a larger one is usually carried back to a perch.

The food items in the stomachs of 45 *A. lineatopus* are shown in table 1. The anoles were collected over a period of a week in an area 10 x 50 yards in Mona. They were killed shortly after capture,

TABLE 1.—*Food items in the stomachs of 45* Anolis lineatopus

	Number of prey individuals
Arachnida	33
Diplopoda	3
Orthoptera (including roaches)	16
Dermaptera	3
Hemiptera (largely Homoptera)	68
Lepidoptera (both larvae and adults)	21
Coleoptera (only adults)	16
Hymenoptera (largely ants)	95
Miscellaneous	8

measured, and their stomachs removed and placed in alcohol. Subsequently the contents were removed and examined. Some food items were found intact but many were represented by a scattering of more resistant parts. A count of the minimum number of prey individuals present was recorded.

A count of prey items is perhaps the best count to indicate food preferences since each capture is weighted equally. It has the disadvantage of ignoring the significant fact that one large insect may supply more food than several small ones. Table 2, which shows the prey by size, makes some correction for this.

Table 2.—*Relation between prey size and lizard size* (first figure in each entry is number of prey individuals; figure in parentheses is number of stomachs)

Lizard size (snout-vent)	Prey size					Total food	Total stomachs
	<0.5 cm		0.5–1.0 cm	1.0–2.0 cm	>2.0 cm		
	Ants	Others					
26–30 mm	12(5)	44(8)	4(2)			60	8
31–40	28(8)	28(10)	4(4)	1(1)	1(1)	62	11+1 empty
41–50	30(9)	25(10)	9(8)	11(8)	2(2)	77	13
51–71	19(6)	3(2)	3(3)	8(6)	3(3)	36	11

Casual observations add dragon flies, Diptera, termites, small snails, and small frogs to the list of prey found in stomachs.

The variety of major types of invertebrates present in appreciable numbers demonstrates that *A. lineatopus* is not a specialist in any particular taxon. The only lizards known to specialize in this manner are those, like *Moloch*, that feed on ants, though some, like the *Cnemidophorous* in parts of Texas, which eat largely termites (Milstead, 1957), may be facultative specialists.

In addition to animals, a few bits of vegetation, a small stone, and a piece of shed lizard skin, probably its own, were found in stomachs. The vegetable material and the stone may have been taken by the lizard along with an insect but the following two incidents suggest other ways in which nonliving material may be taken.

Once, I observed a small male run two feet to a dead insect being carried jerkily by ants. After a minute or so of watching, he picked up the insect, shook off the ants, and ate it.

On another occasion, about one foot from a young adult male, I observed the green base of a hibiscus flower (a cylinder 2½ cm long and 1 cm wide) fall to the ground. The male jumped down to the ground, grabbed and then released the flower except for a small piece that he chewed for some minutes.

Anolis lineatopus feeds on a wide range of sizes of prey, the larger individuals eating more large prey than do the smaller ones.

The sizes of prey found in the stomachs of 45 lizards examined are recorded in table 2 in the following categories: <5 mm; 5–10 mm; 10–20 mm; and >20 mm. Entire insects were measured directly. Fragments were compared with entire insects, either from stomachs or in collections at the University of the West Indies. A few items whose size could not be estimated were omitted.

The increase in number of large prey with increase in lizard size probably reflects a greater ability of large lizards to handle large prey, since food is swallowed whole.

The decrease in the number of small prey and the increase in relative numbers of ants (which is marked only in the largest lizards) must reflect changes in the attitude of a lizard towards potential prey. Ants, unlike most of the insects *A. lineatopus* catches, forage up and down the branches, tree trunks, and fence posts where the larger lizards regularly perch. To catch these ants, a lizard need move only a short distance, if at all. Apparently larger lizards differ from the smaller in taking small insects only when they can do so with minimum effort.

The decrease in number of prey per stomach with increased lizard size is probably largely a reflection of the increase in size of the prey items; however, the smaller lizards are growing more rapidly than the larger ones and so may require more food. In the smallest size class, both sexes are growing rapidly and, when the females' growth slows down, they begin to produce eggs, an activity that must require considerable food. Dessauer (1955) calculated for *A. carolinensis* that "In the course of its 5-month laying season, the individual *Anolis* female must lay down the equivalent of her own total body protein for egg production" (p. 12). The largest lizards are adult males that are growing very slowly though expending considerable energy in display. Harris (1964) found, however, that an *Agama agama* took about the same weight of food per gram of lizard regardless of lizard size.

There are differences in micro-habitat associated with anole size (see p. 17) that may affect what is easily available for food to different sized *A. lineatopus*.

Whatever the reasons for it, *A. lineatopus* of different sizes living in one relatively small and quite uniform area differed in what they had eaten. The smallest took large numbers of small prey, which were predominantly not ants, and the largest took fewer prey, many of which were large, plus an appreciable number of small prey, which were mostly ants. The change from one type of food to the other seems to occur gradually.

Harris (1964) showed conclusively that in *Agama agama* the different size classes of lizards were taking largely different sized prey. Since adult males are larger than adult females and share the same home ranges, this difference must reduce the possibility of intersex competition for food.

Kennedy (1956) demonstrated differences between juvenile and adult *Sceloporus olivaceous* in size of prey and suggested that this produces "a minimum degree of intraspecific food competition between juvenile and adult *S. olivaceous* which is highly advantageous in the rapid development of juvenile lizards . . ." (p. 345). Blair (1960), however, in writing of the same species in the same area concluded that the juveniles never approach the limit of their food supply.

A difference in food size between adults and juveniles has been reported for lizards as varied as *Eumeces fasciatus*, Fitch (1954), and *Basiliscus vittatus*, Hirth (1963a).

A habitat difference between juvenile and adults like that seen in *A. lineatopus* seems common in iguanids. It occurs in at least *Basiliscus vittatus*, Hirth (1963a), *Iguana iguana*, Hirth (1963b), *Uta stansburiana*, Tinkle et al (1962), *Sceloporus olivaceous*, Blair (1960). This habitat difference must certainly reduce the possibility of one sort of intraspecific competition for food. It also reduces the possibility of the adults eating the young.

Certain falcons are sexually dimorphic in size and the larger females catch larger prey (Cade, 1960). Storer (1952) has discussed the possibility that this reduces intersex competition for food. Rand (1952) has reviewed a number of additional types of sexual dimorphisms in birds that may also reduce intersex competition for food. In birds as in lizards it is difficult to prove the applicability of these ideas to any particular case however plausible they are in general.

To evaluate food as a limiting factor in the ecology of these anoles would require a knowledge of both the food requirements of the animals and the availability of food to them. Blair (1960), for *Sceloporus olivaceous* adult females, and Milstead (1957a), for four species of *Cnemidophorus*, concluded that food was at least potentially limiting. Their arguments are convincing, but their proof is not rigorous. For *A. lineatopus* I suspect that food is potentially limiting but the data are adequate only to demonstrate that in the study areas food is neither superabundant nor in very short supply.

My impression is that insects of suitable size are common in Jamaica but this idea must be treated cautiously for not all of the insects present are available to *A. lineatopus* as food. Some insects are too active or too wary to be frequently caught. Others are nocturnal and still others too hard or protected by a nasty taste or smell.

Of the 45 stomachs examined, only 1 was empty of food, suggesting that most *A. lineatopus* catch enough food to keep their digestive systems working most of the time; however, this can be said only of the period when they were collected—early in the dry season, a period when insects appeared abundant.

A captive *A. lineatopus* will live at least several days to a week without food, so presumably in the wild an individual could survive short periods of famine. I rarely saw *A. lineatopus* catch something to eat, and I have the impression that most days it catches only a few insects and some days perhaps none at all.

In contrast to this slow rate of feeding is the response of *A. lineatopus* to food offered them. In my study area, these lizards became very tame and freely took insects tossed to them from a few feet away, running several feet to do so. In a typical session of 45 minutes one afternoon, I tossed insects of moderate size into an area of about four square yards. During this time, 17 insects were captured by eight different lizards, two of them catching 3 insects and one catching 4. This suggests that the slow rate of feeding usually seen is not because *A. lineatopus* are satiated but because suitable insects are not available.

We saw in the field no thin or emaciated individuals among these lizards.

The wide variety of prey taken by *A. lineatopus* means that available food is distributed throughout the habitat and is not densely concentrated in certain areas. Several lines of circumstantial evidence indicate that probably few, if any, established resident *A. lineatopus* starve to death but at the same time that a superabundance of food is not available to them.

WATER.—Probably all the water *A. lineatopus* requires, beyond that present in its food, it gets by licking drops of dew or rain from leaves and twigs with the tip of its tongue. The only report I know of lizards having difficulty securing water is Evans (1951), who reports *Ctenosaura pectinata* making long excursions to drink.

Rain is a frequent occurrence around Kingston. Even in the dry season when no rain falls, dew forms almost every night and remains in the shade until mid- or sometimes late morning. Water is thus available to *A. lineatopus* almost every day.

Anolis lineatopus were only occasionally seen to drink in the field but in cages they were seen to drink frequently.

As I sat watching some marked *A. lineatopus* one afternoon, a light rain began to fall. Only one, an adult male, reacted. He climbed a branch to an orchid and licked several times at one of the wet leaves.

An *A. lineatopus*, which would eagerly take tossed insects, completely ignored the drops of water that formed when I watered the study area. Apparently even during this period in the dry season, when there was not enough rain to keep the grass green, *A. lineatopus* were not short of water.

TEMPERATURE.—*Anolis lineatopus* in the Kingston area has a preferred body temperature (or eccritic temperature) range of 28°–31° C. Sixty-one of 85 lizard temperatures taken under a variety of environmental temperatures fall within this 4° range. Like many other lizards which have been studied (Bogert, 1959; Fitch, 1956b; Inger, 1959; Ruibal, 1961), this species maintains its temperature within this range by behavioral thermoregulation when environmental conditions permit.

I have continued to use the familiar term "preferred body temperature" despite the demonstration of Licht, Dawson, and Shoemaker (1965) that observed field temperatures in some species differ from those chosen in gradient experiments and their suggestion that the term "preferred temperature" be restricted to experimental studies.

The *A. lineatopus* temperatures used here were taken over a wide range of air temperatures but always when the sun was shining. On each occasion a thermal gradient was available to *A. lineatopus* as it was to the lizards in Licht's and his coworkers' experimental setups. On most occasions, the environmental temperatures available, considering substrate as well as air temperatures, extended both above and below the observed *A. lineatopus* range. It seems likely that the observed body temperatures approximate those that would be found in an experimental gradient. Certainly my observations should be more similar to those of an experimental gradient than to the results obtained by measuring all lizards regardless of weather.

The cloacal temperatures of *A. lineatopus* were taken with a Schultheis quick reading 0°–50° C thermometer within a few seconds of noosing.

The body temperature of an *A. lineatopus* is almost always close to and above the air temperature in its vicinity (fig. 1). Body temperatures are higher at high air temperatures than at low air temperatures, but the difference between air and body temperature is greatest at low air temperatures as the following figures (in centigrade) show:

air temperature	*mean body temperature*	*difference*
24	27.5	3.5
27	29.4	2.4
30	31.0	1.0

The *A. lineatopus* temperatures show a slightly greater range (24°–32° C) than do the air temperatures (24°–30° C) but a much more central tendency (variance of air temperatures=6.34; variance of lizard temperatures=3.92).

The distribution of *A. lineatopus* temperatures is skewed so that there are fewer records (7) above the preferred body temperature range (28°–31° C) than below it (14) and the total range extends only 1° above, but 4° below, the preferred range.

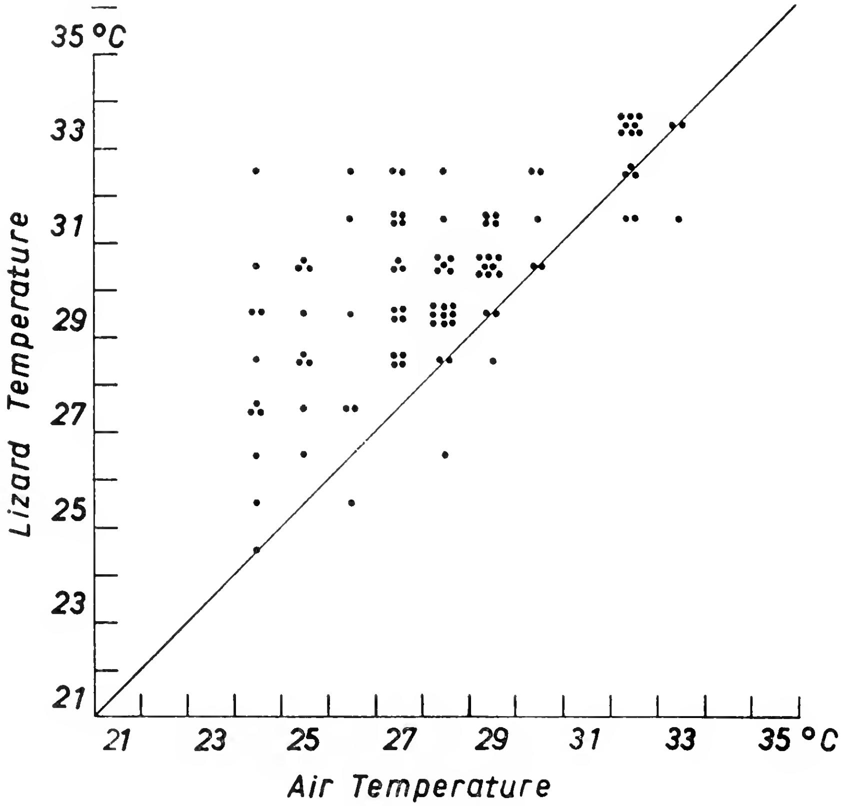


FIGURE 1.—*Anolis lineatopus* cloacal temperatures plotted against air temperature in immediate vicinity at time of capture (temperatures have been recorded to nearest 0.2 degree and have been rounded to nearest degree for plotting).

Heath (1964) in his report on the temperatures of beer cans has shown that body temperatures above the ambient air temperatures do not necessarily demonstrate thermoregulation. But the already described relationships of body and air temperature combined with the behavior patterns reported below are convincing evidence that *A. lineatopus* thermoregulates.

Color change in *A. lineatopus* may play a role in thermoregulation. Casual observation indicates that in the early morning, when *A. lineatopus* are sunning themselves, they are darker than they are during the heat of the day. Since this involves a gradual change in shade rather than an abrupt change in hue, it is difficult to measure in the field and I collected no quantitative data on the point.

The lizard's behavior in moving into and out of the sun was more conspicuous and more easily recorded than the color changes and probably more important in thermoregulation.

The following extract from my field notes shows the sort of behavior frequently seen:

> 30 January—Barbican brush heap, 900 hrs. By this time the *lineatopus* are mostly sitting in the shade. I have the impression that they are avoiding hot perches more than the sun itself. A large male is on a branch which is shaded but he himself is largely in the sun.
>
> One adult female, on the other hand, is sitting in a small patch of shade on a branch in the brush heap. Most of her time is spent in these patches of shade, where she usually sits on top of the branch. When she does leave the shade for a sunny branch, she usually runs along the top, but when she stops she moves in to the shade on the side. Sometimes when she runs along a sunny branch she will stop and run very quickly back to the shade patch as if she had suddenly become too hot.

Table 3 shows the results of seven censuses of adult male *A. lineatopus* along a stone aqueduct that runs north and south. These lizards moved into the sun when they were cool and avoided the sun and hot substrates when they were warm. They seemed more careful

TABLE 3.—*Distribution of adult males on a stone aqueduct under different weather conditions* (aqueduct runs north and south and all data was collected in the morning; temperature readings are given in centigrade)

Weather conditions	Air temperature	East side (in sun)		West side (in shade)	
		Substrate temperature	Number of lizards	Substrate temperature	Number of lizards
Sunny	28.4	30.6	10	28.4	4
cool	28.0	30.8	2	27.0	0
	26.0	31.8	7	25.4	2
			19		6
hot	29.6	41.0	1	29.0	13
	29.8	36+	1	30.0	13
			2		26
Cloudy	26.0	28.0	4	27.0	6
	25.6	25.6	4	25.4	7
			8		13

about avoiding very hot conditions than in seeking warm ones when it was cool.

Anolis lineatopus may remain active at body temperatures appreciably below its preferred body temperature range. Most lizards studied (Bogert, 1959; Fitch, 1956; Milstead, 1957) become inactive at low temperatures but *A. lineatopus* do not do so, and I have seen them on cloudy days and around lights at night feeding, fighting, and copulating at environmental temperatures below 25° C when their body temperatures must have been circa ambient.

In contrast to these observations of activity at low temperatures are those made during the very early morning. *Anolis lineatopus* left their exposed sleeping sites shortly after dawn but well before sunrise and moved into spots where they were concealed. They moved up onto their usual perches only after sunrise, when they began to bask.

Studies on other lizards have shown that the preferred body temperature is usually not far from the upper lethal temperature and this is probably true in *A. lineatopus*. On analogy with other lizards one would expect a thermal death point somewhere in the vicinity of 40° C. Obviously *A. lineatopus* cannot occur in places where its temperature would be forced above the thermal death point; it should be noted that on the sunny aqueduct mentioned above (table 3) one of the stones of the aqueduct had a temperature of 41° C.

The effects of temperatures below the preferred body temperature are almost completely unknown not only in this species but also in most lizards. At very low temperatures, *A. lineatopus* becomes sluggish and torpid, as the following illustrates. One male cooled in a refrigerator was sluggish when cooled to a body temperature of 13° C though still active at 19° C.

Presumably deleterious effects of moderately low temperature are associated with the slowing of temperature-dependent physiological processes such as heart rate, oxygen consumption, rate of enzymatic action (Bartholomew and Tucker, 1963, 1964; Bartholomew, Tucker, and Lee, 1965; Licht, 1961).

Hardy (1962) has reported that in *Cnemidophorus sexlineatus*, at lower temperatures, defecation is delayed and individuals are less efficient at detecting prey, particularly motionless prey, and take several times longer to dig tunnels. No similar changes were seen in *A. lineatopus*, but it was noted that *A. lineatopus* are shyer at lower temperatures and it was suggested that this might be a behavioral compensation for the slowing of muscle or nerve reaction at lower temperatures (Rand, 1964b).

Preferred body temperature range may be an important ecologically limiting factor, for this subspecies is absent from dark forest where sunlight is not available and also from higher elevations where temperatures are lower.

In the lowland edificarian and disturbed areas where these studies were made, there are probably few places from which these anoles are excluded because of generally low temperatures. They do not occur where there is no protection from overheating in the sun.

PREDATORS.—Every animal in Jamaica that preys on small land vertebrates or large insects probably eats *A. lineatopus* at least occasionally, but in the areas studied the predation pressure does not seem to be heavy.

From my observation, the most important predators are domestic cats. One well-fed mother cat that was living with us brought her kittens at least one and sometimes several anoles every day, many of them adult *A. lineatopus*. However, this made no obvious diminution in the population of anoles living around the house.

I also saw dogs catch and kill *A. lineatopus*, and some of them probably do this regularly. Chickens also eat these lizards. I found an *Anolis* in the stomach of one of the few snakes I examined, a *Dromicus callilaemus*. Even though this species of snake is moderately common (one could almost always find one in a couple of hours of searching), it is a ground-living species and probably not an important predator on any *Anolis*. Other snakes are rare in the study area.

Birds are probably important predators on small *Anolis;* Wetmore (1916) reports that in Puerto Rico he found *Anolis* in the stomachs of most of the insectivorous birds, even as small as the tody, and this situation probably applies to Jamaica also. The most common of the larger insectivorous birds around Kingston—mockingbirds, anis, and kingbirds—probably take young and female but few adult male *A. lineatopus*.

The birds that might be expected to feed on adult males, the larger cuckoos, herons, hawks, and owls, are relatively rare in the study areas and probably are thus of relatively little importance.

The common toad, *Bufo marinus* (I counted 25 on the lawn one evening), certainly could eat small to moderate-sized *A. lineatopus*, but, since the toads are nocturnal, they probably catch few.

Anoles themselves eat lizards. *Anolis grahami* at least occasionally eat young *A. lineatopus* and the larger *A. valencienni* and *A. garmani* probably regularly eat at least adult females and young males of *A. lineatopus*. Both these larger species are relatively common (an hour or two search in the correct habitat would reveal at least one of each), but both are primarily lizards of tree crowns and consequently do not feed in the places where *A. lineatopus* are most common.

I only once saw an *A. lineatopus*, a 60 mm male, catch and eat one of its own species, about 20 mm long, but I have several times seen an adult male chase and attempt to catch a young *A. lineatopus* and I have also taken a small *A. lineatopus* (just above hatchling size) from the stomach of an adult male. Cannibalism is probably relatively rare, partly because the young lizards are too active to catch easily and partly because they avoid the principal perches of the adult males. The difference in perch between young and adult males may be in part a direct result of chasing by the adult males.

Predation probably is not an important factor in controlling population density of adults resident in favorable habitats. Predation is probably heavier on juveniles, on dispersing individuals, and on those living in unfavorable habitats.

ESCAPE BEHAVIOR.—Most of my information regarding the reaction of anoles to potential predators relates to their reaction to people. It is possible but unlikely that they react differently to smaller predators.

I noted that the first reaction of *A. lineatopus* to an approaching danger is usually to remain still, sometimes flattening against the perch. If the danger approaches closely, the *A. lineatopus* runs around the perch to the other side and either up out of reach or down into the vegetation at the base. Where possible, adult males usually run upward, small *A. lineatopus* more frequently dodge around on the trunk or even leave the tree to hide in the cover on the ground.

Adult males, when they became familiar with me, did not flee at my close approach but displayed as they would at another male.

A captured lizard usually tries to bite and, if successful, holds on. An adult male, when seized, frequently shows most of his agonistic displays (see p. 38 et seq.), raising dorsal and nuchal crests, lashing his tail, opening his mouth, protruding his tongue, and sometimes holding his dewlap open but never flashing it as does a male displaying to another male.

A captured lizard frequently defecates; the feces produced are usually a pasty material, though they may be very watery or sometimes a normal, dry, compact feces. This material is not pleasant to smell nor presumably to taste but it does not smell very unpleasant.

ELIMINATION OF WASTES.—As many arboreal animals do, *A. lineatopus* defecate on whatever perch they happen to be and the feces usually fall to the ground. As might be expected in a species where olfaction is of little importance, the feces do not seem used in marking as Hardy (1962) has suggested they are in *Cnemidophorus sexlineatus*. The fecal pellets are roughly cylindrical, about 1 cm long, dark in color, and dry and compact to touch. There is a small white cap on the end extruded first; presumably the dark material is fecal material from the intestine and the white cap is nitrogenous wastes from the kidneys.

Habitat Requirements

The three main habitat requirements, perch, cover, and sleeping site, must be satisfied in some way or other within the home range of each *A. lineatopus*. These features of the habitat are essential to the operation of the normal behavior patterns that enable *A. lineatopus* to satisfy its fundamental requirements and also important to those associated with social behavior and reproduction. It is probably these habitat requirements that are used as cues in habitat selection by *A. lineatopus*.

Harris (1964), writing on *Agama agama* in Nigeria, states: "Three important structural components the environment must provide are: (a) suitable display posts, (b) a roosting place and (c) conveniently situated refuges from predators" (p. 132). These categories are almost identical to those used herein for *A. lineatopus* though the structures in the habitat that satisfy these demands are quite different.

PERCHES.—An *A. lineatopus* spends its days waiting on one or another of its perches. From its perch the lizard sees most of the prey which it catches, most of the other lizards which it courts or chases, and most of the predators from which it flees, and it is from its perch that most of its display is given. The perch also provides a sunning site and usually shade as well.

A wide variety of objects are used as perches, among them trees, fence posts, rocks, walls of houses, bushes, and hedgerows. The large majority of *A. lineatopus* seen were within six feet of the ground, and relatively few were seen on slender twigs and branches. In general, adult males perch farther from the ground and on larger diameter perches than do smaller individuals, which are usually seen in bushes, hedges, and brush piles very close to the ground and which seem to avoid the large trees and fence posts, etc., that the adults prefer. Collette (1961) describes similar intraspecific differences in perch preference in *A. sagrei* and *A. porcatus*. Intraspecific differences between juvenile and adult habitats seem widespread in iguanids (see p. 9) (For a more detailed discussion of perches, see Rand, in press). The sorts of perches that are occupied most commonly are herein called preferred perches, and those that were occupied less frequently are referred to as less or subpreferable.

The same individual may be seen on the same perch day after day; most, if not all, lizards use only one or a few perches as the center for their activity. Blair (1960) noted similar behavior in *Sceloporus olivaceus*, particularly in the females. *Anolis lineatopus* may spend most of its time on only a small part of one perch, as O'Brien et al (1965) describe for *Sceloporus undulatus*. I have called the perch or perches where an individual spent most of its time its "usual" perch or perches.

Anolis lineatopus usually rests on the side of a vertical perch or on the upper surface of a slanting or horizontal one, most frequently with the head pointed toward the ground, a habit associated, I suspect, with the large amount of food taken on the ground, as I suggested for *A. cybotes*, a species with similar habits, in Hispaniola (Rand, 1962). Though *A. lineatopus* may spend long periods on the same perch, it seldom spends more than 15 minutes without shifting position or without displaying. Even between shifts the lizard is usually alert, and in one 4-minute period when I watched an adult male on his perch, he moved his head 12 times and the eye that I could see also 12 times (the eyes move independently of each other). During this 4-minute period, the longest time without any movement was 45 seconds and usually only 10 or 15 seconds elapsed.

The sort of perch an anole uses varies from species to species so that sympatric species occupy different microhabitats (Collette, 1961; Oliver, 1948; Ruibal, 1961; and Rand, 1962, 1964a). This probably acts to reduce interspecific competition (Rand, 1964a) just as the different foraging zones do for sympatric wood warblers (MacArthur, 1958).

COVER.—Cover near the ground is a more important habitat requirement for female and juvenile *A. lineatopus* than for adult males. Very few *A. lineatopus* maintain home ranges that include no cover at all. Cover takes several forms: dense vegetation, grass, herbaceous plants or ferns that grow around the perch; a pile of dead sticks; a layer of large dead leaves; or occasionally a pile of rocks. These provide protection against temperature extremes (p. 14) and predators (p. 16).

SLEEPING SITES.—*Anolis lineatopus* sleep during the night in exposed situations above the ground, generally at elevations of 1 to 10 feet, usually at the ends of branches, the larger usually climbing higher than the smaller individuals. They sleep on leaves, small twigs, and sometimes on grass blades that frequently are slender enough to bend double under the weight of the anole. Many arboreal and semiarboreal iguanids have similar sleeping habits, among them *Iguana iguana*, Hirth (1963b), *Basiliscus vittatus*, Hirth (1963a), at least some *Sceloporus olivaceus*, Blair (1960), and *Urosaurus ornatus*, Cowles and Bogert (1936).

Sleeping *A. lineatopus* are usually visible from outside the bush or tree and consequently are exposed to any flying predator hunting by sight at night; however, they are concealed from any predator that approaches from inside the tree and is forced to climb the branches to reach them. The small diameter of the sleeping perches presumably would protect them from any large climbing predator, and even a small predator would probably be unable to reach a lizard without shaking the perch enough to awaken it.

Though easily awakened at night by a light or by movement of the perch, the lizards are slow to leave their perches and usually do so only when they are shaken quite violently.

The sleeping sites differ sharply in character from the preferred diurnal perches; the sleeping sites are places this species seldom visits during the day except when catching an insect or when engaged in a dispute with another anole.

Some individuals seem to use the same leaf or twig as a sleeping site night after night. Most, however, are not so regular, though they tend to sleep in the same bush, tree, or bunch of grass. There is definitely not the same attachment to a particular sleeping site that there is to the daylight perch.

Anolis lineatopus left their sleeping places soon after it became light and usually did not settle down to sleep until it was too dark for them to be seen even from a few feet away. Blair (1960) reports a similarly long period of activity for *Sceloporus olivaceus* during the summer as does Hirth (1963a) for *Basiliscus vittatus.* Perhaps this is characteristic of lizards sleeping, as these do, in exposed sites in a warm climate.

On one occasion, January 27 in Barbican, I watched a male *A. lineatopus* go to sleep. I first noticed him at 6:13 P.M. when he ran up the stem of the croton and stopped just below the terminal bunch of leaves. The sun had set but the landscape was still bright. A minute and a half later he climbed up among the leaves and out along one of them and stopped in a typical alert position, head raised and neck bent. Two and a half minutes later he flattened out against the leaf, still facing its tip. Six minutes later he turned around facing the stem of the leaf and flattened against the leaf. The sky was still light but the landscape dark. By 6:30 the first stars were out and it was almost full dark. With the flashlight I could see that the lizard's eyes were still open but he was in his normal sleeping position.

Both Mertens (1939) and Rand (1962) noted in Hispaniola that certain species of *Anolis* sleep with their hind legs flexed while others sleep with these legs stretched out along the body. *Anolis lineatopus* may sleep in either position and quite frequently a sleeping *A. lineatopus* was found with one leg flexed and the other extended backward.

Home Range and Activity Range

An *A. lineatopus* seldom travels far and most of the area it visits is visible to it from its usual perch.

I use the term "activity range" for the area visited regularly during the day including the usual perches but excluding the sleeping site when it is outside of this area. "Home range," as used here, includes both activity range and sleeping site. The activity range is described in terms of its horizontal extent and, since *A. lineatopus* are largely arboreal, reference to its vertical extent is also included. I have followed the suggestions of Milstead (1961) and, in calculating activity range size, have omitted the occasional visits that certain *A. lineatopus* made to perches well outside of the area where they were usually seen, but I have plotted these visits on the maps included in this paper.

Anolis lineatopus may sleep in the same area where it spends the day, perhaps climbing up and out onto one of the branches of its principal perch. It may leave the area where it spends the day, however, if there is no suitable sleeping site, and travel several yards to find one. *Anolis lineatopus* that have mutually exclusive activity ranges may all use the same sleeping sites.

Of 15 adult females living in Barbican [fig. 6] for which I have adequate day and some night records, 7 were recorded sleeping only within their activity ranges, 6 both in and outside of their activity ranges, and 2 only outside. The sleeping places usually were less than 5 feet away from where the female spent the day, but for one female they were 10 and 12 feet away. Of the 10 adult males [fig. 4], 5 were recorded sleeping only inside their activity range, 3 both in and out, and 2 only outside their activity range. Two males regularly traveled 10 feet to sleep but for other males the records outside of the activity ranges were mostly 3 to 5 feet away.

The concept of an activity range with a definite size is useful since it gives a datum for comparison with other animals. It is, at best, a crude approximation of the space actually utilized by the lizard. First, it takes only slight account of the vertical range of the animal and, for an animal that spends most of its waking hours above the ground, this is important. Second, the individuals do not visit all parts of their activity ranges equally nor do they always range out in a regular manner from a single center. Finally, an activity range has definite boundaries only where it adjoins the activity range of another *A. lineatopus* of about the same size (see p. 46 et seq.).

Both the size and the shape of an activity range varies with the size and sex of the individual and with the number and distribution of perches available.

For adult males the usual activity range varies between 3 and 10 square yards, seldom probably is less than 3 and sometimes probably as much as 20 square yards. It usually extends vertically from 1 to 3 yards, again sometimes less but probably never less than 1 foot and seldom more than 5 or 6 yards.

The shape is influenced strongly by the distribution of the perches used. Where a single perch is used and the surrounding area is uniform, the activity range is roughly circular with the perch in the center. The activity range of the adult male (no. 4) mapped in figure 2 approaches this. He lived on an isolated tree and in the 40 times he was observed over a period of 21 days, he was on the trunk of the tree below 20 feet (only 6 times going higher than 8 feet or to the ferns at the base, which extended only 3 feet out from the tree).

Figure 2.—Record of observations of adult male *Anolis lineatopus* (63 mm) on isolated Indian almond tree, August 22 to September 15 (dots=observations on near side of tree, x's=records on opposite side; preponderance of records on near side primarily reflects usual position of observer).

His activity range was 3 square yards on the ground and extended upward about 3 yards.

In areas with more perches available, the activity ranges are larger in horizontal dimensions. In the Barbican brush heap shown in figure 3, the three resident males had areas of approximately 13, 8, and 6 square yards; the first of the males using a small tree regularly climbed to 6–8 feet, while the other climbed only to about 3 feet. The activity ranges of these males were ovals except that the largest had an elongate projection along the fence.

The other males at Barbican [fig. 4] had activity ranges that fall within the 3–10 yard size range. The relationship of perches to activity range shape is conspicuous in figure 4. The activity range of no. 2 was located on the front porch of my house. He used the L-shaped railing as a perch; the observation records of him outline the railing just as the concentration of observations along the fence indicates the position of the fence posts.

On an abandoned stone aqueduct, the males were found living mostly under the arches and usually restricting their activity to a single arch. Those 16 males on which we have adequate data had activity ranges varying from 4 to 16 square yards in area and mostly between 4 and 8 square yards. They extended vertically between 2 and 10 feet. The activity ranges were mostly quadrangular in plane view, reflecting the shape of the area under an arch.

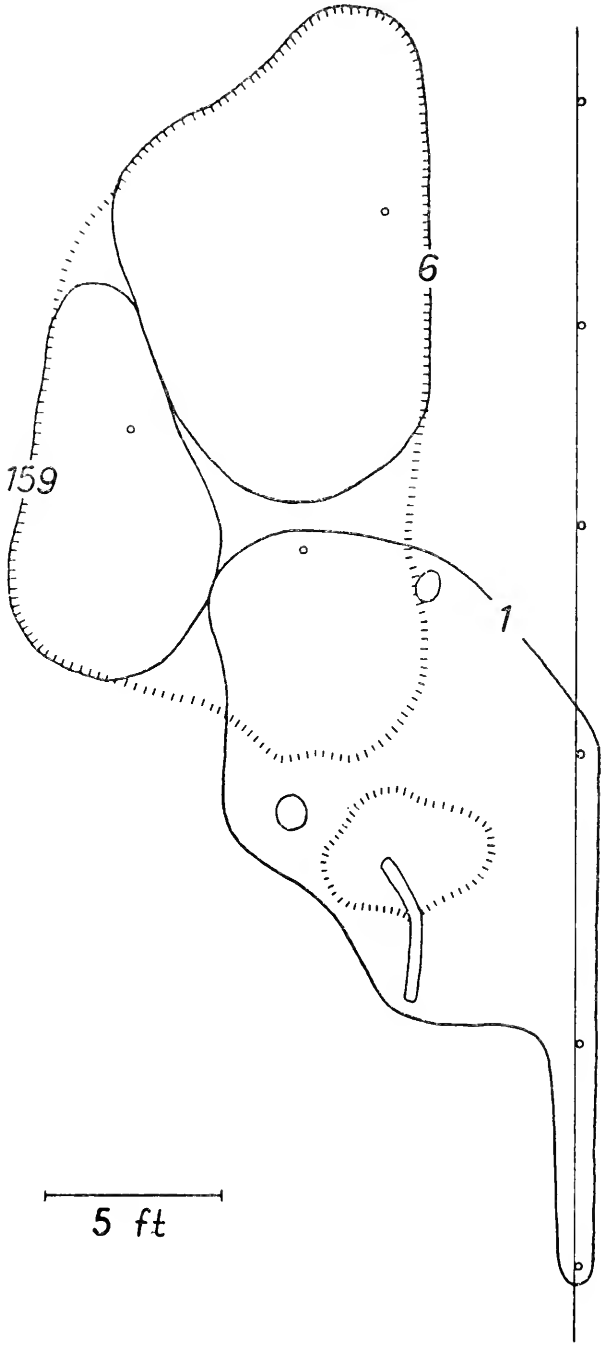
The size of the activity ranges of the adult females is usually considerably smaller than that of those of the adult males, and again structure of the habitat affects size and shape. In general, the female activity ranges averaged about 1 to 2 square yards, sometimes being as much as 3 or 4 square yards and probably sometimes only 2 or 3 square feet. In vertical extent the females usually ranged from 1 to 5 feet and probably sometimes more.

In the isolated tree shown in figure 2 there were 9 resident females. Of these, 8 concentrated their activities below 3 feet, in the ferns at the base and the rock border around it, occasionally climbing the tree to the height of 6 or 8 feet. One female concentrated her activity on the trunk and the side branches between 5 and 9 feet above the ground and only rarely came down into the ferns. For each of these females, the activity range was about 1 square yard in horizontal extent.

In the Barbican brush heap [fig. 5], which was more complex in perch distribution, 3 adult females (nos. 59, 145, and 162) had activity ranges of 1, 1, and 2 square yards and ranged vertically between ½ and 4 feet. The other females in Barbican [fig. 6] have activity ranges that are usually between 1 and 3 square yards in area.

The activity ranges of lizards below adult size are somewhat smaller than those of the adults of the same sex and increase as the lizards grow.

FIGURE 3.—Activity ranges of three adult males (no. 1=59 mm; no. 6=63 mm; no. 159=58 mm) in Barbican brush heap, January 23 to February 23 (heavy continuous lines= approximate activity range boundaries, fine lines=physical features, remaining lines= boundaries of brush heaps).


6
159
1
5 ft

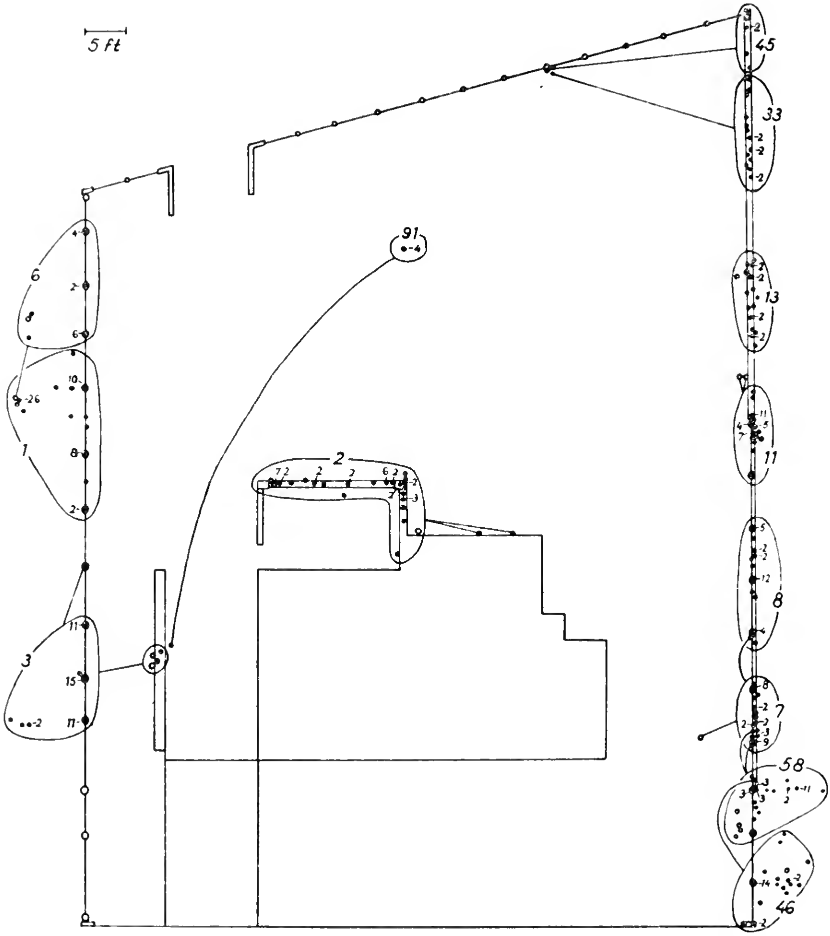


FIGURE 4.—Distribution of adult males larger than 50 mm seen four or more times at Barbican in fenced yard around author's house September 30 to November 7 (dot=day record of each position where lizard was sighted, circle=night record; small number adjacent to dot=more than one record in same position; lines around records for each lizard enclose their activity ranges but indicate boundaries only roughly; observations a long distance from activity range are joined by line that shows only which lizard was involved and not path it took to reach place observed). Three of the males were present for only part of this period. All but no. 91 were marked by October 1. He appeared October 19 on a small, previously unoccupied, tree and was seen there until October 24, when he was found dead in the carport (probably killed by our dog and perhaps carried there by him). No. 2 was found dead on November 1. No. 33 disappeared about October 30 and at about this time no. 45 moved along the wall to occupy no 33's area. These records of no. 45 following no. 33's disappearance have been omitted. (No. 1=59 mm; no. 2=56 mm; no. 3=59 mm; no. 6=62 mm; no. 7=62 mm; no. 8=67 mm; no. 11=61 mm; no. 13=65 mm; no. 33=64 mm; no. 45=67 mm; no. 46=63 mm; no. 58=67 mm; no. 91=55 mm.)

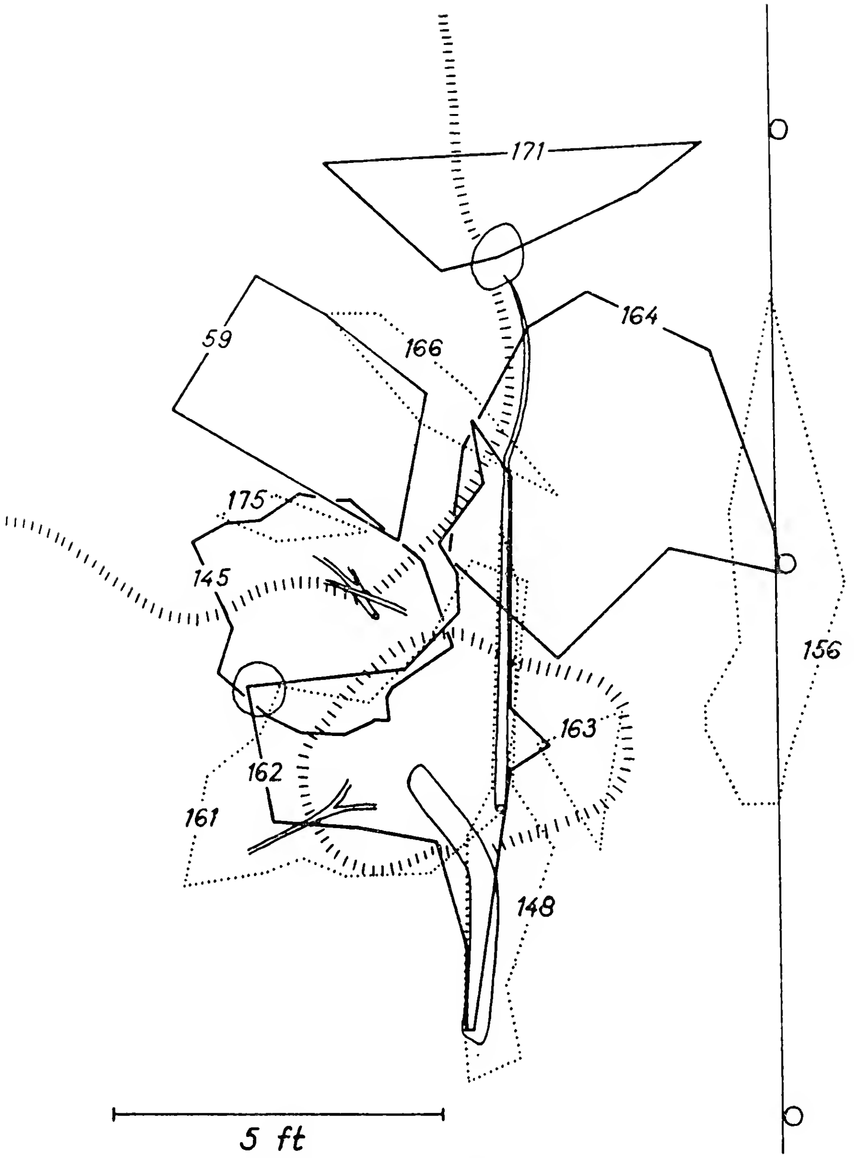


FIGURE 5.—Activity ranges of females and juveniles in part of Barbican brush heap (see fig. 4 for activity ranges of adult males; activity range boundaries were constructed by linking marginal records for each lizard; heavy solid lines = larger individuals, dotted lines = smaller lizards, thin solid lines = structural elements, remaining lines = boundaries of brush heaps; period covered = January 23 to February 23, except for nos. 162, 148, and 163, for which boundaries represent activity ranges before shifts discussed in test (pp. 49 and 52) occurred; in the following list, dates of measurement are given because certain lizards show appreciable growth: no. 59 female = 41 mm, January 23; no. 145 female = 43 mm, January 9; no. 148 female = 26 mm, January 9, to 28 mm, February 1; no. 156 female = 25 mm, January 10, to 28 mm, February 7; no. 161 female = 29 mm, January 10; no. 162 female = ca. 39 mm; no. 163 female = 26 mm, January 24, to 28 mm, February 9; no. 164 female = 33 mm, January 26, to 34 mm, February 9; no. 166 male = 22 mm, January 30; no. 171 male = 31 mm, February 9, to 35 mm, March 11; no. 175 female = 24 mm, February 9).

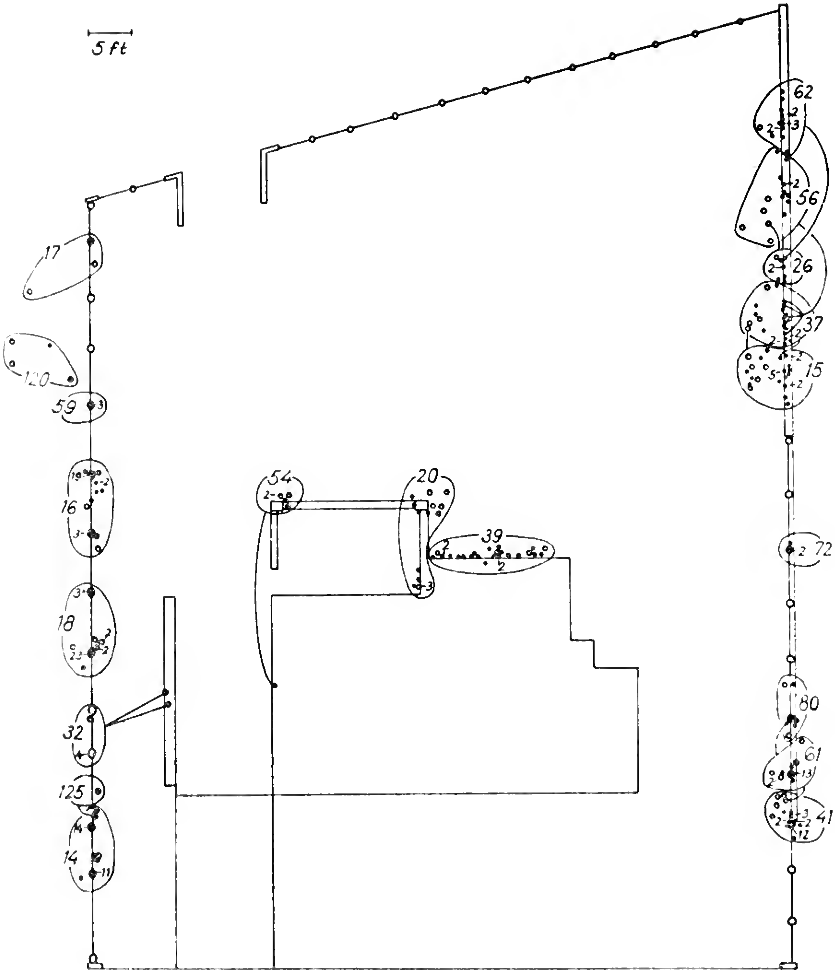


FIGURE 6.—Distribution of adult females in Barbican September 30 to November 7 (same area and lineal elements as figure 5; all lizards seen more than twice have been mapped; no. 14=44 mm; no. 15=44–45 mm; no. 16=41–42 mm; no. 17=42 mm; no. 18=42–43 mm; no. 20=42–43 mm; no. 26=43 mm; no. 32=42 mm; no. 37=43 mm; no. 39=39–40 mm; no. 41=44–45 mm; no. 54=42 mm; no. 56=43 mm; no. 59=39–40 mm; no. 61=42 mm; no. 62=44 mm; no. 72=43 mm; no. 80=45 mm; no. 120=42 mm; no. 125=41 mm).

The best data on young females come from the Barbican brush heap (fig. 5), where the activity ranges of 6 small females were plotted. These varied in area between 1 and 16 square feet and their shape was strongly influenced by the distribution of the larger branches in the brush heap. The larger activity ranges were mostly held by the large individuals.

The best data on young males come from a study of the Mona hibiscus hedge (fig. 9, table 4) where the activity ranges of 7 were studied. These ranged from about 4 to 18 square feet, being about 4 to 10 for the smaller individuals and about 10 to 18 for the larger.

Since even adult male *A. lineatopus* activity ranges seldom reach 150 square feet, they are well below average size for land vertebrates. No birds or mammals are known with home ranges nearly as small as this; however, at least one frog has a home range of about the same size—*Scaphiopus holbrooki* with an average home range of 108.4 square feet (Pearson, 1955).

Temperate North American iguanids have small home ranges but even the species with the smallest, *Uta stansburiana*, with an average adult male home range of 2600 square feet (Tinkle, et al., 1962), has a range considerably larger than *A. lineatopus*. In contrast, two tropical lizards have home ranges that lie between that of *Uta stansburiana* and *Anolis lineatopus*—*Basiliscus vittatus*, Hirth (1963a), and *Agama agama*, Harris (1964). It may be generally true that tropical lizards have smaller home ranges than do their relatives in temperate regions.

Typically *A. lineatopus* visits all of its principal perches every day, frequently more than once. The frequency of forays that it makes from the principal perches is inversely related to the length of the

TABLE 4.—*Activity range use in Mona hibiscus hedge* (areas in square feet; see p. 28 for discussion)

Lizard number	S-V length (millimeters)	Total area April 10–June 8	Number of records	"5-minute census" results			Comparison of polygon areas	
				Area of polygon enclosing—			Ratio of—	
				100% of records	75% of records	50% of records	50% of records to 100% of records	50% of records to total area
3 ♀	33	6.6	63	5.1	2.4	1.1	.22	.17
4 ♂	ca. 37	9.8	64	4.7	2.4	0.8	.17	.08
5 ♂	43	17.7	64	2.7	0.2	0.1	.04	.006
7 ♀	36	6.5	60	6.5	4.3	2.3	.35	.35
8 ♂	31	4.0	64	3.2	0.6	0.2	.06	.05
10 ♂	43	15.7	54	8.5	2.9	0.3	.04	.02
11 ♂	45	11.5	64	7.4	2.8	0.6	.08	.05
12 ♂	52	49.0	51	36.0	10.8	4.6	.13	.09
13 ♂	61	shifted	63	15.9	2.5	2.5	.16	
15 ♂	ca. 41	4.0	63	3.1	0.7	0.2	.06	.05
25 ♂	36	6.8	55	6.2	2.0	0.3	.05	.04

forays. To measure the utilization of activity range, I recorded at 5-minute intervals the position of each *A. lineatopus* present in a small area of hibiscus hedge during 10 periods of about ½ hour each April 18–23. These records for each individual were compiled and 3 convex polygons drawn, one connecting the outermost points, the next, the smallest including 75 percent of the observations, and a third, the smallest including 50 percent of the records. All the records (April–June) were added and a polygon enclosing them was drawn. The 100 and 75 percent polygons are shown in figure 9. The area of each polygon was calculated. The results (table 4) show that each anole spent half his time in a very small area compared with that which it visited. Fifty percent of the records fall in areas ranging from 4 to 35 percent of the respective areas enclosing all of the census records. In 9 of the 11 cases it is less than 20 percent and in 6 it is less than 10 percent.

The addition of other records for April, May, and June made a great increase in area in only 1 case. In the other 9 cases it less than doubled the area.

The principal perches of *A. lineatopus* and the area immediately around them form what might be called the core area of the activity range, following the usage of Kaufmann (1962). As he found in the raccoon-like coatimundis, the core area is not only the part most heavily used but also the part of the home range with the least overlap with those of others (see p. 46).

The activity range of an adult *A. lineatopus* seems relatively permanent and certainly shows no seasonal variation. Subadults and particularly young males are much more mobile.

In the abandoned aqueduct, that I observed, 5 adult males marked on October 19, were found the following June 1 and all were in the same places where they had been marked. In the yard at Barbican, of the 16 adult males seen more than once in September and October, 7 were still present in the middle of March. Of these, 3 had shown slight shifts to adjacent areas and 4 had shown none. Of those 9 which had not been seen in March, 2 were dead, but it is possible that the other 7 had shifted their areas outside of the study plot.

Of the 24 adult females seen more than once during September and October, 13 were seen in March. Of these, 3 had moved in the interim, all to adjacent areas. Again it is quite possible that some of the females not seen in March had moved rather than had died.

Smaller shifts, which did not involve abandoning the original area, were more common. Perhaps the commonest were brief excursions lasting less than a day and peripheral to the usual area. These were recorded in both adult males (up to 20 feet, 7–10 feet being more common), and females (up to 13 feet, 4–5 feet being more common). Also, not infrequently observed were shifts involving the abandonment of part of the area and certain perches and extending the area to new perches in some other direction. Finally, at least 2 of the females made temporary shifts during the period of September to November 7, abandoning the original area for an adjacent one for a few days and then returning.

A number of the adults marked in September through October but not seen in March probably were marked during temporary shifts and occasional excursions into the study area.

I have no data for longer than 6 months but several members of the faculty of the University of the West Indies have told me of *A. lineatopus* that have lived in the faculty's houses and used the same pieces of furniture for perches over several years. These stories, based on unmarked animals, are inconclusive but not improbable.

The reasons for the shifts observed in the adults include changes in the structure of the environment through the cutting and growth of vegetation and interactions with other adults.

It is possible that changes in available food supply affect the area utilized, a concentration of insects attracting a lizard to a new area and a scarcity forcing a lizard to abandon an area, but I have no evidence on this point.

Both young males and young females may hold activity ranges several days or weeks and perhaps longer, but their activity ranges tend to be less stable and less permanent than those of established adults.

Twenty-five young males in Barbican [fig. 7] were marked from September through November 7. Only 17 of these were seen more than once and 9 of these were seen again in March. All 9 had made changes in their areas. Unlike the adults, only 3 of these changes were to adjacent areas, the other 6 were to distant spots, over distances of 45, 48, 35, 35, 45, and 85 feet, respectively.

Even during the period of intensive observation (September through November 7), disjunct shifts were common. Of the 17 young males seen twice or more in this period, 8 showed changes. Six of these were disjunct with distances of 54, 65, 25, 52, 70, 35 feet, respectively. That these shifts average no farther over the short September-November period than over the long September-March period is indicative only, I think, of the small size of the study area.

The young females in this area show similar instability but less strikingly so than do the young males. Twenty-nine young females were marked. Of these, 14 were seen more than once and, of these, 5 were present in March. Of these 5, 2 show changes, neither disjunct. Of the 12 females seen more than once during September through November 7, only 2 show changes and both of these are disjunct, one of 54 and the other of 55 feet, respectively. The young females are very small and thus frequently missed, and, as the mapping technique was too crude to show very small shifts, these records understate the amount of change. Even so, these young females seem to be more stable than the young males, at least in terms of long distance shifts.

Though the activity ranges of young *A. lineatopus* are more liable to change than those of the adults, the lizards do not usually wander randomly. The brush heap area included the areas of 6 small females and 1 small male. Between January 23 and February 23 4 of these 6 females shifted their activity ranges but in each case only to an adjacent area.

In one of these 4 shifts, the lizard was chased from her original activity range by another *A. lineatopus*. In the other 3 cases, the causes of the shifts are unknown but may relate to the changing requirements of the lizards with age and growth.

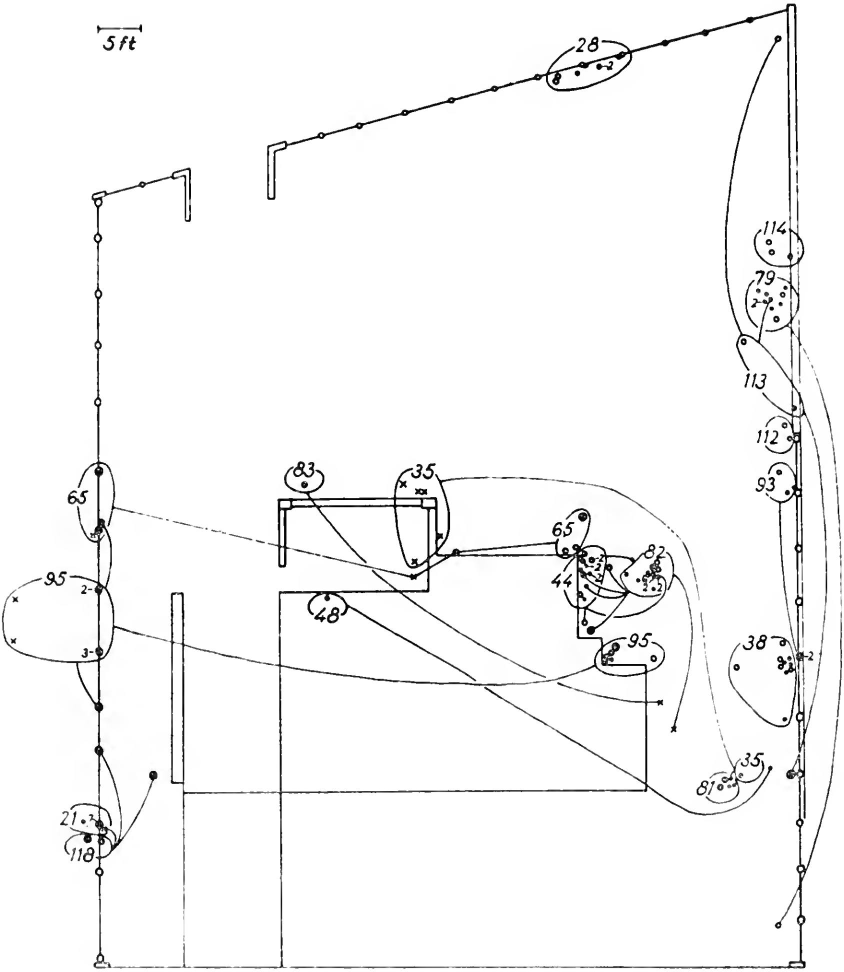


Figure 7.—Distribution of young males at Barbican (same symbols as fig. 5 for period of September 30 to November 7; x's=sightings of lizards several months later, March 8 to 14; all individuals seen more than once during first period and all seen in both periods are mapped; unlike most adults in figs. 5 and 7, these young males showed important growth and first and last measurements are given for them where available; no. 21=47 mm, September 26; no. 28=31 mm, September 26, to 37 mm, October 31; no. 35=44 mm, September 27, to 59 mm, March 10; no. 38=32 mm, September 27, to 38 mm, October 24; no. 44=31 mm, September 29, to 38 mm, October 29; no. 48=44 mm, September 30; no. 65=42 mm, October 5, to 62 mm, March 13; no. 79=29 mm, October 9, to 30 mm, November 2; no. 81=44 mm, October 9, to 65 mm, March 13; no. 82=19 mm, October 9, to 47 mm, March 10; no. 83=18 mm, October 16, to 40 mm, March 11; no. 93=23 mm, October 19, to 57 mm, March 12; no. 95=37 mm, October 19, to 59 mm, March 10; no. 112=22 mm, October 24; no. 113=45 mm, October 42, to 60 mm, March 14; no. 114=37 mm, October 24; no. 118=28 mm, October 29, to 43 mm, March 9).

In the Mona hibiscus hedge studied from April 10 through June 1 there were 10 small males. Of these, 4 changed their activity ranges and the other 6 remained roughly the same.

The data for Barbican indicates that the adults of both sexes have permanent activity ranges and such shifts as they do make are usually to adjacent areas. There is some data from the study area in Mona that contradicts this, though it is a contradiction in detail rather than in substance. When I moved to Mona in mid-April, there were only a few large males that were living on the larger trees, particularly trees with vegetation near the base, a bed of ferns, or a bush. Only a few of these males were marked—those resident in the vicinity of the hibiscus hedge that were being studied in detail—but casual observations were made on the others. It became obvious in the period of mid- to late May that there were many more adult males present and that they were living on trees which had previously been unoccupied. Many of them were smaller than the males which had been present in mid-April. Some of these in one area were marked and their movements watched for about two weeks (fig. 8). These data supported my impressions that there were a number of unestablished adult males moving about in the area. The data show also that there were certain males that did not change their activity ranges during the observation period. The latter males are mostly larger than the former. My interpretation of the data is that the smaller males had recently matured whereas the larger males were older. The older males had been occupying the preferred perches and were successful in keeping the smaller individuals from establishing there, forcing them to spend their time on less favorable perches. That the young males were living in subpreferable areas, coupled with the possibility that they have less site attachment, accounts, I think, for their movements. This is essentially the explanation offered for the situation observed in Barbican. There is a striking difference, however, in the size of the individuals involved in the two situations. In Barbican the males that made activity range shifts were mostly subadults the size of females; in Mona they were fully adult. I think there is a temporal factor herein that explains at least part of the difference. The study in Barbican was terminated in March and that in Mona was not started until May. I think that, if I had remained in Barbican until May, I would have seen an increase in the number of small adult males as the marked juvenile males matured and that these either would have occupied the activity ranges that were not occupied by adult males or would have wandered through the area. Alternatively, had I started my study in Mona in October, I believe I would then have seen a great many movements by young, subadult males.

This study was not designed to investigate either seasonal changes suggested above or dispersal in these lizards; data, therefore, are fragmentary. Clearly both topics are important and need further investigation.

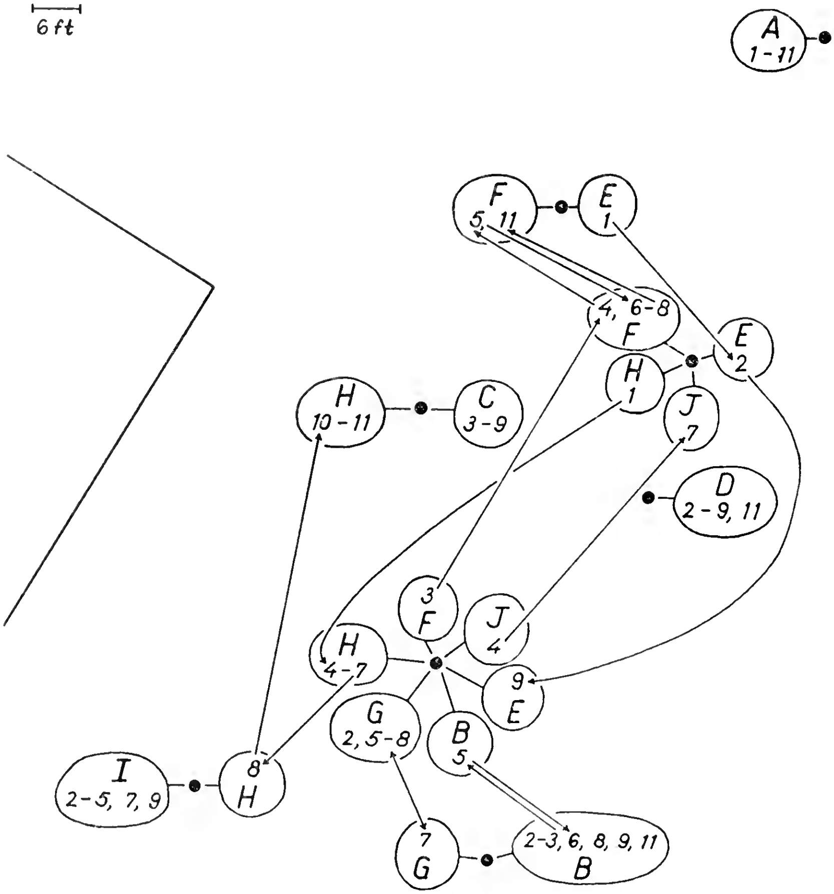


Figure 8.—Distribution of adult males in an area in Mona, May 24 to June 8 (dots=positions of trees on which lizards were seen; lizards: A=68 mm; B=63 mm; C=62 mm; D=60 mm; E=60 mm; F=59 mm; G=57 mm; H=57 mm; I=56 mm; J=51 mm; dates seen: 1=May 24; 2=May 25; 3=May 26; 4=May 28; 5=May 29; 6=May 31; 7=June 1; 8=June 3; 9=June 4; 10=June 5; 11=June 8).

Homing.—Though *A. lineatopus* shows a great deal of site attachment, the only information I have on homing is negative. This is very slight but in the absence of other data is worth recording.

An adult male was moved 200 yards and, after being caged for several days, was released on a small tree unoccupied by any other adult male. He established an activity range there and during the two months under observation showed no sign of attempting to return home.

SPATIAL RELATIONSHIPS BETWEEN ACTIVITY RANGES.—The size, shape, and location of an *A. lineatopus* activity range is influenced not only by the distribution of the habitat requirements but also by the distribution of other *A. lineatopus.*

Even casual observations show that *A. lineatopus* are not distributed randomly with respect to one another. This is particularly obvious along fence rows, where, on almost every fence post, there is one large male but very rarely two. A similar though less conspicuous relationship occurs in the distribution of the adult females.

The simplest situation of this sort that I studied was observed in a series of poui trees planted along a road through the faculty housing of the University of the West Indies at Mona.

The trees had been planted in a strip of grass at about 12 yard intervals, about 4 yards from a hibiscus hedge on one side and about 2 yards from the paved road on the other. They ranged in size from 4 to 12 inches (most of them 8 or 9 inches) in diameter and about 20 to 30 feet high. The spacing of the trees was such that no lizard included two in his activity range. All of the females and most of the males probably had no other principal perches than the trees and the vegetation at their base.

During one afternoon (May 20), I examined the trees along both sides of a kilometer of this road, looking carefully at each tree and examining the vegetation growing at the base. I caught every *A. lineatopus* that I could and sexed, measured, and then released it. A total of 55 trees were examined and 72 *A. lineatopus* seen. Sixty-one were caught, sexed, and measured, plus five more I was able to sex confidently and estimate the size sufficiently to use the data.

The four *A. lineatopus* that I could not size or sex accurately have been omitted from the following discussion as have the other *A. lineatopus* on the same trees with them. This reduced the data analyzed to 51 trees with 62 *A. lineatopus.*

Of males, 32 were sexually mature (i.e. greater than 50 mm snout-vent length), 7 were probably not sexually mature (i.e., less than 50 mm snout-vent length). Twenty-two of the 23 females were probably sexually mature (i.e., greater than 36 mm snout-vent length).

Of the 51 trees, 18 had no adult *A. lineatopus* on them at all, 13 had one, 19 had two, and 1 had three.

The observed distribution departs from random distribution in two ways: there are fewer trees with two adults of the same sex and more with two adults of opposite sex.

Using binomial distribution, the expected number of trees with 0, 1, and 2 lizards were calculated independently for each sex on the assumption that the presence of a lizard on a tree did not affect the probability of another lizard being found on the same tree. These distributions were then compared with the observed distributions (table 5) and the probability that the differences were due to chance were calculated, using an X^2 test. These results show that there are significantly more trees with only a single male (at the .01 level) than would be expected if they were distributed randomly, and fewer trees with two and with no males.

The observed distribution of the females differed from the expected in the same direction (table 5) but not enough to be statistically significant (at the .05 level), perhaps because of the smaller sample size.

Table 6 shows the relationship between adult males and adult females. Trees with no adults and trees with an adult of each sex occur more frequently than would be expected if the distribution of the sexes was independent, while trees with a single male or a single female occur less frequently.

TABLE 5.—*Results of a count of the number of* A. lineatopus *on a line of trees comparing the number of adults per tree with the expected distribution if the adults are distributed independently of one another* (the expected distribution is calculated from the binomial theorem; the sexes are treated separately; the distribution of the adult males differs from the expected at the .01 level, that of the females does not)

	Number of trees		
	With none	With one	With two or more
Males			
observed	21	28	2
expected	27.07	17.32	6.61
Females			
observed	30	20	1
expected	32.99	14.51	3.50

TABLE 6.—*Distribution of males and females with respect to the opposite sex and the null hypothesis (in parentheses) that their distributions are not related*

Females	Males			
	0	1	2	Total
0	18 (12.35)	10 (16.47)	2 (1.18)	30
1	3 (8.24)	17 (10.98)	0 (0.78)	20
2	0 (0.41)	1 (0.55)	0 (0.04)	1
Total	21	28	2	51

This line of poui trees was somewhat unusual in the small number of subadults found, 7 males from 36 to 49 mm and 1 female of 29 mm. The single small female was found on a tree with an adult female and the smallest of the young males. The largest of the young males was found on a tree with an adult male of 62 mm and an adult female of 44 mm. The remaining 5 young males, 40–46 mm, were all on trees that had no other lizards on them.

The distribution of *A. lineatopus* at Barbican during September through November shows a picture similar to that described above but more complex.

The distribution of the adult males is shown in figure 4. They occupy areas that are nearly mutually exclusive though sometimes a male was seen in the activity range of another. The activity ranges of the males in part of this area are mapped in greater detail in figure 3. Again there is little overlap even though in the area where the males meet in the brush heap there are no physical barriers. In fact, all 3 of these males regularly slept in the same tree.

The distribution of adult females in the yard at Barbican (fig. 6) shows a similar mutually exclusive distribution though with more overlap than shown by the adult males. Of the 20 females mapped, all but 3 of them were within the observed activity ranges of adult males.

The distribution of the young males (fig. 7) again shows an almost mutually exclusive distribution, though small ones may overlap with larger ones. The larger subadult males generally show an exclusion also with females. Unlike the females, 7 of the young males lived in areas where there was no adult male.

In contrast to the line of poui trees, the Barbican yard had more females than males and, whereas in the former area there were several males without females, in Barbican there were several females without males.

Figure 2 shows only a single large male living on an isolated tree, but there are 8 adult females and 3 young males also living there. One female lived on the tree trunk and some of the lower branches and seldom visited the ferns on the ground. Seven of the 8 females lived in the ferns at the base of the tree, dividing the area among them so that there was little overlap, though in two cases 2 females occupied the same space at different times. Many of these females also visited the lower tree trunk, where little spatial separation was evident, but none of them used this as a usual perch.

Of the 3 smaller males, 1 had an activity range in the ferns that was largely separated from that of females living in the same area. He also climbed up among the lower branches of the tree. The other 2 small males had activity ranges on the branches of the tree largely distinct from that of the first small male, from all the females, and generally from the large male. These 2 overlapped in space considerably but there is quite a difference in size between them, the larger almost approaching adult size

In addition to the four areas described above, two more were studied that contained a number of young *A. lineatopus* of various sizes. In both of these the spatial relations were more complex than when only adults are considered.

The first of these, Hibiscus hedge, had resident in it: 8 subadult males of various sizes, 1 adult female, and 2 subadult females. It was also visited by 3 adult males. The activity ranges of these 11 lizards (omitting the adult males) is given in figure 9. The first impression of this figure is one of utter confusion. Closer examination, however, reveals several patterns. Though the outlines of many of the activity ranges overlap, there is little overlap between the areas in which the lizards spent 75 percent of their time. Between lizards of approximately the same size, little overlap occurs even at the outer limits of the activity ranges. This exclusion of lizards of the same size operates regardless of sex.

The lizards can be separated into three size classes: the largest with 1 male 49 mm long, which ranged over almost the entire area; the medium-sized lizards, 3 males ca. 44, 42, 42 mm long, which were mutually exclusive; and the smaller lizards, 7 in number, 3 females of 35, 32, 30 mm, and 5 males of 40 to 30 mm, which were also mutually exclusive.

The section of the Barbican brush heap shown in figure 5 had 1 adult male, 4 adult females, and 7 smaller lizards (5 females and 2 males) present. Again their distribution (omitting the adult male) looks confusing until they are sorted by size into two groups: a larger one containing 4 females of 43 to 34 mm and 1 male of 31 mm; and a smaller sized group of 6 females of 30 to 22 mm. Again, though there is considerable overlap between lizards of different sizes, there is little overlap within the size classes. Again, for this size range of lizards, sex is irrelevant. It should be noted that the size groupings used herein

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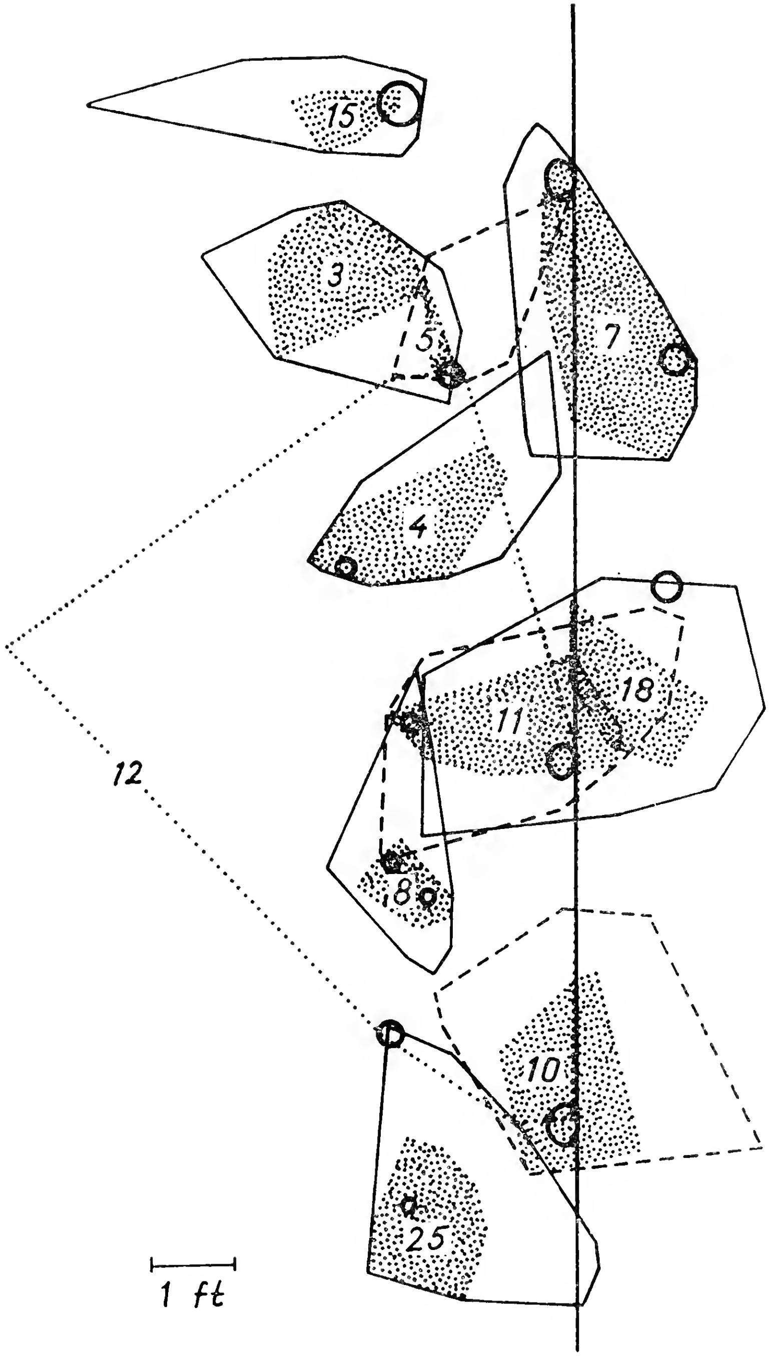
FIGURE 9.—Distribution of females, juveniles, and young adult males in Mona hibiscus hedge; this area also was visited by several larger adult males (circles=fence posts and certain important bushes; several types of lines distinguishing different size classes of lizards based on censuses conducted April 18–23=activity ranges; stippled areas=places where lizard spent 75% of its time (see pp. 28 for explanation); stippled area for no. 12 overlaps those of nos. 8, 10, and 11 and has been omitted for clarity; no. 3 female=32 mm, April 10; no. 4 male=36 mm, April 10; no. 5 male=42 mm, April 10; no. 7 female=35 mm, April 10; no. 8 female=30 mm, April 10; no. 10 male=42 mm, April 10; no. 11 male=44 mm, April 10; no. 12 male=49 mm, April 10; no. 15 male=40 mm, April 11; no. 18 male=36 mm, April 11; no. 25 male=36 mm, April 17).


15
3
5
7
4
18
11
12
8
10
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1 ft

bear little resemblance to those used in the first case and, in fact, any division seems to be arbitrary.

A basic rule in distribution of *A. lineatopus* seems to be that no two lizards of the same size can have widely overlapping activity ranges. This general rule seems to apply at all sizes, from the smallest studied, 22–24 mm, to the largest adult males, ca. 70 mm, and to apply regardless of sex. *Anolis lineatopus* of different sizes, however, may have widely overlapping activity ranges. Usually the activity ranges of adult males overlap those of adult females, which frequently in turn overlap those of small juveniles. The activity ranges of the small males frequently are like those of similar sized females, but also, and much more frequently than females, they are in areas that are uninhabited by other lizards, either male or female, and some of which, because of the structure or situation, seemed subpreferable. The distribution of adult *A. lineatopus* relative to one another resembles one of the common patterns seen in vertebrates, that of territoriality. The distribution of the juveniles with respect to one another, particularly to the adults, is more novel.

Social Behavior

The regular arrangement of activity ranges with respect to one another is largely the result of direct interaction between individual *A. lineatopus.* These interactions fall into two categories, agonistic behavior and courtship. These interactions, and the display associated with them, are common and make up most of the social behavior of the species. As is general in lizards, parental care, flocking, play, allogrooming, and alarm signalling are absent. Perhaps important in certain circumstances but hardly true social behavior is predation by adult male *A. lineatopus* on juveniles of the species (see p. 15).

An adult male *A. lineatopus* probably spends more time in display than in any other activity except sleeping and watching. One male that I watched for about 11 hours gave 181 displays (averaging about one every 3½ minutes). During this time he was involved in two conflicts with other adult males, copulated twice, and courted unsuccessfully several additional times. In the 8 hours from 8:00 A.M. until 4:00 P.M. there were only 5 periods longer than 10 minutes when no display was seen, the longest being about 30 minutes.

Before describing agonistic behavior and courtship and discussing their effects on the spatial organization of the population, it is necessary to digress briefly into a description of the various displays observed in *A. lineatopus.*

DISPLAY.—No analysis is given here because the displays of West Indian *Anolis,* including *A. lineatopus,* are under study by Dr. R.

Ruibal (in press). "Display" is used here in its usual nontechnical sense.

The displays of *A. lineatopus* can be described under the following categories: back jumping , step bobbing, bobbing, dewlapping, orientation, posture, jaw fencing.

Back jump: The lizard suddenly and violently extends all four legs so that it pushes itself away from the perch and backward along it. A series of one to three of these may be given in sequence. I have seen it only infrequently and always in long disputes between adult males, most often shortly before they meet to lock jaws or between bouts of jaw locking.

Step bobbing: In this display the head and anterior part of the body is raised stiffly in a series of short steps and then lowered in a similar manner, producing a slow, jerky bob that is usually repeated several times in sequence. Step bobbing is somewhat more common than the back jump. It is given by juvenile and adult males (and perhaps females) usually in disputes wherein both lizards are displaying, occurring early as well as late in a dispute. It occurs more rarely in dispute situations wherein the opponent is not displaying and only very occasionally in situations wherein no opponent is visible. It can be combined with dewlapping.

Bobbing: The head or head and shoulders are moved up and down rapidly several times. This is the most common *A. lineatopus* display. It is given in courtship by both sexes and in dispute situations by males and females, both juveniles and adults. The displays included herein are variable in form and, though I did not do so, it may be possible with careful study to separate a male courtship bob from this category, as Greenberg and Noble (1944) did for *Anolis carolinensis* and Kastle (1963) did for *Norops auratus*. A great deal of bobbing by all *A. lineatopus* is not obviously either dispute or courtship. Similar bobbing occurs commonly in iguanids and agamids. Interpretations of its significance are varied. Greenberg and Noble (1944) called it a subordination gesture in *Anolis carolinensis;* Noble and Bradley (1933) called it an aid to vision, increasing depth perception. Carpenter (1962), in *Sceloporus undulatus* and other iguanids, calls it assertion display, and Harris (1964) suggests that in *Agama agama* it functions to keep the group members aware of one another's position. Evans (1936a) suggested that in *Anolis carolinensis* it served as a cue given by a female to a male to indicate her sexual receptivity.

I have recorded the behavior associated with 57 instances of bobbing by marked females and subadults during two sessions of two hours each (tables 7, 8). The most striking correlation is with movement. *Anolis lineatopus* usually bobbed after it had shifted its

TABLE 7.—*Relationship between head bobbing and shifts in position in females and young males*

Apparent reason for shift	Before shift	During shift	After shift	No shift	Total
To feed		7	15		22
To flee or avoid another lizard	1		3*		4
To chase or approach another lizard	3	2	10		15
Unknown	1		7	7	15
Total	5	9	35	7	56

*Plus one instance of step bobbing.

TABLE 8.—*Occurrence of head bobbing in dispute situations among females and young males*

	Neither bobs	Only winner bobs	Only loser bobs	Both bob	Total
Approach-avoid	8		1		9
Chase-flee	3	10			13
Mutual display	1			2	3
Total	12	10	1	2	25

position and did so whether it had moved to chase away another *A. lineatopus*, flee from one, or catch something to eat. Juveniles and young males bobbed as frequently as did females and in a similar manner. In dispute situations the winning or dominant lizard usually bobbed, the loser or subordinate seldom did so.

In *A. lineatopus* bobbing is not a subordinate gesture nor a signal of female sexual receptivity. It is probably not an aid to depth perception. Bobbing probably serves to advertise (or assert) the presence of the displaying *A. lineatopus* to others in the vicinity. It would thus serve much the same function in *Anolis lineatopus* that it does in *Sceloporus undulatus* and *Agama agama*. Presumably it is also analagous to the singing of territorial birds and the sign posting of many mammals.

Dewlapping: The dewlap is flashed—extended to its maximum, as a gular fan, exposing the yellow and orange skin between the more dully colored scales—several times in sequence and then relaxed. In Evans' (1953a) terminology there are 5–12 flashes per volley. The dewlapping display is given by adult males (very occasionally by subadult males, see page 54). This display is commonly seen and is given in courtship and agonistic situations. Like bobbing, it seems also to serve as an advertisement display.

Orientation: Though orientation by itself is not a display, certain stereotyped changes in orientation are important components of almost all displays. In courtship a male orients toward the female, who is usually oriented away from him. He may turn his head to one side so that his dewlap is more visible to her. In a dispute, *A. lineatopus* frequently does not face its opponent directly but turns so that it presents a side view. The amount of turning varies from turning the head slightly to one side, through a position in which the lizard is at right angles to its opponent, to one in which the lizard is facing almost directly away from its opponent. In disputes in which both lizards are displaying, they frequently approach one another obliquely rather than directly.

In watching a prolonged fight between two males, it is possible to predict, on the basis of the angle of each, which one will attack next. Lizards that are parallel to one another will usually display rather than attack. The closer a lizard is to facing his opponent, the more likely he will approach the other; the farther away he is facing from his opponent, the more likely he will retreat.

Posture: Associated with lateral orientation are postural displays that increase the apparent size of the lizard when seen in side view. In lizards of all sizes the sides are pulled in or flattened so that the back is arched and the belly extended with the result that the body appears deeper. The throat is gorged: the base of the hyoid is pulled down so that the throat appears swollen. Frequently the mouth is opened slightly and the tongue, which is short and broad, is raised and pushed forward so that the tip appears as a small ball between the ends of the jaws.

Finally, and in the males only and most conspicuously in adults, the tissue along the center of the neck and back can be raised into nuchal and dorsal crests. The total effect of these changes is to make the lizard, when seen from the side, appear almost twice as bulky as it normally is. The postural displays are all associated with disputes and do not occur in courtship.

Jaw fencing: Though fighting is not properly considered display, combat between *A. lineatopus* adult males is usually so ritualized that is should be considered here. Each male approaches the other slowly until the two are an inch or so apart, head to head. They lunge repeatedly at each other's snout for a moment or so, as if fencing for a hold. They then lock jaws, one biting the other's snout and the latter biting the former's lower jaw. The two lizards then strain against one another, each apparently attempting to dislodge the other from the perch. When one succeeds, the other may fall to the ground or dangle in midair for a moment. Alternately, one lizard may attempt to escape, opening his mouth and scratching with a front foot at the other's snout. This wrestling with locked jaws may last for several minutes and may be repeated two or three times. Usually one of these encounters is decisive and the loser retreats immediately after the bout. I have never seen a defeated lizard so injured or exhausted that it was unable to run away.

Damage sometimes results from these bouts and blood is drawn, though the wounds are restricted to the snout. Some males are found with a swelling on one of the mandibles, probably wounds from this sort of combat that have become infected. (Schmidt, 1928, suggested the same thing for *A. cristatellus* in Puerto Rico.) The infected wounds apparently are painful. One noosed male with an infected jaw repeatedly bit and released my finger rather than biting and holding as a male normally does.

The preceding descriptions of display provide a foundation for discussing the role that social behavior plays in the spatial organization of *A. lineatopus*. Two sorts of social behavior seem important: courtship and agonistic behavior.

Courtship.—This behavior brings together male and female when they are ready to copulate. Evidence suggests that it also influences males and females to establish and maintain overlapping activity ranges and in effect to form pair bonds.

This pattern, a male with a home range shared by one or several females that are his mates, is common among vertebrates. It is perhaps most common among birds and mammals in which the male and female share in care of the young. It seems widespread in lizards, particularly iguanids (*Anolis sagrei*, Evans, 1938a, Oliver, 1948; *Sceloporus olivaceous*, Blair, 1960; *Uta stansburiana*, Tinkle, et al, 1962; *Basiliscus vittatus*, Hirth, 1963a; and *Agama agama*, Harris, 1964). The role of courtship in establishing this pattern is far from clear. Blair (1960) feels that the males of *Sceloporus olivaceous* seek out the females. In *Agama agama*, Harris (1964) has evidence that it is the females that make the choice, joining a male that has established a home range. Hunsaker (1962) showed experimentally that in the *Sceloporus torquatus* group it was the male bobbing display that was attractive to females, and Hunsaker suggested that this influenced them to settle near the male. Perhaps dewlap displays of the adult male *A. lineatopus* are similarly attractive to females.

Though the male *A. lineatopus* spends a considerable amount of time chasing and bobbing and dewlapping to females, I observed copulations infrequently. Chases, though frequent, are seldom persistent, and I never saw a male catch a female that was trying to avoid him.

In the consummated courtships seen, there was relatively little display and the whole process seemed very casual. All of the copulations I observed between marked lizards occurred within the home ranges of the lizards involved. For example, at Barbican (figs. 4, 6), an adult male (no. 1) was seen in copulation with three females (nos. 16, 59, 145), all of whose home ranges widely overlapped his. None of these females was seen to copulate with any other male though this may happen. Among the lizards on an isolated tree (fig. 3), one female was seen to copulate with the adult male and also, on another occasion, with a smaller (ca. 47 mm) but obviously adult male. The activity range of the large male overlapped that of the female while the activity range of the small male overlapped that of the female to some extent.

The following description from my field notes illustrate these consummated courtships:

> 29 October—Barbican. No. 3, adult male, was sitting on a fence post and No. 18, an adult female, on the adjacent fence post about 7 feet away. They had been sitting in these spots for at least ½ hour ignoring each other. The male displayed occasionally: bobbing first, then continuing to bob he began to flash his dewlap, stopped bobbing, and continued flashing dewlap, then stopped; a few bobs were given without any dewlapping. The female moved several times but I saw no display on her part. Then, with no obvious preamble No. 3 climbed along the barbed wire from his post to hers. He stopped on the wire for a moment then proceeded to her post, approached her from behind and straddled her with both fore and hind legs and seized a tiny bit of the loose skin on the back of her neck and they walked together a few inches down the post. They stopped and he twisted the base of his tail under hers and apparently inserted his left hemipenis. Shortly he released his hold on her neck. They remained still except for two short series of bobs by the female. After perhaps 2–3 minutes they separated, both dragged their vents on the post and then the male returned along the wire to his original post.

Once the male had left his original post he did not display and his earlier displays seemed the usual advertisement displays. I had been watching the male but was aware of the female for about a half hour before the male approached her and I noticed no display behavior on her part. The only unusual thing she did was not avoid no. 3's approach. About an hour later these two were in copulation again.

Before any of this happened, I had placed another female, tied to a string, on the male's fence post and, though she was in full view of him, he seemed to ignore her completely.

The other 10 courtships that I saw followed this pattern almost exactly, differing only in that the male occasionally stopped in his approach to the female and dewlapped. In each of these I was impressed by the small amount of display on the part of the male and its almost total absence on the part of the female. The only movements by the female that could be considered display were noted in two of the courtships; in these, just before the male seized her neck, the female moved her head from side to side.

There may be an inviting or receptive display on the part of the female but I was unable to recognize it. Certainly the females do not bob to indicate their receptivity as Evans has recorded for female *A. carolinensis*.

Copulations were observed from August 24 to May 30. They seem to occur throughout the year.

The above description of a copulation mentions that the male copulated with a female that was resident in his area even though there was an adult female closer to him and tethered so that she could not escape. On another occasion, a different male approached about 10 feet, apparently in response to my placing a female stake-out in his home range. When he reached the vicinity of the stake-out and had inspected her, he mated with a free female that was nearby and with which I had seen him before. I tried tethering females within the home ranges of males on several other occasions and in no case did a male attempt to mate with them.

These observations suggest the possibility that the males recognize the females that live within their home ranges as individuals. The observations can also be explained by saying that a female tied up is not a suitable mate or that the tethered females were not receptive while the free-living ones were and that the male could detect this.

There are two other data relevant here. One is that adult male and adult female home ranges overlap intersexually more frequently than one would expect on chance (p. 33). Apparently adults of one sex or the other, and perhaps both, prefer to live in a home range which overlaps that of an adult of the other sex.

The final piece of evidence is the very simple and almost casual way in which copulation occurs and the small amount of display that immediately precedes it. A great deal of display is given by the males in the presence of the females to which the females do not react overtly. If it has any effect on them at all, it must be a cumulative effect over a period of time. This is possible since all of the copulations that I observed involving marked lizards took place within the normal home ranges of the lizards involved. The cumulative effect of the display may result in keeping the female aware of the male's presence, in bringing her into sexual receptivity (as in many birds), or in reducing her fear of or aggression toward him. The studies of Hunsacker (1962), showing that there are two displays in *Sceloporus*, one which attracts the females to stay near the male and another which is precopulatory, suggest that the cumulative effect of display postulated for *A. lineatopus* may occur widely in iguanids.

Since the lizards live together more or less permanently and the females usually mate with a single male (the male with the one or more females that have home ranges within his), there exists what might be considered a pair bond. The evidence that the male *A. lineatopus* may recognize the females as individuals suggests that this pair bond is comparable to that in birds and mammals. A pair bond of some sort has been reported in the largely monogamous *Uta stansburiana*, Tinkle, et al (1962), in certain populations of *Sceloporus merriami*, Milstead (1961), and *Crotophytus collaris*, Fitch (1956a), and in *Cnemidophorus tigris*, Milstead (1961). Kastle (1963) suggests that his captive *Norops auratus* recognized one another as individuals.

The large amount of unconsummated courtship and the very small amount of immediate precopulatory display then could be interpreted together as display that serves to help maintain the pair bond. This is a function of "territorial" display that is quite well established in bird literature.

This discussion of the possible pair bond in *A. lineatopus* is speculation but it suggests a very interesting line of investigation.

The adult males, in addition to courting females, also courted young males that were of female size. I was unable to distinguish between the approach of a male and his display to these young males and that exhibited toward adult females. This contrasts with the situation in *A. carolinensis*, wherein Greenberg and Noble (1944) reported that they could distinguish the approach of an adult male to a female from his approach to any other male.

In no case did I see a homosexual mating though I saw one male start precopulatory behavior with an adult male stake-out. Homosexual matings are reported for caged *A. carolinensis* by Noble and Bradley (1933). These matings probably were due to the crowded conditions under which the lizards were being kept.

The only difference I could detect between females and young males in their response to courtship is that the males always ran and the females ran except when they were receptive. (There is some difference in their shape, particularly when a female is carrying a large egg.)

On one occasion I saw an adult male interrupt a copulation as follows:

18 May—Mona. This evening just about suppertime my attention was attracted by rustling in the leaves. When I looked I saw a male holding a female by the neck; as is typical of the terminal stages of courtship, they were walking along slowly. Just then another adult male ran over and jumped up in a bush nearby and bobbed, then he jumped towards the pair and all three disappeared around a flower pot. By the time I maneuvered to where I could see them

again, the pair had separated. Clearly one male had been attracted by the courtship of another and had successfully interrupted it.

This was seen only once, probably because males by their aggressive behavior keep other males out of the area where mating takes place.

Agonistic behavior.—The information on the role of agonistic behavior in the spatial organization of *A. lineatopus* populations is more abundant and more direct than is that on the role of courtship.

Two factors are most important in agonistic behavior: relative size and location. First, *A. lineatopus* is most aggressive toward others of similar size while much less so toward those that are either much larger or much smaller. Second, *A. lineatopus* is most aggressive within its activity range and particularly on its usual perches. As a result, *A. lineatopus* of similar size have activity ranges with little overlap. Greater overlap in activity range is possible between individuals with greater differences in size. *Anolis lineatopus* (particularly females and subadults) behave aggressively toward anoles of other species just as they do toward their own species.

Though the basic pattern is quite simple, the relationships among *A. lineatopus* in the areas studied were complex. Because of the wide range of sizes present, each individual behaved somewhat differently to each of its neighbors.

Collias (1944) has said that individual aggression may be expressed as either of two types: dominance hierarchies and territoriality. This dichotomy has been widely used in studies on lizards (C. C. Carpenter, 1962; Greenberg and Noble, 1944; Evans, 1951, etc.). The behavior of *A. lineatopus* can not be assigned to either of these categories because it has important aspects of each of them. By either a simple definition of territory as "a defended area" (Noble, 1939) or a more complex operational definition—"an area or space in which a particular individual dominates certain categories of intruders who dominate it elsewhere. An individual dominates another when it drives it away, excludes it or supplants it at will" (Rand, in press)—every *A. lineatopus* holds a territory, defending it against neighbors of the same size. At the same time, each is a member of a straight line dominance hierarchy that consists of all those anoles of different sizes whose home ranges overlap its own home range.

Territorial behavior in some form or other is a common behavior pattern in iguanids and has been reported from almost every species that has been studied in detail. Adult males are always involved, and sometimes adult females as well. In a few cases, principally Blair (1960), Fitch (1956a), and Oliver (1948), it has been reported in juveniles.

The establishment of dominance hierarchies is a common phenomenon in caged iguanids: *A. carolinensis*, Evans (1936), *Crotophytus collaris*, Greenberg (1945), *Urosaurus ornatus*, Carpenter and Grubits (1960). Dominance hierarchies in the field also have been reported in *Ctenosaura pectinata*, Evans (1951) and *Sceloporus grammicus*, Evans (1946).

The brief report on the social behavior of *A. sagrei* given by Oliver (1948) suggests that that species is very similar to *A. lineatopus* in its social behavior.

Anolis lineatopus differs from the usual territorial pattern in vertebrates chiefly in the involvement of a variety of sizes of juveniles that hold territories and defend them against one another and, in the case of large subadult males, against adult females. The laboratory studies of Greenberg (1947) show that juvenile green sunfish may hold territories and suggest that in the wild they may behave as do *A. lineatopus*. The basic pattern in *A. lineatopus* and some of the possible complexities can be described effectively by presenting abstracts from my field notes.

In the following series of examples I have begun with interactions between individuals of similar size living in adjacent activity ranges. In these first two cases, the disputes were brief. They occurred on the mutual range boundary or at the point when one *A. lineatopus* entered the activity range of the other and ended when the former left. Either lizard invaded, always as a by-product of some other activity, but the resident always was both the aggressor and the winner.

(1) Hibiscus hedge, Mona [fig. 9]—Seven disputes between No. 4, a 36 mm male and No. 7, a 35 mm female, with activity ranges which overlapped very slightly.

13 April. No. 4 chased a smaller lizard (No. 6) out of his own area and well into that of No. 7. No. 7 charged at No. 4 and he retreated back toward his usual perch.

18 April. Both lizards met at the boundary between the two areas and displayed repeatedly at one another. First No. 7 retreated into her area and No. 4 remained where he had been displaying. After several minutes No. 7 came back toward No. 4 and displayed. No. 4 returned the display and then retreated to his usual perch. No. 7 did not chase him.

20 April. Twice a larger lizard (No. 5) chased No. 4 who fled into the activity range of No. 7. The first time, No. 7 charged at No. 4 and the second time charged, then stopped and displayed. Each time No. 4 fled back to his own activity range. The second time, he stopped when he was well within it to display back at No. 7. In neither case did No. 7 carry her chase beyond her usual activity range.

27 April. The two lizards were seen displaying to each other on the boundary area but a bit nearer one of No. 7's perches than to No. 4's usual perch. No. 4 retreated.

1 May. The two lizards were again seen displaying to each other in the same general area as on 27 April but a bit nearer No. 4's usual perch than last time. This time both retreated with No. 4 moving away first and then No. 7.

(2) Hibiscus hedge, Mona [fig. 9]—A similar set of disputes between No. 4 and No. 18; both 36 mm males. On 14 April both No. 18 and No. 4 at different times were seen chasing the same smaller lizard, No. 6. Once No. 4 chased No. 6 into No. 18's activity range and followed him. No. 18 charged at No. 4, who ran back into his activity range. Twice No. 18, in chasing No. 6, ran into No. 4's area. Each time No. 4 displayed at No. 18 who displayed back and then retreated.

In the preceding two examples the encounters were brief and no changes in activity range boundaries resulted. These were the most common type of disputes seen between similar sized individuals and seemed to serve to maintain the status quo. Occasionally disputes were observed that produced changes in activity ranges. These were longer and often renewed on successive days. Two examples are given below; the first resulted in only a minor boundary change.

(3) Barbican brush heap [fig. 3]—No. 1, 59 mm male; 6, 62 mm male with adjacent activity ranges with one small area of overlap, a stake that was a preferable perch on the North edge of No. 1's activity range and the South edge of No. 6's.

Two encounters illustrate the original situation, when neither male was using the stake frequently.

15 January, 0905 hours. No. 1 sitting on stake well up in view, bobbing occasionally. 0910 hrs. No. 6 appears in the center of the brush heap and runs a foot or two towards No. 1, stops and bobs. No. 1 runs down from stake into brush heap, No. 6 moves back a bit, but No. 1 continues towards tree.

1005 Hrs. No. 6 comes over in brush heap to level of stake, apparently to chase No. 152 (a smaller non-resident adult male). No. 1 comes down from tree through brush to about one foot south of No. 6, tail twitching, dewlaps. No. 6 dewlaps, then retreats a couple of inches. No. 1 jumps towards stake, now on a small twig west of stake. No. 6 retreats toward center of brush heap, bobbing.

[The next day the situation changed:] 1540 hrs. No. 1 runs over into brush heap, bobbing and tail twitching. He goes beyond the stake a short distance [he was probably chasing a non-resident male which I did not see]. No. 6 leaves his perch in the north end of the brush heap and runs toward No. 1, and bobs. No. 1 retreats toward stake and No. 6 moves a bit nearer and bobs again.

1546 hrs. No. 1 jumps to stake, crest up.
1548 " No. 6 dewlaps, his crests are not yet up.
1549 " No. 1 bobs.
1549 ½ " No. 1 dewlaps.
1551 ½ " No. 6 bobs, then jumps east, moving at right angles to No. 1.
1553 " No. 6's crests are up a little.
1555 " No. 6 bobs.
155 " No. 1 dewlaps; No. 6 dewlaps and back jumps, crests now full up.
1608 hrs. No. 6 bobs.
1609 " No. 6 turns and moves west about 6 inches, directly north of stake, side-on to No. 1.
1610 hrs. No. 6 moves about 2 feet farther west; dewlaps.

1611 hrs. No. 6 down into brush heap out of sight.

1613 " No. 6 moves directly toward brush heap, stops one foot away; it begins to rain.

1618 hrs. No. 1 dewlaps. No. 6 is now 3 feet NNW of stake.

1620 " No. 6 runs by stake, but angling toward No. 1, to 2 feet northeast of stake; No. 6 dewlaps, crests full up; No. 1 dewlaps.

1625 hrs. Both display.

1631 " No. 6 moves diagonally a short distance towards No. 1.

1632 " No. 1 dewlaps; No. 6 bobs.

1634 " No. 1 dewlaps.

1637½" No. 1 twitches tail, jumps down into brush heap away from No. 6; No. 6 moves a bit closer; No. 1 jumps back to stake obliquely approaching No. 6; both display dewlapping.

1639 hrs. No. 6 moves a bit closer, mouth open, tongue out; they are now about 1 foot apart, No. 1 on stake, No. 6 on a branch in brush heap.

1645 hrs. No. 1 dewlaps.

1647 " No. 6 displays.

1648 " No. 1 jumps at No. 6, they lock jaws and struggle violently; No. 6 is knocked off his perch and runs 1 foot away.

1649 hrs. No. 6 dewlaps.

1650 " No. 6 bobs; No. 1 twitches tail.

1651 " No. 1 moves back to stake; bobs.

1653 " No. 6 moves about 6 inches further away.

1656 " No. 6 moves back to the north part of the brush heap, then down into brush heap, bobbing.

No. 1, apparently as a result of this encounter, established his claim to the stake and thereafter visited it frequently without being challenged by No. 6, which I did not again see on the stake.

17 January—0900 hrs. No. 1 is on stake, No. 6 on his perch in north part of brush heap. Neither has crest up nor is displaying more than usual.

Anolis lineatopus may expand its activity range slightly at the expense of another as did the adult male in the case above, or it may drive the original lizard out completely as did the juvenile female in the following example.

(4) 27 January—Barbican brush heap [fig. 5], 900–1020 Hrs. No. 148, small female, invaded the activity range of No. 163, small female, and drove her out of it. These lizards have occupied adjacent activity ranges for at least a week. Until today I had seen no conflict between them.

Two small females, Nos. 163 and 161, have divided the small brush heap between them, No. 161 on the west side and No. 163 on the east side. No. 148 has spent its time both north and south of this brush heap, passing without hindrance through it along a central branch which lies between the activity ranges of Nos. 163 and 161.

This morning No. 148 entered the activity range of No. 163 and bobbed at her. No. 163 bobbed back. No. 148 jumped in No. 163's direction and No. 163 retreated east and eventually out of her activity range.

Between 900 and 1000 hrs. while I watched, No. 163 tried twice to re-enter her old activity range and each time No. 148 drove her out. They never came to grips or even displaying at close range. A dash by No. 148 in No. 163's direction sent No. 163 fleeing.

No. 161 ignored all this going on within 2–3 feet of her. When No. 163 retreated from her activity range she approached the fence where another small female lives (No. 156). This female ignored No. 163 today.

1400–1430 hrs. No. 163 made another attempt to enter her old activity range and retreated once more before No. 148's approach.

29 January, 815–830 hrs. No. 163 was back in her activity range this morning but No. 148 soon chased her out again. No. 163 fled toward the fence again but this morning No. 156, who had ignored her on 27 January, chased her back towards the brush heap. No. 148 chased her back toward the fence. No. 156 again chased her away. This time No. 163 moved to a small plant on bare ground midway between the fence and the brush heap and spent the rest of the morning there. No. 148 moved north out of No. 163's old activity range and spent the morning on the branches on the southeast edge of the big brush heap.

Encounters between similar sized individuals sometimes involved a resident and another *A. lineatopus* that was a stranger to the area. Presumably most of these strangers are the subadult and young adult males (p. 31). Probably most *A. lineatopus* that change their home range are attacked when they cross or attempt to settle in an area that is already part of the home range of an *A. lineatopus* of similar size.

In some of the encounters between residents and strangers, the stranger fled quickly, as in the following two incidents.

(5) 2 February—Barbican brush heap [fig. 4]. A stub-tailed adult male appeared within the activity range of No. 159 (adult male). No. 159 approached him to within about 6 inches, both had crests up and both bobbed and dewlapped.

The intruder ran by No. 159, leaving 159's activity range and into that of No. 6 (adult male). No. 159 followed, actually invading the edge of No. 6's activity range, to display at the intruder, who ran a bit farther then climbed down inside the brush heap and disappeared.

After a few moments, No. 159 retreated into his own activity range.

No. 6 had ignored this whole business from his perch on the other side of his territory.

(6) 19 February—Barbican brush heap, 0832 hrs. An unmarked bobtailed adult male appears in the small brush heap. No. 1 is on rock and probably cannot see intruder.

The bobtail hops into shade of log.

0835 hrs. Bobtail hops onto log.

0841½ " Bobtail moves to tree out of sight of No. 1.

0846 " Bobtail moves into full view of No. 1 at 2 feet up on tree.

0849½ " No. 1 begins bobbing, giving several series of step bobs.

0850½ hrs. No. 1 runs toward tree; when No. 1 is still 4 feet away, bobtail jumps to ground on the other side. No. 1 stops in brush heap, step bobs and dewlaps.

0851 hrs. No. 1 jumps 6 inches further towards tree, bobtail runs 2 feet further away.

0851½ hrs. No. 1 moves onto tree. Bobtail leaves area completely, going south.

The intruding lizard, however, is not always defeated.

(7) 6 September—Mona. No. 26 (49 mm male) came to ground [from the

tree where he usually was seen] and ran towards another tree nearby. No. 17 (44 mm female) who was on the ground in his path jumped to the tree [where she usually was seen]. No. 26 changed direction and chased No. 17 around and up the tree. No. 17 fled and No. 26 came back down the tree to sit on No. 17's favorite perch.

Some of the fiercest fighting that I saw occurred between a resident and an intruder that did not retreat when attacked.

(8) 29–30 August—Mona. A large male *lineatopus*, No. 31, was marked on 26 August on a large tree. He measured 67 mm. in snout-vent length He was next seen on 29 August on a tree about 15 yards away fighting with an unmarked, probably resident, male. The fight included some jaw locking and No. 31 apparently won.

The following day No. 31 and probably the same unmarked male were fighting on the same tree. "This is serious fighting: no display, just biting." First seen on the tree trunk, they soon locked jaws and fell to the ground where they remained for a couple of minutes fencing and biting at each other, not only at jaws but at necks also. Both climbed back onto the tree trunk and the fighting continued, the lizards standing head to head and lunging sideways. They locked jaws and fell again, the unmarked male catching a small plant with his hind legs and letting No. 31 swing past to crash against the trunk with an audible thud, then hang suspended from his jaws. They hung so for better than a minute and then separated. The unmarked lizard ran up the tree and No. 31 up the one next to it. They worked their way up the trees in installments, each male on his move getting higher than the opponent on the adjacent tree. At each stop they displayed, dewlapping and bobbing, until finally they worked their way up into the crown and out of sight.

On September 1 and 2 No. 31 was seen back on the tree where he was first marked.

These accounts of disputes or aggressive encounters between similar sized individuals have illustrated the forms these encounters usually take and the conditions under which they usually occur. It should be stressed further that some sort of dispute occurs on almost every occasion when two similar sized *A. lineatopus* meet. They may not fight when both individuals are outside of their activity ranges or both are frightened. It is sometimes possible for a lizard to remain within the activity range of another of the same size for some time but only if the intruder remains out of sight of the resident. This is possible only in areas where the habitat is structurally complex with many hiding places. Even under these conditions I believe the situation is only temporary.

At the other extreme from these aggressive encounters between similar sized *A. lineatopus* are the relationships between individuals of very different sizes. These may have widely overlapping activity ranges and show very little, if any, aggressive behavior toward one another.

This is particularly true if one individual is an adult male and the other a female. In this case, the male chases the female in courtship.

The female usually ignores the male except for moving to get out of his way and avoiding his courtship unless she is ready to mate.

There may be little aggression even if both lizards are not adult, provided they are quite different in size.

(9) Hibiscus hedge—Mona [fig. 9] No. 11, 44 mm male and No. 8, 30 mm female, held widely overlapping activity ranges and were both seen frequently in sight of each other over a two month period. During this time only three incidents were recorded which could be considered interactions and in each of these No. 8 moved out of the way of No. 11 who happened to approach the perch on which she was sitting. A similar relationship existed between No. 162 (a 40 mm female) and No. 161 (a 29 mm female) in the Barbican brush heap.

Between the above-described extremes of tolerance and intolerance are a number of cases in which a smaller lizard is tolerated by a larger one in parts of the latter's activity range, usually those areas the larger individual visited less frequently, but the latter attacked in other areas particularly on its usual perches.

(10) Barbican brush heap [fig. 6]. Nos. 145 and 162, 43 mm and 39 mm females, demonstrate this. No. 145 held an activity range centered on a small tree. No. 162 was a 39 mm female who spent most of her time in the small section of the brush heap east of the tree, though a number of times I saw her visit the tree itself.

24 January—No. 162 jumps from east brush heap to tree where No. 145 was sitting. No. 145 immediately chased No. 162, who ran up tree. No. 145 did not follow. Twenty minutes later No. 162 runs back down tree and jumps to east brush heap too quickly for No. 145 to do anything.

25 January. No. 162 climbs tree; No. 145, who is in brush heap north of tree, ignores her. No. 162 climbs to 10 feet (unusually high for a female) and stays there for about 40 minutes. During this time No. 145 had moved from north of the tree into the brush heap east of the tree. When No. 162 came back down to the brush heap where No. 145 was, they bobbed at each other for about 15 minutes before No. 162 retreated down into the brush heap.

29 January. No. 145 comes down tree and into east brush heap. No. 162 is in this brush heap about one foot from No. 145 but may not see her. No reaction, and about ½ hour later No. 145 returns to tree and then to north brush heap.

31 January. No. 162 is hopping from east brush heap over towards tree. No. 145, who was in brush heap north of tree, comes over across ground to between No. 162 and tree and bobs. No. 162 runs back to brush heap.

Later No. 145 moves to east brush heap where No. 162 is; they ignore each other.

1 February. No. 162 moves from east brush heap to tree, No. 145 comes from north brush heap to chase her and No. 162 runs up to 9 feet in the tree.

5 February. Both Nos. 162 and 145 are seen in east brush heap. No. 162 bobs at No. 145 but No. 145 runs back to tree but not in response to No. 162.

12 February. No. 145 chases No. 162 from tree. No. 162 runs across east brush heap to rock beyond it. Until today No. 162 has spent most of her time in the section of brush heap just east of the tree with very infrequent excursions north and further east. Today No. 162 moved northeast and was involved in a long and rather violent fight with a lizard well north of where she usually ranges.

13 February. Both Nos. 162 and 145 are seen in east brush heap. They are about one foot apart, lateral to one another, with throats gorged and sides flattened. Both bob. No. 162 moves back and forth at right angles to No. 145 and bobs several times. No. 145 moves to the perch she uses most when she visits east brush heap. No. 162 moves south away from No. 145, and then back past her and out of this section of the brush heap entirely.

Today again No. 162 spends quite a bit of time after this dispute with No. 145 northeast of the section of the brush heap where it occurred and is seen chasing a smaller resident lizard on a fence post which No. 162 has previously seldom visited.

15 February. No. 145 comes from the brush heap north of tree and chases No. 162 out of the brush heap east of tree. No. 162 flees northeast. This is the first time I have seen No. 145 come to this section of the brush heap expressly to chase No. 162.

20 February. No. 145 comes from north of tree to the east brush heap to display to No. 162. No. 162 flattens sides and gorges throat but runs and then down into brush heap.

23 February. Last day of observations. No. 162 seen in small brush heap, No. 145 in brush heap north of tree.

At the first of the study period, No. 145 chased No. 162 from the tree and they largely ignored one another in the brush heap east of the tree, though sometimes bobbing at one another. About February 12–13 they began to display more vigorously to one another in the east brush heap and no. 145 was seen to come to the brush heap to chase or display to No. 162. At about this time No. 162, which had concentrated her activities in the small section of brush heap, began to spend more time north and east of it, chasing and fighting with the other lizards she encountered. Until observations were discontinued, however, she still visited the east brush heap section. This coincidence suggests that the increased number and intensity of disputes with No. 145 in the east brush heap was a factor in No. 162's moving into new areas that No. 145 did not visit.

I have described a variety of interactions that can occur between different individual lizards and under a variety of conditions. I would like to present some of these accounts here and describe the relationships of a single lizard to the others around him.

(11) No. 5 was a subadult male in the Mona hibiscus hedge [fig. 9], 42 mm long when first measured on 10 April and 46 mm long when last measured 8 May. Between these two dates he was seen on 24 different days and interactions recorded with eight other lizards. He used as a principal perch a hibiscus bush and frequently visited a nearby fence post and the ground around both. During the observation period no changes in his activity range were noted.

The activity range of No. 5 overlapped that of three smaller lizards and his relationship with each of these was slightly different.

(11a) No. 3, a 32 mm female, lived entirely within the area visited by No. 5. She spent most of her time on the dead leaves on the ground but frequently visited the hibiscus bush, which was No. 5's principal perch, throughout the period of observation. She usually made these visits when No. 5 was elsewhere and when he returned she sometimes fled back to the ground but more usually No. 5 chased her away, not pursuing her on the ground but merely chasing her out of the hibiscus. Several times No. 5 came to the hibiscus from somewhere else, the fence post, the ground, in order to chase No. 3 away; on other occasions when he returned for other reasons to find No. 3 there he would chase her.

No. 5 usually seemed to ignore No. 3 when she was on the ground, though once when she ran towards the hibiscus bush he chased her away before she reached it. I never saw him leave his perch to chase her except on this occasion. However, if he happened to encounter No. 3 while he was on the ground for some other reason, most frequently to catch an insect, he would frequently chase her for a short distance. Sometimes she would move out of his way under such situations without his paying any attention, and I never saw her display to him under any circumstances. The repeated chases from the hibiscus, and I recorded 15 of them, did not seem to deter No. 3 from returning to it.

(11b) No. 5's activity range also overlapped that of No. 4, a 36 mm male, who lived primarily on the ground among the dead leaves and used a dead stick as a principal perch. Like No. 3, No. 4 visited No. 5's hibiscus but did so much less frequently. No. 5 chased No. 4 on these occasions and, more frequently than with No. 3, chased No. 4 before he actually reached the bush. Both these differences between No. 3 and No. 4 may have been because No. 4 had farther to travel to reach the hibiscus than did No. 3, but it may also have been because No. 4 was larger and No. 5 more aggressive towards him. No. 5 also occasionally came from the hibiscus over to No. 4's perch and once, at least, seemed to do so in order to chase No. 4, who fled and then hid in the leaves. More frequently, when No. 5 came in this direction to catch an insect he would stop on No. 4's perch before returning to his hibiscus. Sometimes he would encounter and chase No. 4 in the process, sometimes No. 4 would move out of the way without being chased, and once No. 4 displayed at No. 5 when No. 5 neared him in the vicinity of No. 4's perch. On this last occasion No. 5 ignored No. 4 completely. Before the end of the study period, No. 4 disappeared from the study area. Whether he died or moved away I don't know and, if he moved, have no idea of the influence of No. 5's chases.

(11c) No. 7 was a 35 mm female who used as principal perches a corn plant and a fence post nearby. No. 5 also visited the fence post not infrequently but was never seen on the corn plant, so that the overlap between these two was not complete. Relatively few encounters between these two were seen and none on the fence post which they both used. No. 7 did not visit No. 5's hibiscus but we saw three chases, one of them quite persistent, which seemed to start when No. 7 approached the hibiscus. In only one of these could I see why. In this case, No. 7 was chasing a smaller lizard and the chasing carried her into No. 5's vicinity near the hibiscus. In the final chase observed No. 5 was chasing a smaller lizard and his chase brought him close to No. 7. He stopped chasing the smaller lizard and chased No. 7 for a bit.

(11d) The smallest lizard whom I saw No. 5 interact with was No. 6, a 29 mm male [not shown in fig. 9 because it appeared at a later date]. During the period when these two interactions occurred, No. 6 was living on the ground near the hibiscus and being chased frequently by No. 3 and particularly by Nos. 4 and 7. Once No. 6 approached No. 5's hibiscus and No. 5 ran towards him and dewlapped; No. 6 fled immediately. The second time, No. 5 chased No. 6 when No. 4 had chased No. 6 towards No. 5. The first of these encounters is curious because it was one of the two times when I saw No. 5 dewlap, the other was in response to a small stake-out I introduced into his area. No. 5 was not sexually mature and consequently was not dewlapping either in disputes or in advertisement display at this time and he is the smallest male I ever saw dewlap.

(11e) On either side of No. 5 lived two lizards approaching him in size: No. 15, a 40 mm male who lived in an oleander bush on one side, and No. 11, a 44 mm male, who lived in the next hibiscus on the other side. These three lizards seldom entered the activity ranges of each other and never were seen to visit each other's principal perches. Perhaps for these reasons few disputes were seen between them, none with No. 11 and only two with No. 15. In one of these, No. 15 had invaded the dead leaves near No. 3 to catch an insect, as he sometimes did, and No. 3 had displayed to him. No. 15 displayed back and No. 3 in turn displayed. At about this point No. 5 left his hibiscus and ran towards the fight. No. 15 fled back to his oleander but No. 3 remained still, No. 5 returned to his hibiscus. On the other occasion, both No. 15 and No. 5 had left their perches and run out onto the bare dirt beyond the dead leaves in order to catch an insect. This brought them close together and they displayed at one another briefly before each retreated to his own area.

(11f) In addition to these smaller and slightly larger lizards, No. 5 also came into contact with three males larger than himself. One of these, No. 14, a 48 mm male, had an activity range which did not overlap that of No. 5 but was near it. On one occasion No. 14, for some unknown reason, left his home range and visited No. 5's hibiscus, arriving when No. 5 was absent and sat there quietly. When No. 5 appeared and climbed the hibiscus, he made several series of bobs at No. 14 who ignored them. No. 5 did not attack No. 14 but after this few minutes of display ignored the motionless No. 14.

(11g) The next large lizard with which No. 5 had contact was No. 24, a 57 mm male. This male was seen off and on throughout the study period but as far as I could tell never established a permanent activity range during this time. I only saw one encounter between the two. I had tossed a grasshopper towards No. 5, who came to the ground for it. He made several attempts, chasing it across the ground and biting at it. No. 24 came towards the grasshopper, scaring No. 5 who seized it and ran back to his perch leaving No. 24 sitting on the ground.

(11h) The final lizard with which I saw No. 5 interact was No. 26, a 58 mm male, who included No. 5's hibiscus in his activity range and for part of the study period visited it quite frequently. Once No. 5 fled at No. 26's approach when they were both on the ground. Twice No. 5 left his hibiscus when No. 26 climbed it. Three times No. 26 chased No. 5 when No. 26 was sitting in No. 5's hibiscus and No. 5 climbed up into it, approaching him. In each of these cases No. 5 fled immediately. In the final interaction, No. 26 was sitting in No. 5's hibiscus and No. 5 was on the ground. No. 5 ran out to seize a large insect and started to carry it back to his hibiscus. On almost reaching it he apparently saw No. 26, for he changed course and ran part way to the fence post. Before reaching it he stopped, turned and, with the grasshopper in his mouth, step-bobbed at No. 26.

The largest male in the area, No. 13, a 60 mm adult, was not seen to pay any attention to No. 5 or No. 5 to him but No. 13 seldom visited the hibiscus.

The aggressive behavior that has been described has involved so far two *A. lineatopus;* such encounters were the commonest seen. Aggressive encounters, however, were seen between *A. lineatopus* and other species of *Anolis.*

There are a total of seven species of this genus in Jamaica, five of them occurring around Kingston. These lizards all have somewhat different structural or climatic niches (Rand, mss.) but they all overlap to a greater or lesser extent. The commonest species after *A. lineatopus* in the study areas is *A. grahami,* a green species that lives generally higher in the trees than does *A. lineatopus.*

The adult males of the two species are about the same size but rather different in shape and in color. They are quite tolerant interspecifically and frequently both species will live on the same tree. Part of the small amount of interaction is due to a difference in preferred perches but sometimes two adult males sit quietly a foot or two apart ignoring each other. Interactions are seen, usually no more prolonged or intense than the following.

(12) 5 February—Barbican brush heap. No. 1 was on south stake. A male *grahami* ran up stake, No. 1 jumped off and bobbed and dewlapped, his crests raised. The male *grahami* dewlapped and then after a moment jumped off in another direction and eventually climbed a tree.

Interactions between females and subadults of the two species were much more frequent and pursued more vigorously than between the adult males.

(13) The best example of this sort of interaction involved a female *grahami*, No. 165, and several female *lineatopus*. The *grahami* lived on the small tree in the Barbican brush heap and the female *lineatopus* frequently visited it. One of them, No. 145 (*ca.* 43 mm long) used the tree as one of her principal perches, as well as using the brush heap around it. The *grahami* repeatedly chased No. 145 off of the tree over the month of observation but seldom followed her into the brush heap and never came to the brush heap to chase her. The other two *lineatopus* females, Nos. 162 (39 mm long) and 161 (*ca.* 29 mm long) visited the tree less frequently. As has been described, the larger *lineatopus* female (No. 145) chased the smaller ones from the tree, and the *grahami* did this also, once following the smallest female, No. 161, into the brush heap and chasing her about for several minutes.

The behavior of the *grahami* to the *lineatopus* was, as far as I could see, identical to her behavior toward other *grahami* except that she did not start to chase the *lineatopus* unless they were on the tree, but once left her tree to chase a female *grahami* that was approaching it and still 4 feet away.

The interaction between the two species is reciprocal, as the following notes show.

(14) 23 January—Barbican brush heap. No. 145 chased a small *grahami*, 35 ± mm SV, making three charges at it. No. 162 at south end of log displayed to a small *grahami* which ran.

(15) 10 April—hibiscus hedge, Mona. A small female-sized *grahami* came down to the ground to drink from the rain water which had accumulated in a cup-shaped dead leaf. A *lineatopus* of about the same size which was sitting on a stick a few inches away first bobbed and then jumped at the *grahami* who fled.

Not only do *A. grahami* and *A. lineatopus* fight but the male of the latter occasionally courted the female of the former and presumably the male *A. grahami* courts the female *A. lineatopus*.

(16) 12 April—hibiscus hedge. No. 13 (60 mm male) chased a female sized *grahami* from the hibiscus next to his usual fence post to the next fence post, clearly courting it. He has also courted No. 11 (a 44 mm male *lineatopus*) twice this morning.

Though most observations were on reactions between *A. lineatopus* and *A. grahami*, I also saw reactions with *A. opalinus* and with *A. garmani*.

(17) 17 May—south of Lloyds. In the course of making movies of display I placed a male *opalinus* on a fence near another male *opalinus* and, incidentally, near a male *lineatopus* almost twice the size of the *opalinus*. Though these two lizards did not pay any attention to each other, they both reacted to the stake-out. The *opalinus* reacted first to approach and dewlap. The *lineatopus* then ran towards the two and the *opalinus*, apparently frightened by this, ran away. The *lineatopus* stopped a few inches away and dewlapped. After a few moments the *opalinus* ran back to the stake-out and both dewlapped and bit at it.

(18) 12 October—reservoir, Mona. A female *lineatopus* displayed (bobbing) to and chased a male *opalinus* slightly smaller than she was. He fled without ado. Also saw a female *garmani* and a large male *lineatopus* side by side within three inches apart and in sight of each other without any indication of conflict.

(19) 30 May—College Common. This afternoon I saw a male *lineatopus* display to a male *garmani* considerably larger than himself. Both lizards were on a two-inch branch of a poui tree about 12 feet above the ground, the adult male *lineatopus* near the trunk and the adult male *garmani* well out among the smaller branches. As I watched, the *garmani* began to move quite slowly along the branch toward the *lineatopus*. When it reached a point about 2 feet away, the *lineatopus* turned its head so that it was orienting its dewlap towards the *garmani* and began to give dewlap flashes. This display was very like, if not identical to, the initial display to another male *lineatopus*. The *garmani* stopped and then immediately jumped from the branch to another, moving at right angles to the *lineatopus*. It jumped again in the same direction and stopped when about three feet from the *lineatopus*, then bobbed.

The result of these interspecific interactions is to reduce overlap in the activity ranges of lizards of the same size regardless of species, but least so in the cases of adult males. This suggests that the significance of the aggressive behavior may be different in females and subadult males than in the adult males. This point is discussed later.

Not only do *A. lineatopus* display to and chase anoles of other species but also they sometimes display to objects that are not lizards at all. Adult males, when they became familiar with me, would sometimes respond to my approach by bobbing and dewlapping as they would to the approach of another male. This display was never carried beyond the initial reaction though, as mentioned under "Escape Behavior" (p. 16), a male held in my hand would flatten his sides and erect his crests, both of which are part of the aggressive display pattern.

The smaller *A. lineatopus* also display sometimes to objects that are not anoles, as the following note shows.

21 April—hibiscus hedge, Mona. *A. lineatopus* (40 ± mm female) was sitting on a two foot high bamboo stake about six inches from the top. A yellow-faced grassquit lit on the end of the stake. The lizard gorged its throat and flattened its sides. The bird flew away. The lizard's reaction was that typically given on the approach of a somewhat larger lizard.

Agonistic behavior: discussion.—Neither of the well-established concepts, dominance hierarchy and territory, will describe the situation in *A. lineatopus* adequately by itself, nor is there a point intermediate between them that will describe it if one considers dominance hierarchy and territoriality to be end points of a continuum as Davis (1959) suggests. It would be possible to do as Greenberg and Noble (1944) did in their paper on *A. carolinensis* and describe certain aspects of *A. lineatopus* behavior in terms of territory and others in terms of hierarchy; even this approach is not completely satisfactory. It seems to me less important to try to fit observed data into labeled pigeon-holes than to describe that data usefully.

An approach to the description of the situation in *A. lineatopus* is suggested in a paper by Allee (1950), wherein he distinguished between two types of hierarchies ("peck right" and "peck dominance") on the degree of predictability of the outcome of disputes. Extending this approach, one can consider agonistic behavior in terms of the kinds of information necessary to predict dispute outcomes. This seems to me to provide the basis of a more general system of description and analysis than does a dichotomy between territory and hierarchy.

Both territory and hierarchy can be described in these terms: territory as a system in which the outcome can be predicted on the basis of the place where the encounter occurs, and hierarchy as a system in which the outcome can be predicted on the basis of the results of previous encounters.

To my knowledge, this approach has never been developed in quite the way I am doing here, though every useful generalization about the social behavior of a species can be paraphrased as a prediction about what an individual will do under the specified conditions. Ethologists (e.g., Neil, 1964, in his study of *Telapia*) have used the predictive approach, but they have been interested largely in predicting the next action of an animal during a dispute rather than in predicting the eventual outcome. The cues the ethologists use seem largely to be evidence that indicate the internal state of the animal, which in turn determines what it will do. The cues discussed below seem to be involved in actually determining or affecting the internal states of the lizards.

From the discussion in the preceding section, two factors suggest themselves as bases for predictions in *A. lineatopus:* relative size of anole and place of encounter.

Among vertebrates generally these two characteristics, size and familiarity with the site, are undoubtedly among the most important. Probably the only factors likely to rival these are sex, breeding condition, and, in some cases, age. Brown (1963) found that, in Steller's jays, where the encounter took place was the most important factor in determining (or predicting) which of the two birds would dominate.

But this could be modified somewhat by sex, state of reproductive cycle, and state of molt.

In figure 10 the size of the winning *A. lineatopus* is plotted against the size of the losing individual in each of 182 disputes. The figure shows that, in a large majority of these, 155, the larger lizard won; thus, the outcome of 85 percent of these disputes could have been predicted correctly on the basis of the size of the lizards alone, and, where the size difference between the lizards was more than 8 mm, all outcomes could have been predicted. Those cases wherein the difference was less than 8 mm are unpredictable on this basis; this range of differences form what conveniently can be called a zone of uncertainty. (These and the following percentages of accuracy of prediction are merely suggestive. A calculation of confidence limits is mathematically possible but, as the sample was not random, is not statistically valid.)

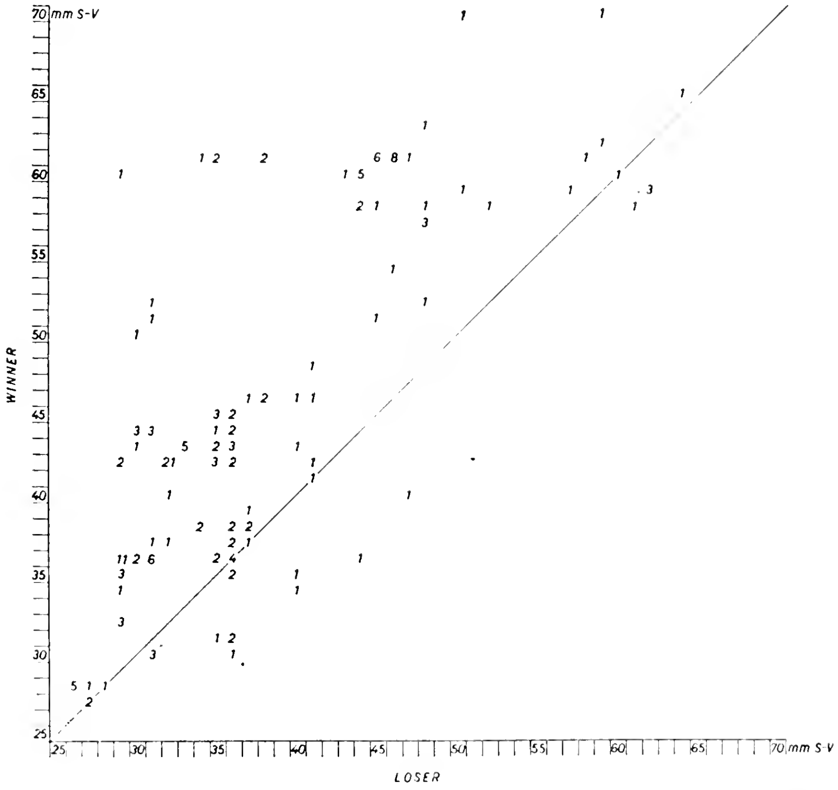

FIGURE 10.—Relationship between size and outcome of aggressive disputes between *Anolis lineatopus* (figures=number of disputes observed).

Using only the place where a dispute occurs as a basis for predicting the outcome is not as satisfactory as using relative size alone. In part, this is because the prediction is most accurate where only one lizard is resident and an appreciable number of disputes has occurred between lizards that are either both resident or neither resident and, in part, because place influenced disputes only where the difference in size was small.

Location, however, can be combined with size as basis for prediction. Because of the nonrandom nature of the sample, an increase in the percentage predictability is probably a less adequate measure of success in predicting than is a decrease in the zone of uncertainty (in mm of size difference).

Table 9 shows the effect of both size of anole and place of dispute on the outcome. It also shows that, where both were resident (table 9A), the larger always won. Where neither was resident (table 9B), the outcome is doubtful when the difference between the lizards is less than 4 mm, which reduces the zone of uncertainty to about half for these cases.

Table 9C deals with disputes in which one lizard was resident, the other not. In these, the resident lizard always won if it was larger than the nonresident, equal to it in size, or only 1 mm smaller. The zone of uncertainty now includes those disputes involving a resident 2 to 8 mm smaller than its nonresident opponent.

Considering both relative lizard sizes and location of dispute, a basis for prediction can be phrased as follows: If the difference between the lizards is greater than 8 mm, the larger will win (81 of 81 disputes); if the difference is 8 mm or less and if neither or both are resident, the larger will still win (26 of 30 disputes); if the difference is less than 8 mm and only one is resident, the resident individual will win (62 of 71 disputes). Using this set of rules, 169 of the 182 disputes (93 percent) could have been predicted successfully.

Obviously factors other than relative size and place of occurrence are influencing the outcome of disputes in the zones of uncertainty. These probably include the past experience of both individuals (including previous disputes between them) and the psychological and physiological condition of the individuals at the time of the dispute. Still, a system, such as the present, that gives a successful prediction level approaching 95 percent is a good description of the factors influencing outcome.

The nature of a dispute, i.e., the form it takes, is also strongly influenced by relative size and place. The closer in size two *A. lineatopus* are, the more likely that a real fight with physical contact will occur and the closer an *A. lineatopus* is to its usual perch, the more vigorous will be its displays. The most prolonged fights oc-

TABLE 9.—*Effect of both relative anole size and place of occurrence on the outcome of disputes* (numbers of disputes are plotted against difference in size of anoles; only those with a size difference of 8 mm or less are given)

Difference in size: Winner-Loser	A Both resident	B Neither resident	Difference in size: Resident-resident	C One resident	
				Resident wins	Nonresident wins
8	6		8	1	
7	6		7	12	
6	3	1	6	6	
5	1	2	5	6	
4			4	2	
3		2	3	4	
2			2	4	
1		5	1	4	
0			0	10	
−1		2	−1	3	
−2			−2		5
−3		2	−3	2	
−4			−4	1	1
−5			−5	3	1
−6			−6	2	1
−7			−7	1	
−8			−8	1	1

curred when an *A. lineatopus* attempted to establish an activity range within the established activity range of a slightly smaller *A. lineatopus.* The least severe conflicts occurred when a small *A. lineatopus* moved to avoid a much larger individual that was ignoring it.

This aspect of disputes is considerably more complex than outcomes, and one important source of complexity is that the adult males have a more elaborate set of aggressive displays than do the rest of the population. No system of predicting the nature of disputes can ignore this factor. The response of an *A. lineatopus* to the initial display of its opponent also affects the nature of the dispute that follows.

The conditions under which disputes occur again show a strong influence of relative size and place. The examples in the preceding section have stressed this point. Again there are complicating factors, e.g., an *A. lineatopus* is much more likely to behave aggressively toward a moving and particularly a displaying individual than toward one that is sitting quietly.

Despite these complications, the same factors that are important in predicting outcomes of disputes have important effects on the moment when a dispute will occur and on the form it will take.

Thus far, predictability of dispute outcomes has been discussed only as a useful way of describing aggressive encounters in *A. lineatopus* and of using relative size of anole and place of occurrence as useful information for predicting. Certain aspects of the behavior of these lizards suggest that the latter two topics have a more fundamental biological meaning.

I have used predictability to mean that an outside observer could foretell the outcome of a dispute. In a large majority of the aggressive encounters I have observed, the lizards behaved as if they themselves were doing the same thing, i.e., predicting the outcome of the dispute. Most disputes were very brief and consisted of one anole retreating as soon as it was threatened or attacked by another or retreating at the approach of another even though the latter showed no aggressive behavior. Disputes wherein both lizards displayed, i.e., behaved aggressively, seldom resulted in physical combat, and usually one lizard retreated without actually testing the strength of its opponent. Even in the fiercest physical combats that I observed, prolonged fights between adult males, fighting was restricted almost entirely to the ritualized jaw wrestling. I have never seen a fight that ended with one anole dead or even physically exhausted.

I am, of course, not suggesting that these lizards are consciously weighing their chances of winning an encounter. The data, however, shows that they are behaving as if they had done so. Phrased differently: A dispute may not be decided by the dispute itself but by the reactions of the individuals involved to circumstances surrounding the dispute, and these reactions may be determined before the dispute starts. Because the lizards themselves behave as if they were predicting the outcome, "predictability of dispute outcome" is more than a convenient way of describing agonistic behavior; it seems to be an important biological or psychological aspect of agonistic behavior.

Having suggested that *A. lineatopus* frequently behave as if they are predicting outcomes, it is possible to ask if they are using the same information that I have found useful. Phrased differently: Are the place where two lizards meet and their relative size important stimuli in determining their behavior in the dispute situations? I think the answer is a qualified yes. Careful experiments would be necessary to demonstrate that this is true, but the field observations certainly suggest it.

That a lizard is more likely to attack an opponent, less likely to flee, and will travel farther to attack when the opponent is in the resident's home range (and particularly when it is on the resident's usual perches) strongly suggests that place of encounter has an important effect on the aggressive behavior of the animal.

The same sort of information suggests that relative size is also important, but here an additional line of evidence is available. In the aggressive displays of these lizards, there are many elements that act to increase the apparent size of the lizard (see p. 41). These elements are developed most highly in adult males but some of the elements, like lateral orientation and flattening, occur in all sizes and in both sexes.

That selection has favored the incorporation of so many devices for increasing the apparent size of *A. lineatopus* into its aggressive displays suggests that it is to the advantage of a lizard not only to be bigger but also to appear bigger. This can only be important if the reaction of an anole to an opponent is based in part on an estimate of its size. (In other words, this sort of display can be important only if apparent size is used by the lizard to "predict" the outcome of the dispute.) Barlow (1963) has shown experimentally that certain fish discriminate between fish of their own size and of those 10 percent larger or smaller. Anoles can probably do at least as well.

In this discussion I have attempted to show that the outcomes of a high percentage of disputes in *A. lineatopus* are predictable on the basis of the relative size of the lizard and on the place of occurrence and that these two factors also influence the nature of a dispute and the conditions under which it occurs. Further, I have attempted to show that the lizards themselves behave as if they were predicting outcomes and were using the same two factors in doing so.

Adaptive Significance of Spatial Distribution

By "adaptive significance" of the spatial distribution of individual *A. lineatopus* in small areas I mean the possible selective advantages that this distribution can have for individual *A. lineatopus* and for the population as a whole. This is equivalent to "function of territory." C. R. Carpenter (1958) and Hinde (1956) have provided extensive lists of the functions of territory in various species of vertebrates. Some of these functions are clearly not applicable because they are related to parental care. The other functions, as Tinbergen (1957) has pointed out, must be divided into those that arise from the fact that individuals have definite activity ranges and those that arise from the distribution of these activity ranges in relation to one another.

One adaptive advantage of an activity range is that the individual can learn thoroughly the structure of the area. *Anolis lineatopus* frequently uses indirect pathways: an anole on a branch may run back up the branch and down the trunk to reach the ground, following a pathway that initially may take it away from its objective. The speed with which these pathways are selected suggests the lizard previously has learned the best routes. *Anolis lineatopus* males living on trees almost invariably run up when frightened; those living on fence posts run down. In each case the anole selects without hesitation the escape route that takes him most surely out of danger.

Residence in an area makes it possible for an *A. lineatopus* to become familiar with the fauna also, to learn good places to watch for insects, and to learn which of the larger animals in the area are potentially dangerous. How important the former element is I do not know, but the changes in reaction to me as a potential predator were striking. Most lizards in the study areas were quite easy to noose the first time I marked them. The next time they were much more difficult. One male became so shy that I could not catch him at all. Most males would allow approach within a few feet but, after several attempts to catch this individual, he would run when I was 30 or 40 feet away.

The effect of familiarity with an area has been reported in a number of other lizards. Fitch (1956) reports a young *Crotaphytus* that usually hid under a particular rock. When he removed the rock, the lizard ran to the same spot where the rock had been and seemed confused at the absence of the rock.

Residence in an area also provides an *A. lineatopus* with the opportunity to learn to recognize other lizards as individuals. Evidence that they do this has been discussed. This familiarity with other individuals over long periods provides the opportunity for pair formation and may reduce the severity if not the frequency of agonistic encounters.

Beyond the advantages arising from the existence of activity ranges, there are a number of advantages that arise from the distribution of these activity ranges with respect to one another (Tinbergen, 1957).

The first of the two patterns in distribution of activity ranges, the overlapping between adult males and adult females, has an obvious advantage in mating. It helps to insure that there is a mate available for a receptive female and it enables the male to find mates without leaving the area with which he is familiar. It may also facilitate mating by allowing the individuals to become familiar with each other and so produce some sort of pair bond.

Interpretation of the adaptive significance of the second pattern, the minimal overlap between the activity ranges of *A. lineatopus* of the same size and the gradual increase in overlap as the difference in size between individuals becomes greater, is more difficult.

There are, I think, three major effects of this pattern. Two are closely interrelated and affect the whole population: the distribution of the population with respect to available food and the control of population density in favorable situations. The third, the distribution of the adult males with respect to potential mates, affects the adult males most directly.

Considering first the lizard's relation to food supply, we have already seen that *A. lineatopus* feeds largely within its home range and largely on insects it sees from its principal perches. I have also shown that there is a tendency for different sized *A. lineatopus* to eat different sized food. The spacing out in an area of individuals of the same size means that there are fewer times when two *A. lineatopus* attempt to catch the same insect and consequently compete directly for food. Also, since the lizards' activity ranges are nonoverlapping, the lizards cover the maximum area possible and a particular insect is most likely to land in the feeding area of one of them. The overlapping of feeding areas of *A. lineatopus* of different sizes means that a greater size range of the insects within an area are potential food to the *A. lineatopus* living there. Thus, both the spacing out of individuals of the same size and the overlap of those of different sizes increases the probability that a given insect will be eaten by an *A. lineatopus* wherever the insect lands.

From this discussion it appears quite possible that one of the important ecological results of the social organization of *A. lineatopus* is in the decreasing of intraspecific competition for food and the increasing of the efficiency with which the available food supply is exploited.

It has been suggested that territorial behavior (which is frequently so defined as to include the social system described herein) has an important function in regulating density in favored areas. In *A. lineatopus* there is a lower limit set by the structure of the environment below which activity ranges cannot be compressed, i.e., the number of available perches. Particularly with adult males, but even with smaller individuals, most perches are indivisible; they are occupied by only one *A. lineatopus* of a particular size. In areas where the only perches are scattered trees or fence posts, the social behavior interacts with the structure of the environment to limit population density. If there were more trees or fence posts, there could be more *A. lineatopus.* But, if *A. lineatopus* peacefully shared perches, there could be more of these lizards in the same number of trees.

In more complex structural habitats, the situation is not so clear. The general constancy of home range size in several rather different places suggests that there is a size limit below which home ranges cannot be compressed. This in turn suggests that even in complex environments, social organization may act as a means of limiting population density. There is another element in the structure of the environment other than available perches that may affect density and this is visibility. In very dense vegetation it might be possible for two *A. lineatopus* to have overlapping home ranges and seldom meet. I do not think this is of great importance, for most home ranges have perches from which much of the area can be seen and it is on these that the lizards spend most of their time. But the presence of a large male in a brush heap for several days, even though he was repeatedly chased by the resident males, suggests that overlapping home ranges are at least temporarily possible. The importance of visibility was emphasized for *A. sagrei* on Bimini by Oliver (1948), who reported that the territories became larger and that less overlap was tolerated when a hurricane increased visibility by defoliating the habitat.

Agonistic behavior of the sort shown by *A. lineatopus* can regulate density only by forcing individuals to move away, since fights to the death are rare, if in fact they ever occur. Subadult, young adult males, and young females do move considerable distances and may settle, at least for short periods, in previously unoccupied areas (p. 29 et seq.). Further, a number of these young males were found to be living in areas that for one reason or another seemed to be subpreferable for the species. It seems likely that they had been forced to move by aggressive behavior on the part of other lizards and forced to settle in unoccupied places because the preferable ones were already occupied.

The evidence suggests that the social organization in *A. lineatopus* tends to set an upper limit to the population density in a particular structural environment and to force the excess lizards, particularly young males and, to a lesser extent, young females, to disperse.

How far these *A. lineatopus* travel during dispersal we have no idea; consequently, it is impossible to judge the importance of social organization in promoting panmixis in the population or in extending the distribution of the species. Certainly that there is dispersal at all reduces the amount of close inbreeding. That the dispersal may take lizards into previously uninhabited areas indicates that it plays some part in extending the distribution of the population.

It has also been suggested that the spacing out of individuals in an area may act to reduce both predation and disease. Both of these are possible but seem unlikely in *A. lineatopus*. In spacing out individuals it is possible that fewer are found by predators, but *A. lineatopus* are most conspicuous when they are displaying and fighting. The increased conspicuousness to a predator must at least partially offset any advantages gained by over-dispersion.

We know almost nothing about disease in lizards but it is possible that the spatial isolation that the social behavior produces may act to reduce the spread of infectious diseases. Two facts, however, argue against its importance. First, only individuals of about the same size are overdispersed and diseases that are restricted to particular sizes within the species must be uncommon. Second, although lizards may be spatially isolated during the day, they frequently sleep in the same places, so that, even if the spread of disease is reduced during the day, it would not be reduced at night.

The final area in this discussion of adaptive significance involves adult males. I have stressed that, while all sizes and both sexes are aggressive, the adult males are more aggressive than any other individuals. The males travel greater distances to attack intruders than do other *A. lineatopus;* they are more persistent in their attacks and they fight more frequently and more fiercely. They have structural modifications, nuchal and dorsal crests, used exclusively in agonistic behavior, that are lacking in females and young.

This sort of difference in behavior is known in other iguanid lizards. In some, the males have larger home ranges from which they exclude other males even though, unlike the *Anolis*, the males are smaller than the females (Blair, 1960). In other species, only the males are aggressive at all (Blair, 1960). In *A. carolinensis,* males defend their home ranges most aggressively during the well-marked breeding season (Greenberg and Noble, 1944).

Finally, in *A. lineatopus* adult males are less tolerant of individuals of their own species and size than are the females and juveniles, but they are more tolerant of males of other species.

I think the general occurrence of aggressive behavior and the spacing out it produces in all sizes of *A. lineatopus* can be explained by the ecological advantages that have been discussed in the foregoing discussion, but the greater aggressiveness of the adult males requires additional explanation. I think the explanation lies in a function of territory discussed at length by Tinbergen (1957), which demonstrates the selective advantage that is conferred on an adult male if he can insure himself exclusive mating rights to certain females by keeping other males away from them. If he can do this for a single female, he insures that he will father at least some offspring, and the more females he can keep isolated, the more offspring he will have and the greater his contribution to the gene pool of the next generation. This being true, there must be a strong selection pressure for any mechanism that will insure a male exclusive mating rights to one or more females. The aggressive behavior of adult male *A. lineatopus* that keeps other males out of the area in which females are permanently living is just such a mechanism. I think that the selective advantage to the individual male of having exclusive mating rights accounts for the greater aggressiveness in the adult males of this species, while the other ecological advantages to the population as a whole of spacing individuals of the same size accounts for the existence of aggressiveness in all of the individuals of the species.

The Life of a Lizard

In this section I want to describe what probably happens to a lizard throughout its life history in general terms of its social relations and its spatial distribution in a densely populated area. There are many gaps in my information that I must bridge with hypotheses. Some of the imagery may be wrong but it is the best I can do to demonstrate as vividly as possible some of the gaps in our knowledge.

A lizard hatches from an egg buried under a log, the edge of a rock, or in leaf litter and soon settles into a home range; how far it wanders before doing so we do not know. The initial activity range differs from those of the adults. The former is smaller, and the hatchling avoids large perches and is not attracted by the presence of an individual of the other sex. The avoidance of large diameter perches is adaptive since these are frequently occupied by adult males that eat hatchlings when the adults can catch them.

These hatchlings are aggressive and soon space themselves out so that their home ranges do not overlap, though the home range of a young lizard may be overlapped by those of several larger lizards. As the young lizard grows, it enlarges its home range. At the same time, there seems to be a shift in perch preference with the result that the growing lizard begins to visit the usual perches of the larger individuals.

Initially, the young lizard is generally ignored by the larger neighbors and avoids them. But as it grows larger and begins to visit their perches, they begin to chase it, both when it visits one of their perches and when they encounter it elsewhere. At first the young lizard tolerates this behavior and flees the larger individual without changing its activity range. Such a situation may last for several weeks and perhaps several months. During this period the same lizard also is chasing from its own activity range others smaller than itself, and it may expand its activity range at the expense of another by chasing it away. The young lizard also may be forced to move by another slightly larger lizard's moving into its area; I believe this action produces some of the long distance shifts recorded for juveniles.

Even if another juvenile does not displace it, this lizard's continued growth soon brings it into more serious conflict with the adults whose activity ranges overlap its own—first, with adult females since they are smaller than adult males. The decreasing difference in size between the adult female resident and the more rapidly growing juvenile seems to produce serious conflicts for two reasons. First, the female becomes less tolerant and begins to chase the young lizard, not only from her preferred perch but in other parts of the home range. Second, the young lizard begins to become aggressive towards the adult and to display back and attempt to chase her. This is probably a gradual change but eventually the young lizard must either defeat the adult and chase her away or—much more likely since the young one is as yet smaller than the adult—be defeated and move. This change seems to occur as the young females are approaching sexual maturity but while the young males are still immature. As either sex approaches adult female size, they begin to attract the attention of the adult male, no longer as food but now as potential mates, and he begins courtship chasing. For the maturing females this probably has no effect on their home range, but for the young males this may be a factor in forcing them to move.

When an *A. lineatopus* of this size moves, it may travel considerable distances, at least 50 to 80 feet and probably more. During this time it must continually come into conflict with other *A. lineatopus* of about its size, and probably it is chased repeatedly from the suitable activity ranges that it visits. These *A. lineatopus* sometimes settle in places that are unoccupied because they are subpreferable, and we find young males living in unusual activity ranges, up in trees, on very small isolated perches, etc.

Because there is a continual mortality among the adults, however, desirable activity ranges are always becoming vacant. If a young male *A. lineatopus* is fortunate enough for this to happen to the female whose home range overlaps his own, then he may not be forced to move at all. But probably and more frequently, he must travel and perhaps visit a number of suitable sites before he finds one from which he either can oust the resident or which he can occupy unchallenged. Probably another frequent occurrence is for a lizard to move into an area that lies on the boundaries of two residents and establish himself in an activity range that includes part of two other activity ranges. Such a course involves defeating both residents but only in parts of their activity range that they do not use frequently and, consequently, do not defend as vigorously as they would their preferred perches.

For an adult female, this is probably her last move. If her new activity range overlaps that of an adult male and contains the requisites in food, temperature, and cover, she probably will remain there the rest of her life, mating with the male, perhaps leaving the area to lay her eggs if no suitable laying site is immediately available, perhaps shifting the boundaries or moving either temporarily or permanently to an adjacent area, but making no further major moves. She will defend the area against intruders of her own size, at first tolerating young lizards and then, as they grow—whether they are her own offspring or not—gradually driving them out.

The problems of a male the size of an adult female are not solved even when he finds a suitable activity range. As he continues to grow, his activity range requirements change; he now prefers a larger perch. He has grown big enough so that no female can chase him from his established area, but he is also growing big enough to challenge the adult male whose activity range may overlap his. Again two things seem involved in the increasing conflict. The large male's interest in him changes from courtship chases to more vigorous aggressive attacks, and he himself becomes more aggressive toward the big male. Though the big male may die or the younger may defeat him and so remain and enlarge his area, it is more likely that the young male will be driven out. The younger male is now adult though small. With the activity range requirements of an adult male, he finds that usually the best, most preferable home ranges are already occupied by larger adult males that will not tolerate him on any of their perches. Again he may have to travel considerable distances, establishing himself temporarily in undesirable sites, perhaps staying within the activity range of a large adult but avoiding him by staying hidden, probably moving several times before he finally finds a suitable place where he can establish; and he, like the female, settles here more or less permanently, making minor boundary changes or occasional shifts to adjacent areas or forays to nearby perches. But he is now an established resident who will court all the female-sized lizards, mate with receptive females, eat the hatchlings, including his own children, if he can catch them, and drive out any intruding adult male.

Daily Routine

In previous sections I have discussed by topic various aspects of the ecology and behavior of *A. lineatopus*. To bring these aspects together and present a picture of the daily routine, this section describes the behavior of a single adult male that I and another observer, working in shifts, kept under surveillance for one full day. We watched him from before sunrise until after sunset and lost sight of him only for two 10-minute periods, though he was out of sight for a few seconds a number of times. During the day, we saw him catch and eat food twice, copulate twice, drive another male from his home range, and dispute with a nearby male over the common boundary of their home ranges.

This male, no. 1, was a marked individual (60 mm S–V) that we had kept under observation for several months. He had a home range (fig. 3) which included a small tree about 20 feet tall that branched at the ground into six trunks, each about three inches in diameter. It also included part of an adjacent brush heap and a small log and three nearby fence posts.

We started observations at 6:05 a.m., when it was just light enough to make notes. The nocturnal frogs were still calling but the cocks had started to crow and mockingbirds were singing. It was still cool (19° C at 6:15). I could see no anoles yet, though I knew from previous nights that many were asleep in the small tree, stretched out along the twigs or leaves near the ends of branches.

At 6:17 a.m. I located the first *A. lineatopus*, an adult male, still in his sleeping position on top of a leaf at the end of a branch but already awake with his eyes open. It was light now and, three minutes later, he left his sleeping site for the inner branches of the tree. During the next 20 minutes, there was considerable movement in the tree as anoles moved about and departed for the adjacent brush heap. The individual we had decided to observe, no. 1, appeared at 6:22 a.m., moving down one of the tree trunks and then across to the brush heap. After about 10 minutes he moved down into the brush heap so that he was almost completely concealed by the tangle of branches above him. He ignored the other anoles moving about him, including a large male that came down the tree and jumped into the brush heap.

By 7:00 a.m. both tree and brush heap were quiet again and none of the *A. lineatopus* were sitting up on the perches where we usually saw them during the day. They had all left their exposed sleeping sites for more concealed spots, where they were waiting quietly.

The sun rose and at 7:16 a.m. its rays struck the brush heap, but no. 1 was still in the shade. He waited only a minute and a half before moving out into the sun and, three minutes later, climbed up onto the surface of the brush heap to sit in partial sunlight for a few moments before moving toward the tree and into full sunlight. About the same time other *A. lineatopus* also began to move, and the area that had appeared empty moments before was now full of anoles basking in the sun. Two large males began displaying to each other across the boundary of their home ranges in the brush heap. Though they continued this for about 20 minutes and were less than five feet from no. 1, they were outside of his home range and he ignored them.

By 8:00 a.m. it had warmed up considerably (24° C at 8:10 a.m.) and no. 1 was moving about frequently and displaying, both dewlapping and bobbing. Though I saw him bob once shortly after he first appeared (6:23 a.m.), he did not display again for over an hour and did not begin displaying frequently until he had been sitting in the sun for some minutes.

About 8:30 a.m. no. 1 dashed for the tree, ran up and, with pauses for display, ran out toward the end of one of the higher branches. He dashed around among the foliage for a confusing few moments and then another male jumped from the tree into the brush heap and disappeared. No. 1 did not follow but moved to one of the larger branches and displayed. The other male had probably slept in the tree and had been late in leaving it. No. 1 finally had seen him and chased him out. During the chase, no. 1 seemed to be trying to get above the other male and to drive him down from the tree.

Now fully active, no. 1 spent most of the rest of the day in the tree (a total for the whole day of 7 hours and 55 minutes) though he visited the brush heap three more times (a total of 3 hours and 30 minutes) and made one sortie to a small log near the base of the tree, spending 11 minutes on it and the ground nearby. One small branch of the tree seemed particularly attractive and he visited it eight times, spending 3 hours and 48 minutes there. This branch was about five feet above the ground and from it he could overlook his entire home range; he had used this same perch day after day. He spent another hour and 57 minutes on other parts of the trunk from which this small branch grew, 1 hour and 47 minutes on a second trunk, 10 and 7 minutes respectively on two more trunks, and 16 minutes in the crown foliage. Two trunks he did not visit at all.

The next few hours were routine. No. 1 sat on one perch for a while and then shifted to another to sit there, moving then either to a new perch or back to the first. Though he did nothing I could interpret as searching, he seemed always to be watching his surroundings alertly. Even when on the same perch he made frequent small shifts in position, up, down, or around the perch, and with even more frequent head and eye movements.

One of the things for which no. 1 apparently was watching was food. During the day we saw him catch only two items. In both cases he ran down the trunk of the tree from his perch and picked up something small from the bark and swallowed it. He may have made more captures during the few periods when he was out of sight but, if so, they must have been few and small because large prey is conspicuously chewed before being swallowed.

Most shifts in position were followed by some sort of display, either bobbing or dewlap flashing. During the day there were only eight periods of 10 or more minutes without display, the longest being about 20 minutes.

Most displays did not seem to be directed at anything in particular and probably served to advertise his presence to any potential intruder or prospective mate, though the bobbing also may have a function in improving his depth perception.

Though most of the observed display did not seem to be directed at any particular lizard, several times we saw him unsuccessfully court a female, chasing her and displaying to her.

No. 1's activity reached its highest peak in the earlier part of the morning, perhaps because he was moving frequently to take advantage of patches of sunlight and shadow to thermoregulate. During the heat of the day all the *A. lineatopus* were less active than they had been in the morning, and they spent longer periods sitting in the same places in the shade avoiding both the direct sun and the perches that had been warmed by the sun. Later in the afternoon, they all again became more active but perhaps not as active as they had been in the morning.

It was midafternoon before no. 1's routine of waiting and watching was markedly interrupted. At 3:48 p.m. he mated with a female that also used the tree as one of her perches. He moved around the tree trunk and came upon her as she rested head downward. He moved up along side of her and attempted to seize the skin on the back of her neck with the tips of his jaws; she moved her head from side to side as if avoiding this but did not run. Shortly after he secured the grip and twisted his tail under hers to bring their cloacas into contact. They copulated for about three minutes and then separated. As usual the successful courtship was casual and with little display.

No. 1 returned to his usual routine until 5:00 p.m., when he moved to the brush heap to display vigorously to another large male that had moved to a stake on the boundary between their home ranges. The resulting dispute lasted about 20 minutes; both lizards dewlapped, oriented laterally, and bobbed at each other. Eventually both retreated, leaving the stake unoccupied. Several days later, no. 1 was able to expand his home range to include this stake but only after a prolonged dispute with the other male. (Details of this dispute are given on p. 48.)

Soon after this dispute the sun set at 5:44 p.m. and shortly afterward no. 1 climbed up the tree into the higher branches. He moved out onto the smaller branches and appeared to be selecting a sleeping site.

Suddenly he came back to one of the main trunks and bobbed at a small unmarked adult female and ran toward her. She jumped to a branch, he followed and seized her by the skin on the neck and walked with her a few steps. They then copulated for two and a half minutes and separated.

No. 1 displayed and then moments later climbed out among the small branches and foliage. At 6:11 p.m. he was stretched out on a very small branch about 10 feet above the ground, apparently ready to go to sleep. It was already quite dark and by 6:13 it was too dark to see him or to make notes.

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An Enzyme Method Of Clearing and Staining Small Vertebrates

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Introduction

Cleared (transparent) and stained specimens are used widely for osteological studies of vertebrates. Many such specimens have been prepared by the Schultze method (Schultze, 1897) or modifications of that method (Davis and Gore, 1947; Evans, 1948; Hollister, 1934; Jensh and Brent, 1966). The Schultze method and its modifications chiefly involve tissue maceration in solutions of potassium hydroxide or sodium hydroxide, staining the bones to give them maximum visibility, and immersion of the specimen in a liquid with an index of refraction similar to that of the cleared tissues.

The method is successful when it is used on fresh or newly preserved specimens, but numerous workers have encountered considerable difficulty in producing good transparent specimens by the above methods after specimens have been stored in various preservatives for several years. Such specimens may remain opaque because of dark stains in the flesh or they may swell and the membranes rupture during the clearing process.

The new method described in this paper substitutes enzyme digestion for the alkaline maceration. It offers several advantages, including ease of clearing the old material. Other methods such as cleaning by dermestid beetles or flesh maceration by boiling are usually not desirable in the preparation of skeletons from small, delicate specimens because the bones may be lost, damaged, or distorted.

Purified trypsin powder was first tested, in distilled water with a trace of potassium hydroxide, on formalin-fixed specimens that had been stored for several years in ethyl alcohol. These tests were slow in producing transparent specimens. The odors given off from the solutions were very disagreeable but the results indicated that enzymes should be explored.

Because the initial preparations remained in good condition during two years in glycerin, tests of various enzyme-buffer solutions were undertaken. Of these, the sodium borate (borax) solution was found to be superior. It supports the most rapid enzyme activity while maintaining a relatively stable and desirable pH over a long period of time, and it inhibits bacterial growth that results in disagreeable odors.

Due to the great variation in specimens and in their preservation, results are not always predictable. The enzyme method generally produces good transparent study specimens from individuals that have been properly preserved and cared for prior to enzyme treatment, except where thick or dense connective tissue is present as in some small species and most large specimens. The enzymes are less harmful to specimens than strong alkalis because the digestion removes muscle tissue and stains and permits slight collapse of membranes over the evacuated areas rather than extensive swelling with its splitting and distortion or disintegration of tissue. Specimens will fall apart occasionally or disintegrate during enzyme digestion as well as in caustic potash solutions. This appears to result from faulty preservation that permitted prior connective tissue alteration or digestion. These specimens are more likely to be usable following digestion than following caustic treatment because the former frees the specimen of bulky and weighty materials that cause damage when it is moved.

I have used the enzyme method successfully to clear several hundred specimens of fishes of more than 100 species, belonging to 40 families, and also several specimens of amphibians, reptiles, and mammals. The method has been of value in restoring glycerin specimens of fishes that had been treated previously with potassium hydroxide. The enzyme method would thus appear to be useful as a means of clearing small specimens of all vertebrates.

I have not tested proteolytic enzymes other than those of pancreatic origin. Their maximum activity is usually at a pH below 7.5 or in strong acids, which may be damaging to skeletal tissue. The pancreatic extracts are inexpensive, breaking down denatured proteins, especially those of muscles, and work best in a favorable, slightly alkaline medium.

There are few published accounts on the use of enzymes in the preparation of osteological material. Moser (1906: summarized in Piechocki, 1961, p. 285) recommended a solution of potassium carbonate and trypsin powder for clearing embryos. The method has remained relatively unknown. In my tests, clearing was slow, solutions rapidly became acid, and there was loss of bone minerals. Piechocki (1961, p. 228) summarized reported uses of papain, pepsin, and trypsin for cleaning flesh from skeletons. The papain and pepsin methods involve the use of acids and were not tested because of probable damage to bones. The trypsin methods include the use of sodium sulphide and higher temperatures than I have employed. My results indicate that sodium sulphide-enzyme solutions have less advantage than borax-enzyme solutions for both clearing and defleshing preserved specimens. Some damage to specimens occurred from rapid pH drop to acid conditions. True (1948) described a slightly acidified pepsin solution for removal of fats and proteins before staining.

I made frequent checks on the pH of all solutions during the process of working out the method. The readings were obtained from a Beckman pH meter, Model G, calibrated at pH 7.0 by use of the "Fisher Standard Buffer Solution" specified as pH 7.00±0.02 at 25°C (monopotassium phosphate-sodium hydroxide buffer, 0.05 Molar). In comparative tests, specimens of one species with presumed identical preservation were used, and specimens of equal sizes were selected insofar as possible. They were placed in solutions of equal volume with similar enzyme content. All reactions were at room temperature, which varied from 22°C to 27°C.

I am especially appreciative for the laboratory assistance of Kenneth Karb, Phyllis Herrington, and Fanny Phillips, and the encouragement received from the staff of the Fish Division in the development of the process.

Materials Required

1. Alizarin red S powder. This material should be one of those certified by the Biological Stain Commission as satisfactory for staining bone. A few grams will be sufficient for several years use in most work.

2. Potassium hydroxide (KOH), U.S.P. grade. The pellet form is the most satisfactory in rapid preparation of solutions.

3. Distilled water.

4. Hydrogen peroxide (H_2O_2), U.S.P. grade. A 3 percent solution keeps better than stronger solutions and has been found satisfactory.

5. Borax or sodium borate powder (sodium tetraborate, $Na_2B_4O_7 \cdot 10H_2O$), U.S.P. grade or better is preferred.

6. White glycerin, U.S.P. grade or better is preferred. The liquid should be obtained and stored in glass containers as it becomes colored in contact with metal.

7. Trypsin powder (purified).[1] This material may be sold also as pancreatic protease and pancreatin. It typically contains a wide variety of enzymes as well as trypsin. The commercial preparation must be free of collagenase contamination and must have been purified to the extent that it is free or nearly free of elastase. One method of effective removal of elastase from pig pancreas preparations that resulted in a good yield of trypsin and chymotrypsin was described by Kunitz and Northrop (1936); see also Baló and Banga (1950). Highly purified and concentrated trypsin preparations are expensive and unnecessary. Extensive purification may reduce or eliminate desirable enzymes that are produced by the pancreas, particularly the chymotrypsins and the wide variety of other proteases as well as lipolytic and diastatic enzymes. The enzyme potency is often expressed as a ratio. The figure 1:80 usually means that one part will digest 80 parts casein when measured by the specified pancreatin test. Other specifications may include the activity of individual enzymes expressed as units per gram.

The dry powder is stable and may be stored at room temperature for a considerable length of time. To insure stability and to reduce possible bacterial multiplication, however, I suggest keeping it in a tightly closed container under refrigeration. One hundred grams is sufficient to clear nearly 100 small specimens, if they are properly prepared.

8. Thymol, N.F. crystals ($C_{10}H_{14}O$).

9. Concentrated formaldehyde solution, about 40 percent by volume, U.S.P.

10. Ethyl alcohol (ethanol), 95 percent, U.S.P. (optional; used in step 10 of "Method" section). Absolute (100 percent) ethyl alcohol is desirable.

11. Xylene (xylol) (optional; used in step 10 of "Method" section).

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[1] I have made extensive use of Fisher Scientific Company's "Purified Trypsin Powder" (1:80 N.F.), Catalog Number T-360. Similarly good results have been obtained from Difco Laboratories' "Trypsin, Difco Certified" (1:250 N.F.), Code Number 0152.

Preparing Stock Solutions

1. Saturate distilled water with sodium borate powder. Mix thoroughly and allow to settle until supernatant is clear. A large volume of the solution can be mixed well in advance and used as needed. When preparing a new supply, break the caked borax at the bottom of the container and add sufficient new powder to insure saturation.

2. Prepare a solution of one-half to one percent potassium hydroxide in distilled water.

3. Prepare the enzyme buffer solution by mixing three parts of the clear upper liquid from the saturated sodium borate solution (1) with seven parts distilled water if the temperature of the saturated borate solution is in the range of 22° to 27°C (about room temperature). This concentration (30 percent saturated borax solution) is estimated to be approximately 0.9 to 1.0 gram sodium borate per 100 ml. of the solution at 25°C.

If bacterial contamination takes place in the clearing process at this strength and the original borate solution (1) is fully saturated, the amount of saturated borax may be increased slightly in new solutions. The solubility of borax in water varies materially with the temperature. The following quantities of saturated borate should be used in preparing enzyme buffer solutions when the saturated solution is at the temperature indicated, based on the saturation rate ("Handbook of Chemistry and Physics").—10°C: use 6½ to 7 parts saturated borate solution and 3 to 3½ parts distilled water for 10 of solution; 15°C: 5 to 5½ parts borate; 20°C: 3½ to 4 parts borate; 30°C: 2½ parts; 35°C: 2 parts; 40°C: 1 part borate in 6 of solution; 45°C: 1 part borate in 8 of solution.

4. Mix the following solutions of glycerin and potassium hydroxide solution (2) or distilled water:
   a. 40 percent glycerin and 60 percent potassium hydroxide.
   b. 70 percent glycerin and 30 percent potassium hydroxide.

The Method

In the following step-by-step process it is necessary to avoid contamination of specimens and materials in order to curtail undesirable organic growth in the solutions. Do not expose specimens to high temperatures. A maximum of 30°C is recommended for most fishes. Slightly higher temperatures should not damage warmblooded vertebrates and those that have lived in a hot environment.

1. Kill specimens in 10 percent formalin (about 4 percent formaldehyde) and leave in this solution for one week to 10 days. This fixing solution consists of one part by volume of concentrated formal-

dehyde solution plus nine parts water and specimens. Buffer in about one day by adding one-half teaspoon of borax powder per quart of solution. Open the abdominal cavity and the gut to expose them to the preservative. Such structures as fur and feathers, which may be difficult to remove later, should be removed at this time. The viscera, most scales, and many other undesired parts preferably are removed after staining to prevent loss of small bony structures.

The best preservation results from killing the animal in the fixing solution. Dead but unpreserved animals should be fixed without delay. Whether they will yield satisfactory specimens depends upon the length of time they have been dead and upon their prior treatment. Short delays, even of less than an hour after death, and exposure to high temperature before fixation may result in specimen contamination, decomposition, and noticable connective tissue breakdown. The destruction of tissues continues slowly when the specimen is under refrigeration and, to some extent, when the specimen is frozen, although some specimens that were frozen for several days have turned out satisfactorily without preservation.

Small specimens that have died immediately prior to the enzyme treatment sometimes result in good preparations without preservation, but fixation is more reliable. If they are not fixed, they should be eviscerated and subjected to the clearing process, beginning with step 3 without delay.

Specimens stored in isopropyl or ethyl alcohol require no further preliminary preparation. Those that were initially fixed in alcohol or that exhibited spoilage before formaldehyde fixation may disintegrate in digestion. Specimens damaged, twisted, or distorted when fixed become good cleared examples that often are not distinguishable from those that were preserved in a more normal position; they usually are chosen for clearing in order to retain the better specimens for other purposes.

2. Pour off formalin or any preserving solution containing the odor of formaldehyde and soak the specimen in repeated changes of water until the formaldehyde is removed. Formaldehyde as well as some metals and some apparent formaldehyde derivatives that are not soluble in water or alcohol inhibit the enzyme reaction (see further comments in step 6). If the specimen is not to be cleared immediately, it should be stored in a 70 percent solution of ethyl alcohol.

3. Bleach the specimen in a solution of 10 to 20 percent stock hydrogen peroxide and 80 to 90 percent stock potassium hydroxide. Because the reaction is enhanced by light, it may be placed in a transparent container over a light box or beneath a lamp. Body cavities containing heavily pigmented membranes should be opened

and their organs loosened or spread to allow access of the bleaching solution.

Bleaching at this time is important. If done later, the evacuated body cavities tend to become filled with bubbles. Remove bubbles, if possible, following bleaching. A small vacuum pump is useful for this purpose. If the bubbles cannot be removed, they will slow the clearing, but they will disappear in a closed actively digesting enzyme solution in a few days.

The enzymes do not extensively remove color pigment (chromatophores and guanin) from specimens, but dark pigment is noted to flow out and materially darken digestion solutions subsequent to partial bleaching. Complete dissolving of the pigment from a specimen, thus, may not be necessary. Bleaching is continued until all dark areas have become decidedly pale, the time varying from about half an hour for poorly pigmented specimens to several hours for specimens with thick layers of pigment (e.g., atherinid fishes).

4. Place the specimen in a buffer solution, adequate to cover it, of volume 10 to 40 times that of the specimen. If the specimen has been in glycerin, use the methods described in the section "Glycerin Specimens" (p. 10).

Large reservoirs of liquid, other than enzyme buffer solution, which are in the evacuated body cavities of a partially digested specimen, should be diluted by placing the specimen in a borax solution for several hours prior to placing it in the enzyme buffer solution. Excess water will dilute the buffer solution; hydroxides, isopropyl alcohol, and ethyl alcohol will tend to elevate the pH of the solution above the optimum. Traces of these liquids that may cling to the outside of a specimen can be ignored.

Excessive volume of the buffer solution will dilute and slow enzyme activity. Insufficient volume will permit a rapid pH drop and resist diffusion of digestion products from the specimen. The adequate volume of buffer solution to use appears to be 10 to 40 times the volume of the specimen. A minimum of 200 ml. of the solution has been found satisfactory for very small specimens.

Several specimens, if properly fixed, may be placed together in one solution for clearing.

Glass and plastic containers both have been used for the process with good results. Containers that can be sealed are preferred as they tend to limit bacterial contamination, permitting longer use of a solution.

5. Add the enzyme (trypsin powder). One-fourth of a teaspoon (about 0.45 grams) of enzyme is adequate for most specimens weighing up to 1 or 2 ounces and requiring 400 ml. of liquid or less for immersion. Larger specimens may require more enzyme. Tiny specimens may

be cleared with materially less enzyme, but it is desirable to reduce the volume of buffer solution if a very small amount of enzyme is used. Mix well but do not froth, close the container, and set the solution aside at 20°C to 30°C (most room temperatures are satisfactory) to clear the specimen. Higher temperatures for digestive activity are not recommended as they invite increased bacterial activity and may denature connective tissue in lower vertebrates.

Enzymes lose potency in the solution and should be added only at the time they are to be used.

6. Leave the specimen in digestion until one-tenth to one-fourth of the muscle tissue remains. Change the digestion solution every week to 10 days. If specimen has been in glycerin, the first digestion solution must be changed in four or five days; the second and subsequent solutions may be retained for a week to 10 days.

The digestion solution may be cloudy (due to some enzyme preparations) or clear, and it tends to remain so unless coagulated or precipitated by some extraneous materials. It will darken gradually with release of stains and pigment from the specimen. Clearing of the specimen will first be noted along the edges of the body and in the thinner portions such as the abdominal wall, the caudal peduncle, and the limbs. The specimen will lose rigidity, becoming very flexible as digestion proceeds. Some small specimens can be cleared adequately in one or two days; larger specimens and those containing enzyme inhibitors may require weeks or months in the solution to become sufficiently cleared.

Although a solution may remain active for several weeks, the maximum activity appears to decline after a week to 10 days. As a general rule, a solution should be discarded before it has been used two weeks to avoid bacterial growth and excessive pH drop.

The odor of the solution will initially be similar to that of trypsin powder. Gradually, inoffensive odors due to the digestion may become evident. Specimens that have been stored in such materials as oil of cloves, isopropyl alcohol, and thymol, even though washed to remove these materials, may impart their strong odors to the solution. Growth of bacteria may result in very offensive odors of putrefaction from the solution, in which case the solution should be discarded. The specimen is then cleaned by placing it in 70 percent ethyl alcohol or stock potassium hydroxide solution for a short time and, beginning with step 4, is returned to a new digestion solution in a clean container. If the odor of putrefaction is again produced, the process must be repeated but an increase in the amount of saturated borax solution is suggested (stock solution 3).

When the specimen is nearly transparent—having lost three-fourths or more of its dark muscle tissue and retaining only a few small areas of yellow or brown muscle tissue as remnants of larger or thicker muscle masses—it should be stained (step 7).

Specimens may not clear or may clear slowly because of enzyme inhibitors. Common indicators of inhibition are a musty odor, due to formaldehyde, or extensive bottom precipitate with the tendency of a cloudy solution to become clear. A bath in stock potassium hydroxide solution for one or two days is suggested to aid in removing the inhibitor. This is followed by repeating the digestion process, beginning with step 4. The purpose of the potassium hydroxide treatment is to remove water and alcohol-insoluble enzyme inhibitors. Alternation of potassium hydroxide and digestion treatments may be repeated until the specimen becomes adequately clear, processes that may require several weeks or months to complete.

Some specimens, typically large individuals but also some small ones, have thick connective tissue and remain opaque even in liquids with a high refractive index. They can be made usable by cutting away the undesired connective tissue after completion of the clearing and staining process.

Poorly preserved specimens may quickly disintegrate. To stop or slow the digestion, about 10 percent formalin may be added to the solution, or the specimen may be transferred (carefully) to 70 percent ethyl alcohol.

Providing the solution has had little digestive activity and has a relatively high pH, no damage to adequately fixed specimens results from their retention in a digestion solution for several days or weeks following clearing. Unless extensive digestion takes place, the 30 percent saturated borax solution is adequate to maintain a satisfactory pH of 7.5 or higher for several weeks in the presence of the enzyme.

7. Prepare a stain solution by mixing a very small quantity of alizarin red S powder in sufficient stock potassium hydroxide solution for specimen immersion. Add alizarin until a deep purple or the desired color intensity is reached. Place specimen in stain solution and let it remain until the bones have become adequately stained.

No advantage is evident in using the specially prepared stain solution described by Davis and Gore (1947, p. 8) or Hollister (1934, p. 92). A solution once prepared may be retained and used to stain additional specimens.

An alcohol stain, prepared by dissolving alizarin red S in 70 percent alcohol and made slightly alkaline by the addition of a few drops of stock potassium hydroxide solution will stain the specimens that started to disintegrate in digestion without further extensive harm. After staining, proceed with them to step 12.

8. Remove specimen from stain solution, rinse in distilled water, and then eviscerate, remove scales and all undesired parts.

9. Rinse specimen in distilled water or soak in borax solution, if large quantities of alkali are suspected to be present in the body cavities, and then return to the digestion solution if it is usable; otherwise, repeat the process, beginning with step 4. Continue digestion until all areas of muscle tissue have disappeared.

Completion of the clearing process following staining is suggested because virtually all of the stain embedded in the soft tissues is removed along with the remaining areas of dark brown or yellowish muscle tissue.

10 (optional). Some oils and fats that remain after the digestion process may be removed by gradually transferring the specimen through a series of ethyl alcohols in varying strengths, beginning with about 40 percent, thence through 70 percent, 95 percent, to absolute alcohol (if available), and then to xylene. After the xylene, the specimen is transferred downward in the alcohol series to water and washed until all traces of the xylene are removed.

11 (optional). Guanin or guanin-like substances may be removed by soaking the specimen in a solution of 2 to 4 percent potassium hydroxide for several days. Guanin is seldom dense, opaque, or troublesome in preserved specimens, especially those preserved in formalin. It is almost insoluble in water, only slightly soluble in alcohol, but it is freely soluble in dilute acids and aqueous potassium hydroxide solutions.

12. Following digestion, many specimens are adequately transparent for study in alcohol. To attain uniformity and to avoid storage problems, specimens are worked into glycerin through a series beginning with 40 percent glycerin in distilled water or in stock potassium hydroxide solution (stock solution 4a), followed by 70 percent glycerin (stock solution 4b) and full strength glycerin. The potassium hydroxide and glycerin mixtures are preferred to create a slight residual alkalinity for long-term storage of specimens. A few crystals of thymol are added to the final glycerin to prevent growth of microorganisms, as the digestion products are an ideal medium for such growth.

For final storage, the specimen is placed in a glass jar with a bakelite top. The jar size should be sufficient to allow complete coverage of the specimen by glycerin but sufficient space between the glycerin and top so that it can be screwed on loosely without danger of glycerin spillage. Metallic containers and tops should be avoided as glycerin reacts in contact with metal, often resulting in colored glycerin.

Glycerin specimens.—Specimens that have not been successfully cleared by any of the modifications of the Schultze method (Davis and Gore, 1947; Evans, 1948; Hollister, 1934) may be improved or completely cleared by enzyme digestion. These specimens are often brown and opaque, especially after long storage in glycerin. Frequently the skin has been split, the tissues are swollen, and parts may remain attached only by narrow strands of tissue. With careful handling and clearing, these poor specimens can often be made very useful unless the fragmentation of connective tissue by the alkali treatment has been extensive. In digestion, much of the bulky material is removed and the swelling is replaced by the collapse of elements, which approximates their normal position. I have cleared many specimens successfully with enzymes, after they had been macerated for varying lengths of time in potassium hydroxide solutions ranging from 0.5 percent to 9 percent, without damage beyond that due to the alkali.

The suggested procedure:

1. For average specimens, dilute the original glycerin and thymol mixture to one-half by addition of distilled water. Let stand for about half a day. Tough specimens may be removed from the original glycerin directly to distilled water or borax; on the other hand, very delicate and badly macerated specimens should have their glycerin diluted more gradually.
2. Place specimen in one or two (depending on size) changes of distilled water or borax solution for one-half day or longer to remove glycerin.
3. Clear specimen by digestion, following the appropriate steps 4 through 12 as described in the preceding section, and repeat as necessary. *Do not* retain the initial digesting solution longer than four or five days as, owing to the presence of glycerin, the first solution rapidly putrefies and becomes acid. Since nearly all of the glycerin and much of the muscle tissue will have been removed in the first digestion solution, the second digesting solution will be more stable and may be retained longer.

Reactions of the Pancreatic Enzymes

The powdered enzyme preparation is usually slightly acid. The proteolytic enzymes present are active from slight acidity to moderate alkalinity, with pH 7.5 to pH 9.0 usually cited as the optimum for trypsin and chymotrypsin.

These enzymes break down proteins, especially denatured proteins, converting them to polypeptides and amino acids; thus, denatured connective tissue is digested. Elastin is not easily denatured but is digested by elastase. For this reason, it is advisable to determine that elastase has been eliminated from the pancreatic enzyme preparation. The other important connective tissue component, collagen, changes to gelatin with heating and is then subject to general proteolytic degradation. Such materials as acids, some chlorine compounds, and strong bases may extensively damage organized collagen fibers and connective tissue structures; degradation in trypsin results from treatment with some of them. Collagenase, which digests native collagen, is apparently not produced by the pancreas. An extensive account of enzyme breakdown of connective tissue is given by Mandl (1961). Limited carbohydrate and fat digestion may be expected.

In solution the enzymes become inactive, and the rate of inactivation of trypsin increases, with increase in pH and temperature, to a rather rapid loss of activity when the trypsin is in moderate to strong alkaline solutions (Tauber, 1950, p. 18).

The reaction rate of enzymes depends partly upon the nature of the substrate, the temperature, and the inhibitors present in solution. Inhibition is increased with increase in acidity or alkalinity or with concentration of a nonsubstrate substance beyond the optimum. Tauber (1950, p. 18) has listed a number of inhibitors of trypsin that are important in this method: charcoal, unsaturated fatty acids, tryptic digests of proteins, pancreatic trypsin inhibitor, hydrogen sulphide, alcohol, formaldehyde, thymol, alkaloids, glycerol, fats, sugar, a number of inorganic salts including heavy metals, ionizing radiation (x-rays, ultraviolet light), and bacteria.

The optimum temperature for digestion is probably near the body temperature of the animal from which the enzymes were obtained. At both lower and higher temperatures the activity is slowed, and at higher temperatures the enzymes may be denatured. To prevent thermal denaturization of connective tissue, avoid heating specimens. Temperatures of 30°C or below are recommended for fishes; somewhat higher temperatures will probably not harm reptiles, birds, or mammals (see Takahashi and Tanaka, 1953; Takahashi and Takei, 1954; Takahashi and Yokoyama, 1954).

The pH of the active digestion solution dropped in all cases that I observed, the rate depending upon the enzyme activity and the quantity of buffer solution used. After most digestion solutions have become virtually inactive, they cannot be restored to any worthwhile degree of effective activity by the addition of either an alkaline solution (to elevate pH) or by the addition of more enzyme. But the relatively inactive enzymes in alcohol solutions may be activated to some extent, even after several months, by slight dilution of the alcohol and by adjustment of the pH toward the optimum.

A number of buffers suitable for enzymatic and histochemical studies are described by Gomori (1955). Tests of a number of alkaline materials, including common chemicals, some of the buffers described by Gomori, and many chemicals used in specimen preservation, were made by me. None showed the digestive activity and pH stability of a 30 percent saturated borax solution, many developed strongly offensive odors, and some appeared to be moderate to strong enzyme inhibitors. Very little digestive activity was observed in solutions with pH readings above 10.0, but with a gradual drop in pH the activity often increased.

Although sodium chloride is an elastase inhibitor (Mandl, 1961, p. 233), it slowed the reaction rate, and no effect on connective tissue from its use was observed. Distinct loss of alizarin staining minerals from fin rays was observed after digestion in the following (all with rather rapid drop to low pH readings, the initial pH followed by final pH in parentheses): dilute trisodium phosphate (10.3 to 4.8); dilute hexamine (hexamethylenamine) (7.4 to 5.5); dilute sodium hydroxide (various dropping to 5.0–6.0); distilled water (6.4 to 5.2–6.0); 0.3 percent potassium carbonate, recommended by Moser (1906) for clearing embryos by trypsin digestion (10.2–10.5 to 5.6–6.5); dilute sodium sulphide recommended by Piechocki (1961, p. 228) for defleshing specimens (10.0 to 6.5). Similar specimens in solutions with pH readings remaining above 7.0 did not undergo this loss. No significant damage to connective tissue by digestion was observed in specimens previously soaked in potassium or sodium hydroxide, but many specimens that had been preserved and allowed to remain in unbuffered formalin exhibited loss of the alizarin staining minerals.

Specimens removed from formalin preservative without washing digested very little, if any; and, in borax solutions, the enzyme coagulated and precipitated at the bottom. These specimens could be cleared adequately only after repeated changes of digestion solution or after being washed in water for several days to remove the formaldehyde. Specimens that had remained in formalin storage for a lengthy period of time generally took longer to clear than did specimens stored in alcohol although the formaldehyde had apparently been removed by soaking in water. Likewise, specimens in alcohol solutions that contained a slight odor of formaldehyde required prolonged clearing.

The presence of 0.033 percent formalin in the borax buffer solution prolonged the clearing time for a specimen several times that of solutions without formaldehyde, requiring several changes of digestion solution, but 0.1 percent or more formalin in the buffer (in which formaldehyde odor could not be detected) appeared to prevent all digestion.

Sodium borate solutions were prepared by using measured quantities of borate and distilled water or by saturating distilled water with borate powder and diluting with distilled water at room temperatures of 22° to 27°C. The percentages used in this paper are percentages of saturation at these temperatures, i.e., the volume of saturated borate solution per hundred of the final enzyme buffer solution. The saturated borate solutions ranged from pH 9.1 to 9.3. In 200 ml. of enzyme buffer solution the addition of about one-half gram of enzyme powder resulted in slight but obvious drops in pH, in solutions below 25 percent saturated, or 0.8 gram borax per hundred. Solutions in the range from 5 to 20 percent saturated often became disagreeably contaminated with bacteria in 10 days. Sometimes, but very infrequently, solutions from 25 to 33 percent saturated developed disagreeable odors in this period, perhaps owing to either excessive initial bacterial contamination from unclean containers or to a failure to obtain complete saturation of the initial borate solution. Generally, solutions from 30 percent saturated upward are expected to prevent excessive bacterial growth over a period of time sufficient to obtain the maximum digestive use of an enzyme.

The rate of pH drop depends on the relative volume of the solution, the quantity of buffer in solution, and the digestive activity. Active 5 percent saturated borate solutions frequently dropped from pH 8.8 or 8.9 to pH 6.7 or lower in 10 days without adequately clearing specimens. Similar 20 percent solutions dropped from pH 9.1 or 9.2 to pH 8.2–8.5, and 50 percent solutions dropped from pH 9.2 to pH 8.9–9.0 in the same time, but both with virtual clearing of specimens. Solutions containing 15 percent or less saturated borate or 60 percent or more took longer consistently to clear specimens than did solutions between these ranges. Saturated solutions of borate required the longest activity. Little difference in clearing rate was noted in 20 to 50 percent saturated solutions, with the best results believed to have been in those 25 to 33 percent saturated. Numerous tests of the 30 percent solution indicate that it remains desirably stable and infrequently drops below pH 8.0, even after several weeks.

Solutions of 2 to 6 grams borate per thousand, corresponding approximately to solutions 20 percent saturated or less, gave similar rapid drops in pH and quickly developed extensive bacterial cultures without adequate specimen clearing. Those with 8 to 16 grams borate per thousand gave results similar to the 25 to 50 percent saturated solutions. Borate solutions of 18 to 22 grams per thousand, corresponding to about 55 to 70 percent saturated, permitted slow clearing, similar to solutions with 6 grams or less. Borax-enzyme solutions of volumes 10 to 40 times that of the specimens have generally been found adequate. Excess volume of solution, several hundred times that of the specimen, resulted in a dilution of enzyme, and it nearly doubled the specimen clearing time. On the other hand, an inadequate volume of solution quickly becomes saturated with digestion products, with accompanying drop in pH and curtailment or termination of digestive activity.

The 30 percent solution has proven superior to all other materials tested in speed of enzyme activity, in maintaining a relatively stable pH, and in preventing or curtailing bacterial activity.

Specimens containing glycerin, when cleared in this enzyme buffer solution, produce a rapid pH drop that may descend to the undesirably acid pH 6.0 in less than one week if the glycerin is not carefully washed from the specimen.

Summary of the Clearing and Staining Method

1. If specimen is not already in alcohol, preserve it in 10 percent formalin for one week to 10 days.
2. Soak all formaldehyde from specimen.
3. Prepare a saturated solution of sodium borate in distilled water.
4. Prepare a stock solution of one-half to one percent potassium hydroxide in distilled water.
5. Bleach specimen in about 10 percent stock hydrogen peroxide and 90 percent stock potassium hydroxide solution.
6. Prepare an enzyme-buffer solution of 30 parts saturated sodium borate solution (supernatant) and 70 parts distilled water of volume equal to 10 to 40 times that of specimen.
7. Place specimen directly in buffer solution or, if necessary, remove any large quantities of alcohol, water, or potassium hydroxide from specimen by soaking it in a borax solution, and then place it in buffer solution.
8. Add about one-fourth teaspoon of enzyme to solution for small specimens, slightly more for large specimens; mix and place aside to clear at about 25° C.
9. Change solution (steps 6 to 8) in one week to 10 days, and repeat until specimen has only a few small areas of opaque muscle tissue remaining.
10. Stain specimen in a solution of stock potassium hydroxide and alizarin dye.
11. Remove viscera and undesired parts.
12. Return specimen to digestion solution (steps 6 to 9) until completely cleared.

13 (optional). Remove oils by working specimen through alcohol series into xylene. When oils have been removed, work back through alcohol series and wash to remove all xylene.

14 (optional). Dissolve dense deposits of guanin in a 2 to 4 percent aqueous solution of potassium hydroxide.

15. Work specimen gradually into full glycerin and add a few crystals of thymol.

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A Comparative Study In Rodent Ethology With Emphasis On Evolution of Social Behavior, I

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Introduction

The rodents exhibit, as an order, a complex series of morphological, physiological, behavioral, and ecological adaptations. During the long history of adaptive radiation within this order, many instances of convergent or parallel evolution have occurred, thus rendering the subordinal classification quite difficult (Simpson, 1959; Wood, 1955). In spite of such diversity, the rodents form a remarkably unified taxon, and such an example of ecological diversity superimposed on a common morphological theme has intrigued many ethologists concerned with the evolution of behavior. Among the more prominent workers, Dr. I. Eibl-Eibesfeldt has contributed much to our knowledge of the subject and is also responsible for the most recent review of rodent behavior (Eibl-Eibesfeldt, 1958).

Eight years ago the present author initiated a comparative study of rodent behavior, partial results of which have been published in several papers (Eisenberg, 1962a, 1963a, b, c) and abstracts (Eisenberg, 1962b, 1964). These earlier, separate papers do not adequately reflect the unity behind the undertaking, and in the present paper current results will be combined with previously unpublished data to establish several theoretical principles that have emerged in the course of the work.

Throughout the studies, the behavior patterns have been analyzed in order to determine which movements were stereotyped and, among these, which conformed to the concept of fixed action patterns. Thus, certain behavioral units meeting acceptable criteria could be treated in the same manner as morphological structures and compared from one species to the next in the classical manner developed by Lorenz (1957) and Tinbergen (1951). The ground rules for such comparative studies have been reviewed recently by Wickler (1961) and need not be reiterated here. In my studies, behavioral evolution was approached at the level of discrete behavioral units; such a description of discrete behavioral patterns allowed the formulation of descriptions of more complicated patterns consisting of predictable sequences of discrete units in time. Further analyses of the frequency of occurrence of different stereotyped units of behavior performed in a social context permitted a description of species-specific patterns of social structure. A knowledge of social structure permitted a partial answer to the following question: Do organisms that evolve independently in different geographical locations toward the same ecological niche also evolve similar social organizations? If the answer were yes, then it would be possible not only to predict a social system from a knowledge of niche requirements but also to determine from comparative studies what major environmental adaptations correlated with a given social system. Thus, the comparison of social systems demanded a description of the behavioral units and, in addition, the description of the different forms of social organization by means of some consistent experimental methodology (Eisenberg, 1964). Working in the laboratory with small rodents was possible only when adequate field data were available to correct for any inadvertent misinterpretation brought about by captivity. Finally, methods of quantification had to be developed that permitted a valid comparison among different species. After several years, it became obvious that simple criteria such as the presence or absence of a given behavior pattern would not suffice in determining relevant species differences. Indeed, it appeared that, under the same stimulus conditions, the different species were all capable of exhibiting almost the same discrete units of behavior and, unless major morphological differences interfered, only the different frequencies of occurrence served to separate species. Relative differences rather than absolute differences in behavior became the rule and led the present author to conclusions quite similar to those of Leyhausen (1965).

The study of social organizations ultimately led to an extension of the comparative method. A given type of social organization has a characteristic structure. The structure is the summation of the form and frequency of each type of interaction within an interacting group. Thus, the social structure reflects the mechanisms of interaction and the adaptive role of the interaction patterns determines the selective advantage of the system at the level of the individual member. On the other hand, a set of complementary emergent properties results when one considers that the social structure itself reflects an adaptation to a given set of environmental relationships that are reflected in the physiology or metabolism of the social group taken as a whole.

Future research on the adaptive nature of whole societies will necessarily have to concern itself with biologically viable societies, i.e., a social unit or series of social units that are maintaining their numbers over long periods of time. In essence, then, conclusions concerning the adaptive nature of groups must be based on groups exhibiting a prevailing reproductive success.

The interrelationships of the various measurable phenomena exhibited at the level of the individual and the group are presented in figure 1.

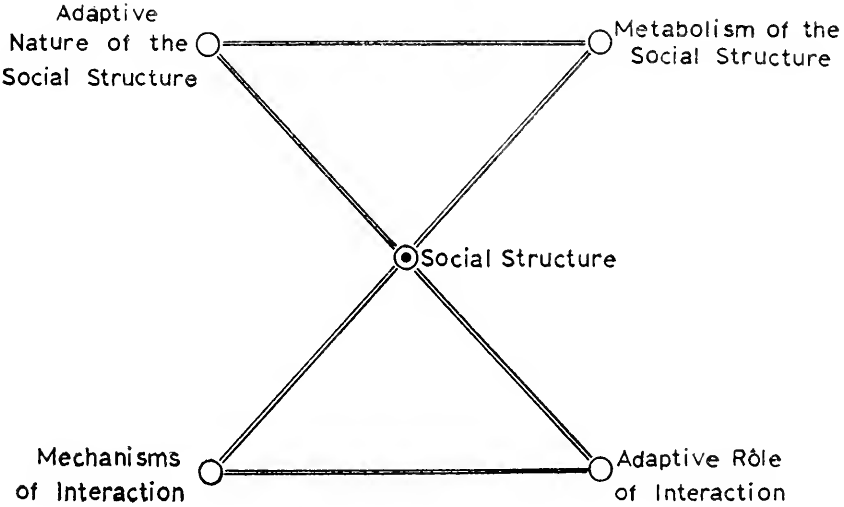

FIGURE 1.—Diagram indicating two possible levels of analysis commonly applied to social structures.

The present report thus demonstrates a method for the analysis of mammalian social structure, the application of the methods to several families showing varying degrees of convergence or parallelism, the reformulation of the term "species-specific behavior," and a discussion of social evolution within the Rodentia.

In a comparative study that spans 3 families and 34 species from three continents, the problems of acquisition and maintenance are of paramount importance. I should like to acknowledge the efforts of my laboratory assistant, Mr. David Williams, who lent his sensitive talents wholeheartedly to the work before us in Vancouver. Specimen donations were also an integral part of this study. I am indebted to Dr. D. Birkenholz of Illinois State University for 3 *Heteromys desmarestianus;* to Mrs. W. Downs of Yale University for 3 *Gerbillus gerbillus*, 2 *Jaculus jaculus*, and 2 *Jaculus orientalis;* to Dr. T. Reed, Director of the National Zoological Park, for 1 *Pachyuromys duprassi;* and to Mr. W. Preston of the University of British Columbia for 12 *Perognathus parvus*. In addition, I should like to cite Mr. Ralph Curtis of Miami, Fla., who was instrumental in arranging the importation of a series of rodents from Pakistan that formed the basis for our dipodid and gerbilline comparisons.

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The Subjects

The choice of the specimens utilized in this study was influenced both by circumstances and design. Initially the behavior of one genus, *Peromyscus,* was selected for study. This North American group includes over 40 recognized species (Hall and Kelson, 1959) that have adapted to a myriad of habitats. As a genus it has lent itself well to comparative ecological, physiological, and morphological studies and offers a wealth of background studies that may be drawn on by ethologists (King, 1967). Four species were selected by the present author for behavioral studies, including two from the Transition life zone and two from the Sonoran life zone (see Eisenberg, 1962a, 1963a). The behavior of this group is the subject of a recent review (Eisenberg, 1967) and will not be redescribed here; however, relevant data will be introduced since this group of four species represents an example of the range of behavioral variation within one genus.

Several questions were raised in the course of the *Peromyscus* study concerning species-specific changes in social behavior resulting from adaptation to desert habitats. For this reason a complete rodent family, the Heteromyidae, was studied in order to correlate generic differences with niche requirements as I compared moist forest-adapted genera (e.g., *Heteromys* and *Liomys*) with desert or semidesert-adapted genera, *Perognathus*, *Microdipodops*, and *Dipodomys* (Eisenberg, 1963b). The results combined with the *Peromyscus* data suggested that any limiting factors a desert environment may impose concerning space requirements of a given individual rodent are not necessarily limiting with respect to the particular species-specific form of the social organization.

To confirm this hypothesis, two Old World taxa of desert-adapted rodents were studied, the Gerbillinae and the Dipodidae. Table 1 contains a list of the specimens included in this study with their geographical origins. Exact capture localities for specimens trapped by the author are included in previous publications (Eisenberg, 1962a, 1963a, b).

Adaptation to an arid environment involves the solution of several severe physical problems including (1) lack of water, (2) widely spaced food plants with concomitant loss of cover, (3) extremes of heat and cold. The behavioral, morphological, and physiological solutions to these problems are varied when the vertebrates are surveyed as a group (Schmidt-Nielsen, 1964), but all mechanisms are geared to the same ends: maintenance of a constant body temperature (at least during active periods), conservation of body fluids, and procurement of sufficient food. A number of small desert rodents have adapted in a similar fashion, providing typical instances of parallel physiological or behavioral evolution. For example, some species of the gerbilline, dipodid, and heteromyid rodents can recover metabolic water in the kidney and live on dry foods alone (Burns, 1956; Kirmiz, 1962; Schmidt-Nielsen, 1964). Furthermore, many desert rodents are nocturnal, construct burrows that are plugged during the day, and cache quantities of food. In several cases bipedal locomotion has evolved (e.g., within the Heteromyidae and the Dipodidae).

None of these behavioral attributes is confined to desert-dwelling species, but the total complex of attributes is unique to a certain type of desert-dwelling form (Eisenberg, 1963b). Within the genus *Peromyscus*, desert adaptation has taken place without the evolution of either bipedality or the ability to reuse metabolic water. The family Heteromyidae exhibits a range of morphological adaptations to a desert environment wherein only the genera *Microdipodops* and *Dipodomys* culminate their evolution with both an extremely specialized gross morphology and the ability to live on metabolic water alone (Eisenberg, 1963b).

Confronted with such a range of adaptations to the same set of problems in the desert, any correlation between behavior and ecology must take cognizance of the multiplicity of variables affecting the overall adaptation pattern. For this reason, tables 2 through 5 summarize the major similarities and divergences regarding reproduction, morphology, habitat, and ecology. Ecological data for the Gerbillinae and Dipodidae are adapted from Ognev (1963), Petter (1961), Zahavi and Wahrman (1957), and Kirchshofer (1958). Figure 2 compares the overall phylogeny for the three major families studied; it is derived from the work of Ognev (1963), Herold and Niethammer (1963), and Wood (1935).

The desert-adapted species show wide divergences when reproduction, maturation rates, morphology, and ecology are compared. The jerboas differ from the kangaroo rats in that some genera of jerboas hibernate and the maturation of the young is prolonged. On the other hand, the dipodids and the genus *Dipodomys* show a close parallel in their morphology and habitat requirements. Certainly the closest correspondence between rodent families occurs when some species of gerbil (i.e., *Gerbillus nanus*) are compared with the heteromyid species of the genus *Perognathus*. In any event, tables 2 through 5 emphasize the differences that may have a bearing on divergences in the form of social organizations (see p. 31).

Methodology

When not under direct observation, the subjects were held as individuals or pairs in glass-sided cages with wire tops and wooden floors. These holding cages were of two general sizes containing floor areas of 90 to 180 square inches. The animals were fed a mixture of sunflower seeds, commercial rat pellets, rolled oats, millet, and fresh lettuce (see also table 1).

The analysis of behavior began with a description of the discrete units that comprise the total repertoire of activity patterns displayed by the subject under study. In order to give the animal ample opportunity to display the full range of its behavior patterns, simulated natural habitat cages were employed. Such cages contained artificial burrows; they are fully described in a previous publication (Eisenberg, 1963b, p. 5). In the present study, the floor areas of the burrow cages included three sizes: 864, 550, and 360 square inches. Nocturnal forms were observed by a red light during their normal dark cycle of activity. Once the behavioral units had been described, the subjects were exposed to several testing situations that may be treated under two headings: (1) behavior patterns of the solitary animal and (2) patterns of social behavior.

The behavior patterns displayed by the isolated animal fall under the general categories of exploratory and maintenance behavior. In order to analyze the differences among species, standard tests were run by allowing an animal to move freely in a glass-fronted arena containing specific artifacts such as stones, hay, a tree branch, and a small amount of food. The arena sizes included floor areas of 748,

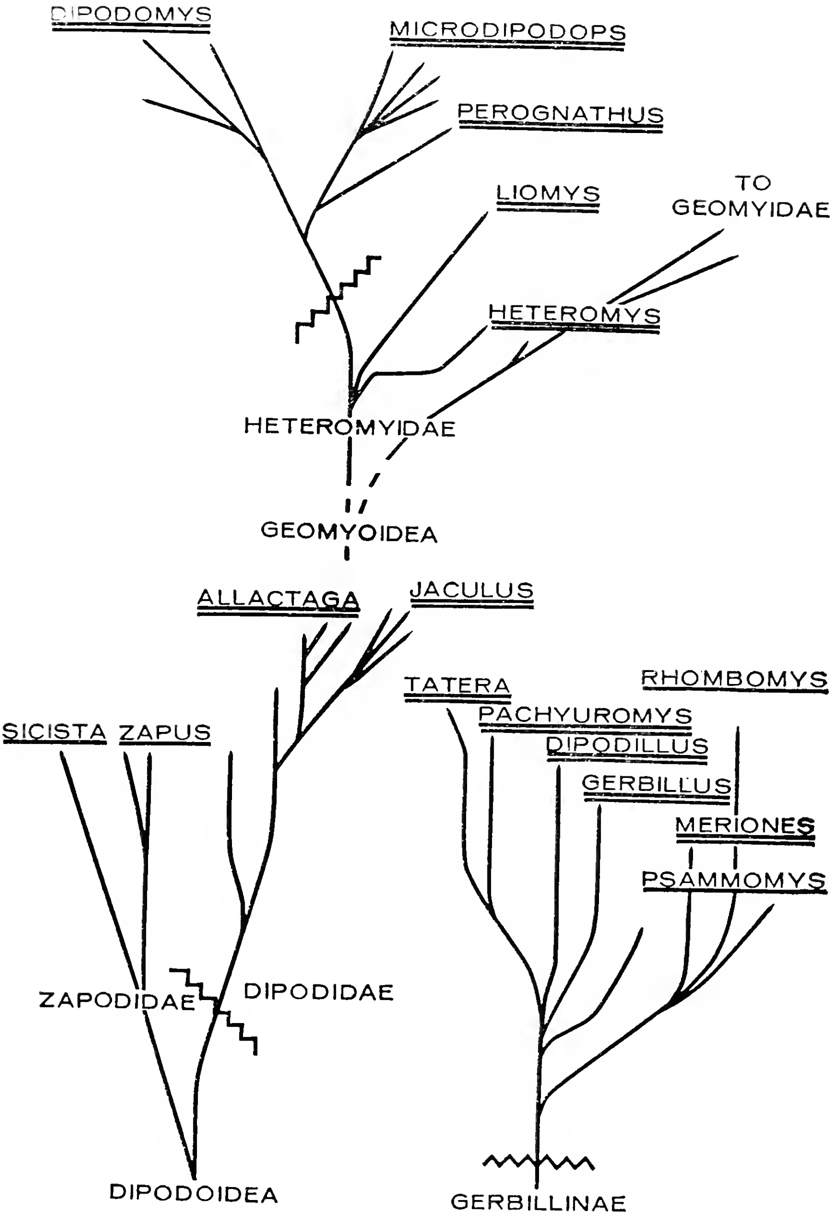

FIGURE 2.—Inter-relationships of major genera from three families of desert-adapted rodents (double underline=all genera included in present study; genera above jagged line are commonly found in arid or semi-arid habitats).

1598, and 2304 square inches. Employing a tape recorder, the behavior was described in a semicoded fashion by an observer concealed behind a screen. The verbal descriptions on tape were transcribed later, employing a constant 10-second time interval to allow further for a consideration of the temporal changes in the behavior patterns. An operations recorder coupled to a keyboard was also employed for recording behavioral units in time. Both data-recording methods are outlined in previous publications (Eisenberg and Kuehn, 1966; Eisenberg, 1963b). Such data were analyzed by various methods that permitted an accurate determination of the changes in the frequency of responses, the duration of specific activity patterns, and the frequency and durational changes over extended periods of time.

A problem in quantification arose in comparing acts that had a brief duration, coupled with a clear onset and cessation, with those acts having a variable duration of imperfectly definable onset and cessation. The more or less brief actions generally were counted and described in terms of straight numbers per unit time. On the other hand, such activities as driving, chasing, fighting, etc., were recorded either in terms of actual duration or were counted for a frequency analysis by employing a 10-second time criterion. Such acts having a duration of 10 seconds or less were treated as one unit; if the duration were greater than 10 seconds but less than 20, the action was treated as two units, and so on. Indication is made in the text whenever the 10-second criterion was applied for a frequency analysis of acts having a long duration.

Patterns of social interaction were also recorded by the general methods just described—by verbal means on tape or with an operations recorder. In addition, a third method involved a weekly check of cages containing freely growing populations. Pairing tendencies, incidence of wounding, litters born, and breeding condition of individuals were censused in this manner. The three approaches to the analysis of social interaction patterns are as follows:

(1) The encounter in a neutral arena: In this situation, two animals were placed simultaneously in a standard environment and the resultant interaction recorded. Such variables as the sex, the age, and the physiological state of the encountering animals could be controlled (see Eisenberg, 1962a, 1963b). The glass-fronted encounter arenas included 748, 1598, and 2304 square inches of floor area. Data from such standard encounter situations permitted species comparisons with respect to differences in the frequency and duration of various social behavior patterns.

(2) The territorial encounter: This was a variant of the simultaneous encounter technique and involved the use of a cage divided into two or three equal compartments as described previously (Eisen-

berg, 1963b, p. 4). The encounter boxes included 1110, 1728, and 1950 square inches of floor area. Utilizing this technique, some measure of the influence of the locus on the outcome of an encounter could be assessed.

(3) The formation of social groups: In this situation pairs or groups were allowed to remain together as a result of either a simultaneous or a territorial encounter. Several measurements were recorded, including the tendency to nest together, the incidence of wounding, the tolerance of the male by a female during parturition and rearing, the effect of the male on the female's estrous condition, and the effect of the adults on the survival, growth, and development of the young. Various cage sizes were employed in the study of the pairing tendencies and the social tolerance during the growth of confined populations. These included cages with floor areas of 180, 328, 550, 864, 1110, 1728, 1950, 2304, 5040, and 6480 square inches. Studies of this nature yielded information concerning species-specific differences in social tolerance. Pair tolerance and the growth of confined populations varied from species to species; the solitary species required a large space coupled with a complex environment in order to reproduce successfully.

Terminology

As the initial analyses progressed, it was found that the behavioral repertoires of the different species were remarkably similar in their gross form. The social behavior of small nocturnal mammals appears to include a reliance on auditory, tactile, and chemical communication, with a reduced role for visual communication. Hence, the evolution of complex movement patterns with concomitant morphological changes that are employed in the visual display of many diurnal vertebrates such as birds, lizards, and certain fishes are reduced in the present group. The role of chemical and auditory signals in the nocturnal rodents is still poorly known and, in the present study, the behavioral units were recorded without direct reference to their communicatory function. As a result, the behavioral inventories show more uniformity than might be expected by students of avian or fish behavior. This uniformity permitted a single list of defined behavioral elements to serve for all species.

Complete ethograms exist for the heteromyid rodents (Eisenberg, 1963b), the genus *Peromyscus* (Eisenberg, 1962a, 1963a, 1967), *Meriones persicus* (Eibl-Eibesfeldt, 1951), and *Gerbillus nanus* (Kirchshofer, 1958); in addition, ontogenetic data exist for *Meriones tamariscinus* (Rauch, 1957) and a behavior study of the jerboa is near completion by Hackinger (pers. comm.).

Rather interesting data on the reproductive behavior of *Pachyuromys duprassi* and other gerbillines are contained in the early work of Lataste (1887). Since the species of *Meriones* and *Gerbillus* included in this study resemble in their behavior the species cited previously, no attempt is made here to include an exhaustive ethogram for them.

The list below includes all behavioral terms utilized in the current study. The list serves for all species although not every species includes all of the behavior patterns in its behavioral inventory. The complete descriptions of these behavioral elements and their functional organization are included in Eisenberg (1962a, 1963b), Eibl-Eibesfeldt (1951, 1958), and Kirchshofer (1958). Both German and English equivalents are presented to avoid terminological confusion.

The postures and movements listed here represent two types of classification. Some of the terms apply to discrete muscular movements consisting of an orientation movement, a stereotyped component, or a fusion of both. Other terms are descriptive in that they indicate a functional unit of motor patterns. Convenience has dictated this mixed presentation. Please note that the functional units described here may well be analogous units when two or more species are compared. It is not intended that the equivalence of terms should necessarily imply homologous motor units.

Eisenberg	Eibl-Eibesfeldt
General Maintenance Behavior	
Sleeping and resting	Schlafen und Rasten
Curled	Zusammengerollt
Stretched	Ausgestreckt
On ventrum	Bauchlage
On back	Rückenlage
Sitting	Sitzen
Locomotion	Fortbewegung
On plane surface	An der Boden
Diagonal	Kreuzgang; Laufen
Quadrupedal saltation	Hoppeln; Galopieren
Bipedal walk	Bipedes Schreiten
Bipedal saltation	Bipedes Springen
Jumping	Springen
Climbing	Klettern
Diagonal coordination	Klettern im Kreuzgang
Fore and hind limb alternation	Stammklettern
Swimming	Schwimmen
Care of the body surface and comfort movements	Körperpflege
Washing	Putzen
Mouthing the fur	Fellpflege
Licking	Belecken
Nibble	Beknabbern
Wiping with the forepaws	Putzen mit den Vorderbeinen
Nibbling the toenails	Nägelputzen
Scratching	Sich-Kratzen
Sneezing	Niesen

Eisenberg	Eibl-Eibesfeldt
General Maintenance Behavior—Continued	
Care of the body surface and comfort movements—Continued	
Cough	Husten
Sandbathing	Sandbaden
Ventrum rub	Bauchreiben
Side rub	Flankenreiben
Rolling over on the back	Wurfen auf den Rücken
Writhing	Schlängelbewegungen
Stretch	Sich-Strecken
Yawn	Gähnen
Shake	Sich-Schütteln
Defecation	Koten
Urination	Harnen
Marking	Markierung; Duftmarkierung
Perineal drag	Rutschen auf der Anal region
Ventral rub	Bauchreiben
Side rub	Flankenreiben
Ingestion	
Manipulation with forepaws	Futterhalten
Drinking (lapping)	Trinken (Lecken)
Gnawing (with incisors)	Nagen
Chewing (with molars)	Kauen
Swallowing	Schlucken
Holding with the forepaws	Handhaben
Gathering foodstuffs and caching	Sammeln
Sifting	Prüfen
Dragging, carrying	Eintragen
Picking up	Aufheben
Forepaws	mit dem Pfoten
Mouth	mit dem Maul
Hauling in	Einholen
Chopping with incisors	Häckseln
Digging	Graben; Lochgraben
Placing	Ablegen
Pushing with forepaws	Nachstopfen
Pushing with nose	Schnauzen-stossen
Covering	Zugraben
Push	Zuscharren
Pat	Festdrücken
Digging	Graben
Forepaw movements	Scharren
Kick back	Auswerfen
Turn and push (forepaws and breast)	Hinausschieben
Turn and push (nose)	Hebeln
Nest Building	Nest bauen
Gathering	Aufsammeln
Stripping	Zerspliesen
Biting	Beissen
Jerking	Hockreissen (des Kopfes)

Eisenberg	Eibl-Eibesfeldt
General Maintenance Behavior—Continued	
Nest Building—Continued	
Stripping—Continued	
Holding	Halten
Pushing and patting	Andrüken der Pfoten
Combing	Abstreifen
Molding	Ausmulden
Depositing	Ablegen
Isolated animal exploring	Einzel Tiere
Elongate, investigatory	Erkünden mit Fluchtmotivation
Upright	Aufrichten; Männchenstellung
Testing the air	Winden
Rigid upright	Sichern
Freeze (on all fours)	Erstarren
Escape leap	Flucht-springen
Sniffing the substrate	Spüren
Whiskering	Vibrissenzucken
Social Behavior	
Initial contact and contact promoting	Kontaktaufnahme
Naso-nasal	Nase an Nase; Schnauzen Kontrolle
Naso-anal	Beschnuppern des Ano-Genital Region
Grooming	Soziale Hautflege
Head over–head under	Kopfunterschieben
Crawling under and over	Überkriechen und Unterkriechen
Circling (mutual naso-anal)	Beschnuppern im Kreisgang; Kreisen
Sexual	Sexual
Follow and driving	Treiben
Male patterns	Männliche Verhaltensweisen
Mount	Aufreiten
Gripping with forelimbs	Stimulieren
Attempted mount	Aufreitversuch
Copulation	Kopulation; Paarung
Thrust	Friktionsbewegungen
Intromission	Einführung
Ejaculate	Ejakulierens
Female patterns	Weibliche Verhaltensweisen
Raising tail	Präsentieren
Lordosis	Paarungsstellung
Neck grip	Nackenbiss
Postcopulatory wash	Sich-putzen
Approach	Annährung
Slow approach	Vorsichtige Annährung
Turn toward	Zuwendung
Elongate	Erkünden mit Fluchtmotivation
Agonistic	Flucht, Angriff, u.s.w.
Threat (proper) (remains on all four legs)	Drohen

Eisenberg	Eibl-Eibesfeldt
Social Behavior—Continued	
Agonistic—Continued	
Rush	Angriff
Flight	Flüchten
Chase	Verfolgen
Turn away	Abwenden
Move away	Weggehen
Bite	Kampfbeissen
Locked fighting (mutual)	Kampfstellung
Fight (single)	Kampfstellung
Defense (on back)	Abwehrstellung
Side display	Breitseitsdrohen
Shouldering	Schieben
Sidling	Drücken mit der Körperseite
Rumping	Schieben
Uprights	Aufrichten
Class I (upright threat)	Drohstellung
Class II	Drohabwehr
Locked upright	
Striking, warding	Pfotenschlagen
Sparring	Pfottentrommeln (Kampfvorspiel)
Tail flagging	
Kicking	Treten
Attack leap	Anspringen
Escape leap	Flüchtspringen
Submission posture	Demutstellung
Defeat posture	Aufgebenstellung
Tooth chatter	Zahnwetzen
Drumming	Trommeln
Pattering (with forepaws)	Pfotentrommeln
Tail rattle	Schwanzzittern
Miscellaneous patterns seen in a social context	
Sandbathing	Sandbaden
Digging and kick back	Scharren und Auswerfen
Marking	Markieren
Ventral rub	Bachreiben
Side rub	Flankenreiben
Perineal drag	Rutschen auf der Anal region
Pilo-erection	Fellsträuben
Trembling	Zittern

Behavior Patterns of the Solitary Animal

LOCOMOTION.—When a series of genera or species are compared, the presence or absence of a behavior pattern is often correlated with a corresponding presence or absence of some morphological feature. This is nowhere better illustrated than with bipedal locomotion. As discussed by Howell (1932), Hatt (1932), and Ognev (1959), bipedal, saltating locomotion occurs when a set of morphological features are present, including modifications in the musculature and vertebral column, reduction in the number of hind toes, lengthening of the hind feet, shortening of the forelimbs, fusion of the cervical vertebrae, and modifications of the tail. To be sure, most rodents possess the ability to stand on their hind legs and walk or even hop for a short distance, but sustained bipedal saltation does not occur as a normal behavior pattern with the absence of certain morphological and physiological correlates. In the group under study, full bipedal locomotion was exhibited only by *Microdipodops*, *Dipodomys*, *Allactaga*, and *Jaculus*. The latter two genera are more advanced in that the first and fifth toes are reduced (*Allactaga*) or absent (*Jaculus*) and in both forms the metatarsals are fused to form a "cannon bone."

COMFORT MOVEMENTS.—Sandbathing: Sandbathing is a complex movement pattern functional in dressing the pelage. It is composed of several distinct behavioral units, including side rubbing, ventrum rubbing, writhing from side to side, and rolling on the back. All these units are part of the total behavioral inventory of most rodents and other mammals; however, the organization of these units into a specific pelage-dressing pattern tends to be taxon-specific (Eisenberg, 1963c). The species-typical movement complex termed "sandbathing" is a normal part of the behavioral repertoire in most rodents that have adapted to arid habitats. It should be understood that sandbathing is not confined to desert rodents alone, but that the frequency of occurrence and stimuli necessary to elicit the pattern are characteristic of desert-adapted species. In the current study, *Gerbillus gerbillus*, *G. nanus*, *Tatera indica*, *Meriones unguiculatus*, *M. hurrianae*, *Pachyuromys duprassi*, *Allactaga elator*, *Jaculus jaculus*, *J. orientalis*, *Peromyscus crinitus*, and all species of *Microdipodops*, *Perognathus*, and *Dipodomys* exhibited functional sandbathing. Dressing the pelage by rolling or rubbing in dry soil may be accomplished potentially by any of the several discrete movements mentioned above. Typically the animals exhibit digging movements with the forepaws and the kicking back of accumulated earth with the hind limbs. Digging movements serve to dust the fur of the ventrum and often, while digging, the animal may exhibit slight forward extensions of the body as it presses its ventrum against the substrate. The components following digging and kick back are classified as a side rub, ventral rub, or rolling over, but this tripartite classification masks some subtle details. Since the side rub and ventral rub commonly occurred in the series of rodents studied, I include a brief description of the variations:

The side rub: This may involve lowering the head to the substrate and sliding forward on the side while first extending and then flexing the torso. The action may be swift with only a slight extension and flexion of the body, or it may involve a movement of both hind legs forward as the torso flexes. During the extension phase, the chin may rest flat on the substrate with the result that the chest is rubbed in the sand. The latter twisting is especially common in the dipodids studied.

The ventrum rub: In this study, the ventrum rub was defined arbitrarily as extension and flexion of the body axis with the ventrum pressed against the substrate. Typically the hind feet are thrust forward even with or beyond either side of the head during the flexion phase. The ventrum and perineal region are thoroughly scrubbed into the substrate. It can be seen from this description that digging and the side rub, plus the twisting of the body, will suffice to dust the entire pelage with soil. The ventrum rub is not always necessary as a pelage dressing component.

Rolling on the back while writhing from side to side was rarely shown by the species studied although it was observed occasionally with *Tatera indica*, *Meriones unguiculatus*, and *Pachyuromys duprassi*.

The frequency of side rubs to ventrum rubs varies in a species-specific manner. Table 6 indicates the trends for seven species from three families. The sandbathing Heteromyidae display a range of ventrum rubbing from 23 to 45 percent, whereas the dipodid *Allactaga* displayed only 8 percent ventrum rubs and the gerbils *Meriones* and *Gerbillus* displayed virtually no ventral rubbing as a component of sandbathing. The discrete components of sandbathing occur in sequences and each single event may be followed by a second event within an interval range of one-half to an unknown number of seconds exceeding 500. The frequency distributions for intervals separating sandbathing acts were plotted. Since the majority of intervals fell within 3½ seconds, this interval was selected arbitrarily as the limiting interval separating acts within the same sequence. For each species, all sequential acts were plotted in a Latin square in a manner described previously (Eisenberg, 1963c). Table 7 portrays the results, which give an indication of how the components of sandbathing are integrated. *Meriones* and *Gerbillus* are prone to alternate side rubs from one side to the other. *Allactaga* seems equally prone to alternate or rub the same side a second time. *Dipodomys deserti*, *Perognathus californicus*, and *P. parvus* tend to alternate sides whereas *D. nitratoides* shows a preference for rubbing the same side. All the Heteromyidae integrate ventrum rubs with side rubs into a functional sequence.

All species exhibit locus specificity in their sandbathing on consecutive days. There is also a pronounced tendency in some species to sandbathe at the locus of a partner during a social encounter (see p. 22). The occurrence of locus specificity and the exchange of loci during an encounter implies that chemical communication is taking place; thus, the functional classification of sandbathing really includes a marking function as well. In addition to the movements involved in dressing the pelage, these animals may have definite marking movements.

Marking: Marking is a functional term including several behavioral units. From a functional standpoint a marking pattern serves to spread some chemical substance at a specific locus. Such a chemical presumably has communicatory value. Many rodents utilize a marking pattern that involves a depression of the anal-genital region in order to bring these glandular areas into contact with the substrate as the animal moves about in its living space. This is termed the perineal drag. Urine and feces may serve as chemical markers in addition to glandular exudates. When special glandular areas are concentrated on other parts of the body such as the flanks or ventrum, side rubbing or ventrum rubbing may be expressed as a marking movement. The perineal drag is a movement common to all the rodent species studied. Ventrum rubbing is a ritualized marking movement shown by the genus *Meriones*. The latter genus is characterized also by a large gland-field in the ventral epidermis.

It should be noted that sandbathing can serve the dual function of dressing the pelage and marking (Eisenberg, 1963b, c); thus, in desert-adapted species the sandbathing behavior tends to be concentrated at a specific locus and can serve as a focus of activity for two or more interacting individuals.

Washing: Washing (autogrooming) is displayed in a typical myomorph fashion (Bürger, 1959). The chief modifications in movement pattern are the results of morphological modifications. Hence, the short forelimbs and short necks of the bipedal genera restrict the movement of the head in the vertical plane and necessitate a rotation of the head when it is washed with the forepaws.

Burrow construction.—The desert-adapted rodents of the families Cricetidae, Dipodidae, and Heteromyidae construct extensive burrow systems that employ basic digging patterns involving the forepaws and hind limbs (Eisenberg, 1963b). The teeth may be used to gnaw into a hard substrate; *Allactaga elator* is most prone to gnaw when constructing burrows. This behavioral trait is reflected in the protruding dentition, which enables *A. elator* to gnaw into a flat surface without a crack or crevice that would permit a starting point for gnawing.

Burrow walls are packed by a pushing and patting motion of the forepaws (Eisenberg, 1963b). This movement pattern is typical for many rodent species, and the nose and incisors may also be involved in packing loose soil. *Tatera* and *Meriones*, when packing, employ the forepaws and nose by jerking the body back and forth in the vertical plane while holding the forepaws rigid on either side of the nose. The forepaws and nose strike the soil and serve to tamp it firmly into place. *Allactaga* and *Jaculus* pack loose soil by raising and lowering the head in the vertical plane, thus repeatedly bringing the snout and incisors against the substrate. This packing method appears to be highly ritualized in the Dipodidae. The heteromyid rodents as well as *Gerbillus* and *Pachyuromys* appear to employ pushing and patting with the forepaws as the principal method for packing the tunnel walls.

Assembly of foodstuffs.—Studies of *Meriones persicus* (Eibl-Eibesfeldt, 1951) indicate a tendency to bite pieces of food (e.g., vegetable matter, stalks, roots, pods) into small pieces, which are then cached. This behavior pattern has been termed "Häckseln" and is here translated as chopping. *M. unguiculatus*, *M. hurrianae*, and *Tatera indica* all exhibited this trait.

The caching of foodstuffs either in the burrow or in discrete loci within the animal's home range is a behavioral trait shared by many species of rodents. The family Heteromyidae is characterized by a persistent tendency to gather and cache great quantities of grain, and this behavioral trait is correlated with the possession of capacious, externally opening, fur-lined cheekpouches (Eisenberg, 1963b). None of the other genera in the current study exhibited such persistent caching behavior, and the dipodid genera do not seem to cache very much at any time during their annual cycle. *Allactaga* and *Jaculus* will assemble dried grasses in their burrows, but this material is generally used in nest building rather than as food (see table 8).

Discussion.—Behavioral and ecological convergences appear to be very close when the genera *Perognathus*, *Gerbillus*, and *Pachyuromys* are compared. Although the genera *Microdipodops*, *Dipodomys*, *Jaculus*, and *Allactaga* are ecologically similar and have evolved a similar morphology correlating with their bipedal form of locomotion, rather profound behavioral and physiological differences separate the bipedal Heteromyidae from the Dipodidae. The most basic correlate appears to involve the reduced caching tendency of *Jaculus* and *Allactaga* with a concomitant tendency to hibernate or exhibit periods of torpor (Skvortsov, 1955, 1964). *Dipodomys* caches seeds and is not known to hibernate.

Since the Heteromyidae are essentially solitary rodents with a very low threshold for the exhibition of agonistic behavior, this tendency toward asocial behavior may correlate with the fact that the genera *Dipodomys* and *Microdipodops* do cache and the fact that the selective advantage of caching is related to a dispersed or solitary social structure.

Sandbathing is a trait shared by all desert-adapted rodents. It would appear that increased sebaceous secretion is a necessary condition to reduce evaporative water loss through the epidermis. In addition, many desert rodents have a dense pelage with a concomitant increase in sebaceous glands as an adaptation to extremes of cold during the desert night (Sokolov, 1962). With the increase in sebaceous glands and secretion, one finds a corresponding necessity to dress the pelage. Since all species of rodents studied appear to dry their fur when it is moistened by means of either extending and flexing the body while lying on their side or ventrum or rolling over, the conclusion is unavoidable that ritualized sandbathing has evolved from the same set of basic movements in all rodent families. It is interesting to note that selection has favored a relatively stereotyped pattern that varies in a species-specific manner (see table 7). The higher taxonomic categories show less uniformity; however, the sandbathing Heteromyidae are remarkably uniform with their tendency to integrate side rubs and ventral rubs. This characteristic tends to set off the Heteromyidae from the Gerbillinae and Dipodidae.

Since sandbathing has the dual function of dressing the pelage and leaving a chemical trace of presumptive communicatory value, the evolutionary origins of sandbathing are inextricably tied to marking. Marking by means of the perineal drag probably had its origin in a common cleaning movement that consisted of wiping the anal-genital area on the substrate after urination or defecation. The stretch involving extension and flexion of the body also frequently accompanies elimination after the animal has awakened from prolonged sleep. Thus, selection could favor a combined ventral rub with perineal drag as a marking movement if the sebaceous secretions of the ventral epidermis had some inherent communicatory function that affected reproductive success or survival of the genotype. Such a ritualized marking pattern appears to have arisen as an independent element in *Meriones*, whereas in the Heteromyidae the ventral rubbing with its marking function has been combined with side rubbing in a functional sandbathing sequence (see table 9).

Patterns of Social Behavior

In a recent review of rodent social behavior (Eisenberg, 1966), I attempted to outline the origins and evolution of the various social systems to be found within the Rodentia. Social systems may be classified into two categories: solitary and communal. The communal systems have several subtypes including monogamous, polygamous, and family band groupings. For convenience, I will restrict the discussion in this paper to three categories: solitary, pair tolerance, and communal. The latter category corresponds to the family band as defined in the previously quoted monograph. It is the central thesis of this section that a given species has a typical social organization that falls into one of the three major categories.

In order to describe quantitative differences among species, three techniques have been employed: (1) the simultaneous or territorial encounter; (2) the maintenance of pairs through parturition; and (3) the study of groups derived from internal recruitment by births (see p. 26). The species-specific social organization is a result of species differences in the ability to tolerate contact with conspecifics. Thus, each species has a social tolerance that, when exceeded, will result in pathologies such as failure of the female estrus cycle, abandoning or destroying the litter by the mother, delayed maturation of the young, fighting to the point of wounding or death, and failure of the male gonadal development. The encounter allows one to make comparisons of the form and frequency of different postures from species to species. It also permits an assessment of the relative amount of agonistic behavior displayed by a given species. The pairing tests allow one to assess the effect of the male on the female throughout pregnancy and parturition. Again one can measure the relative social tolerance. Studies of groups allow one to observe the social tolerance throughout subsequent generations.

As discussed under Methods, most of the behavioral units described in this section involve an interchange of tactile or visual stimuli. Thus, in this investigation, consideration of presumptive auditory and chemical communication patterns has been minimized. It is understood that marking, naso-anal contact, naso-nasal contact, and, to an extent, grooming involve some chemical communication. Although auditory communication was investigated whenever the sounds were below 15 kc, ultrasonic sounds definitely were excluded in this study. Because of the incomplete nature of the sound recordings, a consideration of auditory communication will be deferred in this study.

Aspects of visual communication are difficult to evaluate among nocturnal rodents; however, the striking convergence in color patterns (especially of the tail) between the dipodid genera and the heteromyid genus *Dipodomys* deserves special comment. The kangaroo rats and jerboas have relatively large eyes, and in both groups ritualized upright postures are employed in fighting and during initial contact and courtship (see p. 23 and Eisenberg, 1963b). The white tip on the otherwise black terminal tuft of the tail appears to serve as an orientation point for a male when driving a female or when chasing another male. The white ventrum, displayed during a series of upright postures, produces a sharply contrasting reflecting surface that surely aids in orientation during sequences of mutual uprights and sparring. This latter characteristic is, however, common to all of the species included in this study and is not unique for the kangaroo rats and jerboas.

THE ENCOUNTER.—Encounters were run between males, females, and between males and females. In general, male to male encounters result in avoidance or in fighting, with the subsequent establishment of a dominant-subordinate relationship. Female to female encounters are less predictable and the most informative encounter type is that between a male and a female (Eisenberg, 1962a, 1963b). For the purpose of this paper, I will restrict the data to the male-female encounters under two spatial conditions and two physiological conditions.

The spatial conditions include (1) an encounter in a neutral arena and (2) an encounter in a territorial box (see p. 8). Since the dimensions of the encounter arena influence the outcome (Eisenberg, 1963b), the dimensions will be specified in all tabulations.

The two physiological conditions include (1) the estrous and (2) the anestrous states of the female. In all discussions of male-female encounters the male was judged to be in a sexually viable condition.

For tabulation purposes the behavior patterns are often classified into the following categories: contact promoting, sexual, and agonistic. The composition of each category corresponds to the classification presented on page 10.

Solitary Versus Tolerant Species: If we compare a series of encounters between males and anestrous females for different species, we find evidence for a distinct separation into two social types. One type either avoids contact or, if the arena space is small, engages in agonistic behavior. The second type initiates contact-promoting behaviors such as grooming. Table 10 lists the totals and average frequencies of bouts of the major behaviors displayed during encounters in a neutral arena or a territorial box. A tolerant species such as *Peromyscus maniculatus gambelii* engages in a grooming bout approximately once per encounter even in a territorial encounter, whereas a solitary species in a neutral encounter avoids contact aside from the naso-nasal. Tables 11 and 12 demonstrate a similar separation into contact-prone and avoidance-prone social types, although here the data are selected from a carefully controlled series that utilizes the neutral arena and the territorial box experiments. In the latter situation, contact-promoting behavior drops even further and agonistic aspects become more apparent.

An inspection of tables 11 and 12 suggests that *Meriones unguiculatus*, *Gerbillus gerbillus*, and *Allactaga elator* are more contact-prone, whereas *Dipodomys panamintinus*, *Perognathus californicus*, and *Gerbillus nanus* are more avoidance-prone when the female is in an anestrous condition.

The onset of agonistic behavior is not always immediate. In figure 3, the time course of an encounter between a male and female *Perognathus parvus* is treated in consecutive 100-second intervals. One may notice that on the day preceding estrus the male exhibits contact-promoting and sexual patterns during the first 100-second and third 100-second periods. During the second and fourth 100-second periods, the male exhibits mostly individual behavior patterns that include digging and kick back, sandbathing, exploration, and sitting. On the day of estrus, sexual behaviors predominate throughout the 400 consecutive seconds. The day following estrus shows a gradual tendency for agonistic behavior to increase throughout the encounter. During the first 100 seconds, the male attempts contact and sexual

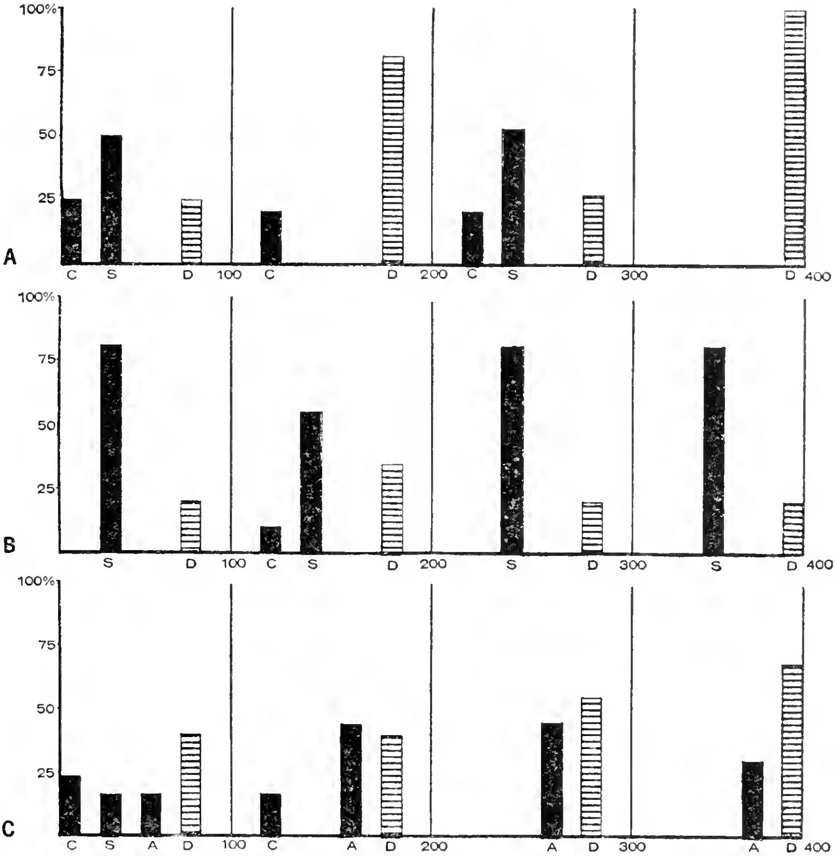

FIGURE 3.—Changing proportions of male *Perognathus parvus* behavior through the estrus cycle of his partner (A=day before estrus; B=day of estrus; C=day following estrus; ordinate=percentage of all acts for each 100-second interval; abscissa=1st, 2nd, 3rd, and 4th consecutive 100-second periods of encounter; S=all sexual acts; C=all contact-promoting acts; A=all agonistic acts; D=all individual behaviors).

behavior; some agonistic interaction also occurs. In the second period of 100 seconds, agonistic behavior increases and some contact-promoting behavior remains. In the third and fourth 100-second periods, the male alternates between agonistic behavior and individual acts of digging and sandbathing.

The reversion to agonistic patterns on the day following estrus was examined in detail by the successive encounter technique. Tables 13 through 15 indicate the reversion to agonistic behavior or avoidance on the day after estrus. The conclusion is evident: certain species of rodents such as the heteromyid *Liomys pictus*, *Perognathus californicus*, *P. parvus*, and *Dipodomys panamintinus* and the gerbillid *Gerbillus nanus* are prone to avoid or react in an agonistic fashion to one another except for the male-estrous female situations, whereas *Allactaga elator* and *Meriones unguiculatus* exhibit contact-promoting behaviors outside of the estrous condition of the female.

Whether solitary or social, chemical communication is implied in such postures as the naso-nasal or naso-anal configurations. In such semitolerant forms as *Meriones unguiculatus*, marking by the male plays an important role in an encounter. The desert-adapted species are prone to exhibit sandbathing during an encounter and in the intolerant species there is generally an exchange of sandbathing loci in order that the male may become familiar with the female's odor before achieving physical contact. The role of sandbathing in social integration has been discussed for the Heteromyidae in previous publications (Eisenberg, 1963b, c). Table 16 includes sandbathing data for three species: *Allactaga elator*, *Meriones unguiculatus*, and *Gerbillus nanus*. It is interesting to note that significant overlap between male and female sandbathing loci occurred only in the *G. nanus* encounters. This is in accord with the general theory since *G. nanus* is the only noncontact species of the three. The species conforms to the pattern of sandbathing during an encounter as outlined in previous publications for the intolerant Heteromyidae. There can be little doubt that chemical substances left in the course of sandbathing by *G. nanus* induce further sandbathing by an approaching conspecific. The exchange of chemical signals is thus a distinct possibility.

A further consideration of tables 12 through 14 points out some interesting aspects of behavior. During a male-female encounter on the days preceding or following estrus, the male exhibits more sandbathing and/or digging and kicking back than on the day of estrus. This is especially noticeable in the encounters with *P. parvus* and *D. panamintinus*. The digging and kick-back patterns exhibit all the characteristics of classical displacement activity and often follow a bout of preliminary sexual behavior or chasing. In both of the preceding examples the primary aggressive or sexual drives are not consummated, and the male switches suddenly to an apparently meaningless pattern of digging and kicking back, often while orientated toward the female.

Species-specific Patterns of Mating Behavior: In a previous publication (Eisenberg, 1963b), a series of heteromyid rodents was compared in order to demonstrate the differences between species and genera when the frequencies of the various mating behaviors were compared. It was found that the same basic components were present in almost all forms studied, but the relative frequencies were quite different. Table 17 presents a comparison of mating patterns for eight rodent species. All data were taken from behavioral records that had terminated in a successful series of mounts. Again the conclusion is unavoidable that, although the potential exists for expression of the same motor units by almost all species, the relative frequency of occurrence of any given unit exhibits unique characteristics for the species in question. Little information can be gained on taxonomic relationships from such an analysis since, in all probability, the quantified movements are not critical releasers as is the case with many birds and fishes. The role of chemical releasers that must act in part to promote sexual isolation in small rodents (Godfrey, 1958) remains to be investigated more thoroughly.

Although complete mating in the dipodids under study was not observed, certain characteristics of their precopulatory ritual render it unique. Males of *Allactaga elator* and *Jaculus orientalis* exhibit the following courtship patterns: As the female sits stationary, the male approaches and touches his nose to hers. The male may then groom the female on the head. If the female remains stationary, the male will hop to the rear and sniff the base of her tail or, if her rump is raised, he will perform an anal-genital sniff. If the female continues to remain stationary, he will straddle her tail and mount; however, she may initiate washing or sandbathing behavior or move away. In the former case, the male will pause and then hop around her to begin again with naso-nasal contact. On the other hand, if she moves away, he will follow and commence driving. While driving, the male *Allactaga* emits a buzzing sound followed by an audible squeak, whereas the male *Jaculus* emits only the buzz. This buzzing sound is unique among all the species studied. The mating behavior of *J. jaculus* has been described in part by Lewis (1965). It appears that the male *J. jaculus* utters a "chirping" call when driving the female. During the mount, which lasts less than a minute, the male employs a neck grip with his incisors. In the example cited, Lewis reports that the couple fall to one side during the terminal phases of the mount. (Compare with *Dipodomys* in Eisenberg, 1963b.)

Copulation involves the same basic movements for all species observed; however, the temporal patterning is variable when unrelated species are compared but uniform for a given species and frequently uniform for a genus. Figures 4, 5, and 6 summarize the copulatory patterns for species of *Meriones*, *Gerbillus*, *Perognathus*, and *Dipodomys*. *Dipodomys* is characterized by a long mount, whereas the other genera exhibit extremely short mounts. The *Perognathus* species and *Gerbillus nanus* generally have one bout of mounting with ejaculation on the terminal mount, whereas the more social *Meriones* exhibits a prolonged mount series with several apparent ejaculations. In this patterning, *Meriones* resembles the golden hamster, *Mesocricetus auratus* (Beach and Rabedaeu, 1959), and the Norway rat, *Rattus norvegicus* (Beach and Jordan, 1956).

Figure 4.—Mount durations and temporal patterning of mounts for two species of *Dipodomys* (vertical bars=mount and its duration; note the protracted mount with terminal ejaculation in this species; A and B=*D. panamintinus;* C=*D. nitratoides*).

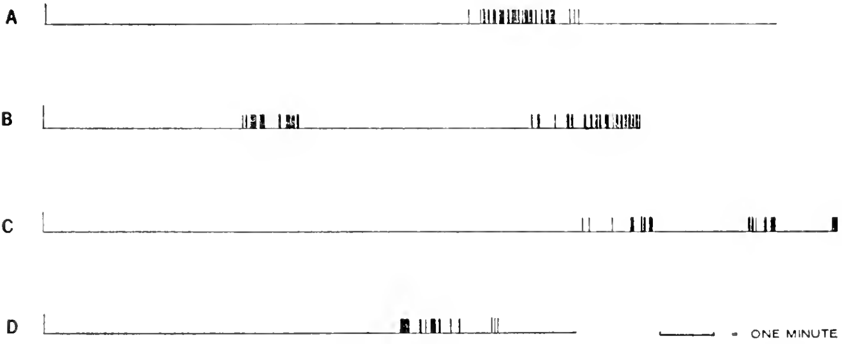

Figure 5.—Mount durations and temporal patterning of mounts for two species of *Perognathus* (A and B=*P. californicus;* C and D=*P. parvus*).

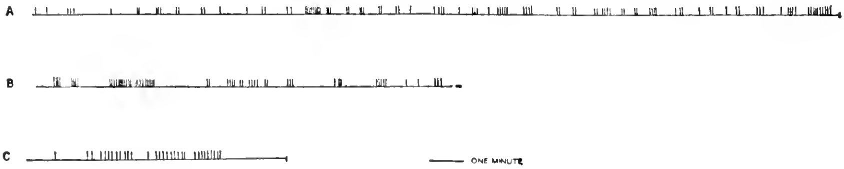

Figure 6.—Mount durations and temporal patterning of mounts for *Gerbillus* and *Meriones* (A and B=*M. unguiculatus;* C=*G. nanus*).

At the time of ejaculation, the genus *Perognathus* exhibits a singular pattern. The male *P. californicus* rolls to one side while, in the case of *P. inornatus* and *P. parvus*, the female generally twists over on her side, frequently throwing the male over also.

This brief review should indicate that considerable uniformity in sexual behavior exists when species of the same genus are compared (e.g., *Perognathus* and *Dipodomys*). Table 18 summarizes the unique features of several rodent copulation patterns. Reference to this table further indicates that considerable variability can exist among the genera of a single family. At this time the adaptive significance of such differences is not apparent although one can surmise that *Dipodomys*, which exhibits such a sustained mount, surely must copulate underground in burrows.

PAIR TOLERANCE.—The data for this section were obtained by allowing a male to remain with a female throughout the parturition and rearing of the litter. Mere tolerance without fighting by a pair in the absence of reproduction was not accepted as evidence for social tolerance (see p. 3). Since the tolerance is in part a function of space, the dimensions of the cage are listed for all experiments. Further, the species ranged in size from 12 grams to 150 grams adult weight. To correct for this size bias, I have listed for each cage size two correction factors that express the area in terms of square inches per gram of animal and square inches per animal.

In general, even females of the most tolerant species will withdraw and nest separately at the time of parturition; however, tolerant species show a compatibility that permits sustained contact without extreme aggression throughout the first few hours after parturition and on through the rearing phase. Table 19 summarizes the pairing tendencies for several species prior to and through the female's estrous period. Those that exhibited solitary nesting tendencies were not paired beyond the mating; the more tolerant species were left together through parturition. This second class of data is summarized in table 20. Table 21 summarizes the data for those species that did not breed for various known and unknown reasons. The conclusions are as follows:

Regardless of the animal's size, given at least 70 to 90 square inches per animal, the normally tolerant species will conceive and remain compatible throughout parturition. The more intolerant species require greater space in order to avoid contact. One can breed the less tolerant species either by providing them with a larger space or by utilizing a series of staged encounters through a female's estrous period followed by total separation through the parturition and rearing phases (Eisenberg and Isaac, 1963).

GROUP FORMATION THROUGH INTERNAL RECRUITMENT.—By allowing a pair to reproduce in a large cage, one can further evaluate social tolerance. In general, reproduction will continue until social contacts reach such a peak that the female fails to cycle or deserts her litter. If one adult male can keep other adults away and reduce the level of contacts to which the sexually reproducing females are subjected, then reproduction will continue. This is true for communal as well as solitary species, but the latter rely on overt aggression more often than do the former and also the solitary species are much more sensitive to social interference than is the case with the more social, communal forms. Thus, a communal species in a confined space generally will exhibit an area in the cage where several sexually active females are nesting and rearing litters. A single sexually active male will have access to these females while the remainder of the population, adults and juveniles of both sexes, dwell communally and fail to reproduce. (See also descriptions for *Mus musculus*, Crowcroft and Rowe, 1963; and *Rattus norvegicus*, Calhoun, 1963a.) Eventually reproduction may cease altogether. Figures 7 and 8 demonstrate the population growth of several species of *Peromyscus*. Note in several cases the tendency to form a stable plateau with a failure of reproduction. Note also, in the case of *P. crinitus*, the wounding caused by male aggression. Although not illustrated in these particular graphs, there is in some cases a slight trend to begin sexual activity at the onset of spring after a fall and winter plateau; however, as shown here the plateau holds. Table 22 includes the results of all population growth experiments with eight rodent species. Note that the rela-

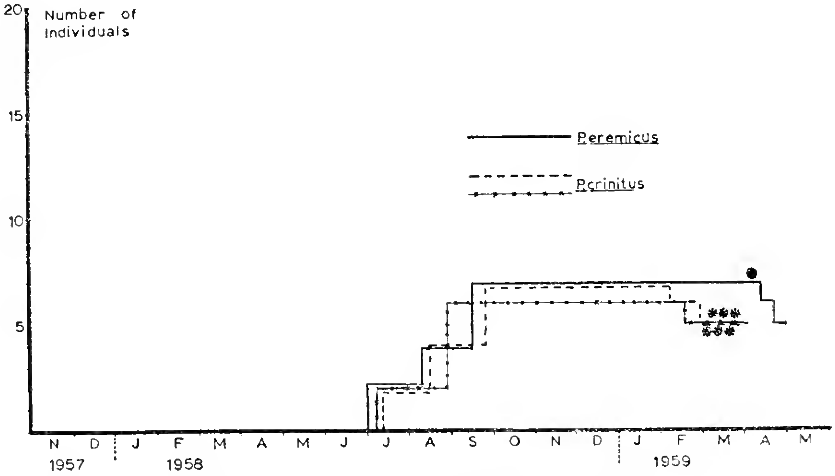

FIGURE 7.—Population growth for two species of *Peromyscus* (stars=number of individuals showing wounds during the spring fighting).

tively intolerant, solitary *Dipodomys nitratoides* ceased effective reproduction with the greatest number of square inches per animal and at approximately the same grams per unit area as did the less tolerant, semisolitary *Peromyscus crinitus.*

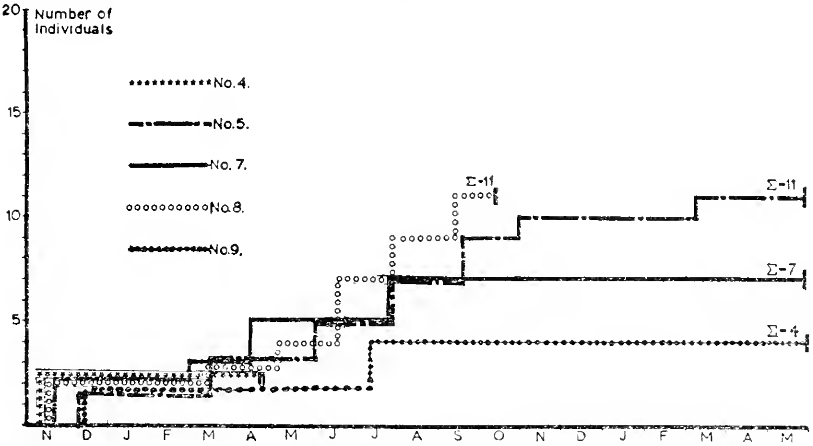

FIGURE 8.—Population growth for *Peromyscus californicus;* note the extreme stability.

An examination of the causes of population curtailment under confined conditions suggests four mechanisms: (1) During a plateau period, the females are generally anestrous with no evidence of normal estrous cycles; (2) the males born into the system show retarded gonadal maturation or even slowed growth; (3) males and even females may exhibit wounds as evidence of abnormal fighting, and such individuals may even die; (4) newborn litters may be neglected or destroyed. It would appear that different species have different thresholds of sensitivity for each of the four suggested pathologies. Thus, a solitary species, when forced to live as a pair in a small cage, may not exhibit reproduction because of a failure on the part of the female to cycle and, although they live compatibly, they are not exhibiting a natural tolerance. In a similar manner, the recruitment failure may be a result of male gonadal failure; agonistic behavior may be so intense that overt fighting and death result; and, if young are born, they may die from maternal neglect or cannibalism.

Lidicker (1965) has published the results of similar population studies utilizing *Peromyscus maniculatus, P. truei, Mus musculus,* and *Oryzomys palustris.* He concludes that species which normally do not experience high densities (or are dispersed in their native habitat) are more prone to exhibit overt fighting and cannibalism of young at high densities. My data concur in suggesting that tolerant species can form high densities with a minimum of agonistic behavior, but I believe the evidence shows that all systems of density regulation are latent in all species and only threshold differences correlate with a given social type (see p. 29).

In both Lidicker's study (1965) and my own, the species of *Peromyscus* show a tendency to increase their reproductive activity in the spring or autumn, following a cessation of reproduction after having achieved a density limit in the previous season. In one case a group of *P. eremicus* partially reared two litters, whereas two other *eremicus* groups showed increased male-male aggression in the spring but the females did not cycle. *P. crinitus* exhibited similar patterns with spring reproduction in one case and male-male antagonism in two cases (see table 22).

One may ask if a normally solitary species can be subjected to early experience that would be conducive to the production of more socially tolerant adult behavior. This may be the case with certain labile species that are adapted to exist at varying population densities. I have found, however, that strongly solitary species will not adapt to enforced proximity even as juveniles. It is true that juvenile groups can be maintained together for long periods of time, but normal reproduction does not take place. In figure 9 one can observe the reversion to agonistic behavior within eight days after a group of *Perognathus parvus* littermates were separated. Not only is normal reproduction affected, but prolonged social experience often appears to have little permanent conditioning effect with this species and others. Littermate groups of typically solitary rodents that did not exhibit normal reproduction included *Perognathus parvus*, *Dipodomys nitratoides*, *Gerbillus nanus*, and *Liomys pictus*.

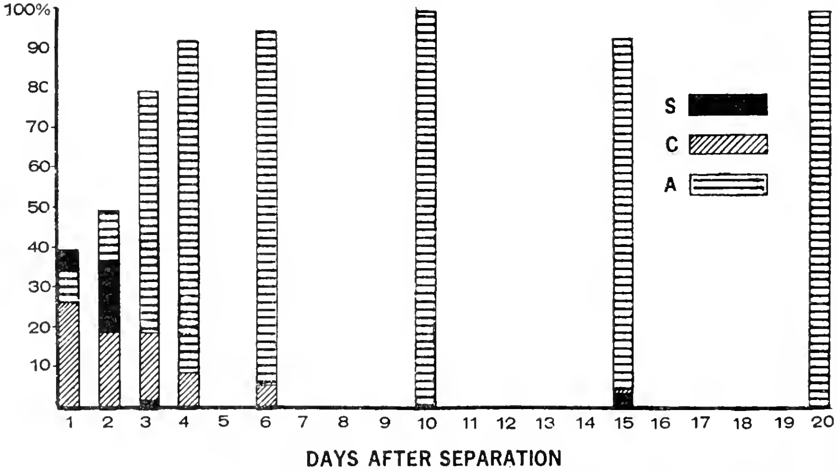

FIGURE 9.—Changing proportions of responses during *Perognathus parvus* littermate encounters after separation at 70 days of age (S=sexual behaviors; C=contact-promoting behaviors; A=agonistic behaviors).

Discussion.—As stated in the introduction to this section, rodent social systems may be classified as solitary, pair tolerance, and communal. The latter two represent in extreme form a closed social grouping, impermeable to outsiders. In reality there are rodent species that, as species, exhibit so-called loose social systems wherein the species may oscillate between a more dispersed solitary formation or a more tolerant, semicommunal system—depending upon the environmental conditions and the population density. The data from the current studies permit me to attempt several generalizations cast against the background of this social classification.

First, it appears that what separates a socially tolerant from a solitary species is the ability of the former to overcome an initially agonistic or avoidance interaction by means of special behavioral mechanisms to insure contact and familiarity without the danger of fighting. Among these mechanisms grooming appears to be important. Furthermore, a social species can achieve contact in the absence of primary sexual stimuli. A solitary species is either unable to achieve contact or, if it does, it is stressed to some extent; and, under conditions of prolonged contact, the physiological mechanisms governing the reproductive capacity break down. This difference between the extreme forms of solitary and social species is not viewed as absolute but rather as a result of differences in sensitivity to contact. Table 23 summarizes this concept whereby the same physiological pathologies are considered for each major social type.

A second generalization concerns the probable outcome of the various social tests if applied to a species of each major social type. Table 24 summarizes these predictions, which are drawn from the data in the previous section. In table 25 the species included in this study are ranked as to social tolerance according to the field and laboratory data.

General Discussion

The behavioral survey of the present study group has shown considerable uniformity in the orientation movements and fixed action patterns. Definite differences in fixed action patterns are usually correlated with corresponding differences in morphology as, for example, in bipedal locomotion. Even in such a markedly specialized behavior pattern, normally quadrupedal species have the capacity to assume a bipedal stance and even hop for a short distance. When we consider sandbathing as a fixed action pattern, we find that it is composed of two to three distinct movements that are part of the behavioral inventory of almost all mammals, and only a unique combination of these components results in a species- or taxon-specific behavior.

When we turn to social interactions, again it appears that the presence or absence of certain movements as an arbitrary criterion will not always suffice to delineate species or serve as a taxonomic tool. This results, no doubt, from the fact that small nocturnal rodents rely less on visual display in communication and, hence, less on visual releasers in sexual isolation with the result that spectacular differences in the fixed action patterns, observable in some avian and fish taxa, are not to be found. Certainly visual communication by movements, postures, and coat color are important in some mammalian taxa such as the primates and ungulates, but they are obviously less important in the small, nocturnal mammalian taxa. Again and again in this study, species-specific behavior patterns are found to be variations on universal neuromuscular patterns. Differences and similarities in the frequency of expression are more reliable indicators of nonrelationship or affinity than is the criterion of presence or absence of expression. In some cases even a frequency analysis fails to indicate affinity above the generic level, for example, in the temporal patterning of copulation. Thus, employing the presence or absence criterion, some behavior patterns will be family-specific, others genus-specific, and even more rarely a pattern will be species-specific; however, analysis of the discrete temporal patterning or relative frequency of occurrence almost always will demonstrate species differences although the adaptive significance of such differences may be unclear (consider again sandbathing). Since such an equipotentiality exists in the repertoires of these mammals—although frequency of occurrence serves to clearly delineate species—I can only conclude that differences in thresholds exist that account for the differential frequencies of expression. Thus, the behavior of a given species may be described in terms of the most probable sequence or set of patterns rather than in terms of its total potentiality for expression. In this sense, species-specific behavior describes the normal expression for a given environment and conforms to Leyhausen's "Verhaltenshäufigkeit" (Leyhausen, 1965).

By applying this definition of species-specific behavior to the social structure observed in different species, it is possible to characterize a given species as belonging to one of several categories of social behavior. For example, *Perognathus parvus* can be kept in groups with little overt fighting. This is especially true if the group is composed of littermates. Although they can tolerate one another, they do not reproduce. Utilizing reproductive success as the criterion for a natural social grouping, we can conclude that, although *P. parvus* has a range tolerance that permits group life without overt aggression leading to wounding, it does not have the ability to reproduce when subjected to social contacts above some minimum level. In the case of this species, the minimum appears to be only the pair association through estrus. Thus, as outlined in the previous section, there are probably several physiological mechanisms that are affected adversely in terms of reproductive success by social contacts. The relative thresholds for these mechanisms varies from species to species depending on their genetic makeup.

The adverse effects of high population densities on the growth and maturation of young rodents has been known for some time (Chitty, 1955), and the cessation of reproduction at high densities through a failure of ovarian and testicular function has been studied from a physiological standpoint by many workers (see Christian, 1963). Recently Calhoun (1963b) has developed an elaborate theory of social behavior based on the concepts of species-specific differences in social tolerance and the evolution of social groups. Wynne-Edwards (1962) has put forth an all-embracing theory on evolution of social groups and the adaptive value of self-regulatory mechanisms whereby populations are kept below maximum numbers by such reproductive failures as outlined previously. I do not wish to examine these various theories from a critical standpoint but only wish to point out that the evidence favors my interpretation of species differences in social tolerance and, further, that these differences have resulted from processes of natural selection to produce a social type adapted to its particular niche. I have attempted to outline a methodology whereby one can study social tolerance by means of several techniques and arrive at some quantitatively based conclusions regarding species differences in sociability.

There remains a further consideration. Given the demonstration that the rodents under study exhibit species-specific social tendencies, what adaptive correlates can one discern? The arid-adapted subfamily Gerbillinae spans the range from a relatively solitary form, *Gerbillus nanus*, to the more tolerant, communal *Tatera indica*. *Jaculus orientalis* and *Allactaga elator* are semitolerant; however, the family Heteromyidae, whether forest-adapted or arid-adapted, appears to be a solitary form. Within the genus *Peromyscus*, the desert species *P. crinitus* is intolerant whereas the equally xeric-adapted *P. eremicus* is more tolerant. Adaptation to xeric habitats with dispersed food supplies is not necessarily in and of itself conducive to selection for a dispersed, solitary existence. Equally important are other aspects of the species ecology including its mode of assembly of foodstuffs, its shelter construction, and its reproductive rate. At this point it seems safe to say that the Heteromyidae have retained the phylogenetically ancient trait of solitary existence because of the adaptive advantage accruing from its defense of cached food. It is not the case, however, that this social trait is always a concomitant of caching.

It is noteworthy that *Gerbillus* (*Dipodillus*) *nanus* resembles the silky pocket mice of the heteromyid genus *Perognathus* in several respects. *G. nanus* is sensitive to crowding, and captive reproduction is possible only by means of a simultaneous encounter technique. During male-anestrous female encounters, the partners exhibit mutual avoidance or agonistic patterns of behavior. Sandbathing as a means of chemical communication is displayed by this species and, after mating, the male and female return to behavior patterns expressing intolerance. All the preceding attributes also characterize the behavior of *Perognathus parvus*, *P. inornatus*, and *P. longimembris* (see p. 22 and Eisenberg, 1963b). Returning again to tables 2 through 5, there is a marked similarity between *G. nanus* and the silky pocket mice with respect to habitat, general ecology, size, and reproduction. This total convergence may well be indicative of a special adaptation syndrome that correlates with the attribute of social intolerance; however, until further comparisons are made on the energy needs and recruitment rates of different desert-adapted species, the selective advantage of the various social systems in all probability will remain obscured.

Summary

Selected species from three rodent families have been studied, including the following genera: Cricetinae: *Peromyscus;* Gerbillinae: *Tatera, Gerbillus, Dipodillus, Pachyuromys,* and *Meriones;* Dipodidae: *Jaculus, Allactaga;* Heteromyidae: *Heteromys, Liomys, Perognathus,* and *Dipodomys.* Species have been selected in order to give a series of forms that have evolved in a convergent or parallel fashion in adapting to desert environments.

The discrete behavior patterns exhibit a profound similarity, but species and generic differences can be discerned. Sandbathing has been selected for intensive study and it has been found that functional sandbathing has evolved independently in all xeritic-adapted forms from the same basic movement patterns. Differences in the frequency of occurrence rather than in the form of the movement have proved to be the most effective criterion for delineating taxon-specific differences.

Social behavior has been investigated with a standard methodology including staged encounters, pair tolerance, and group formation tests. Using reproductive success as the criterion for describing a functional social group, it has been found that each species can be characterized into one of three general social types. The different social types appear to represent different degrees of tolerance for the presence of conspecifics. All social types will exhibit similar social pathologies under social stress, but the more social species have higher thresholds of tolerance. It is proposed that species-specific social tolerance represents an adaptation to average densities that are of selective advantage to the species under consideration. The adaptive correlates of the differing social systems remain, in part, unknown.

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TABLE 1.—*List of species in the present study with geographical origins and comments on maintenance*

Species	Original numbers		Origin	Number of captive bred litters	Comments on maintenance
	Males	Females			
CRICETINAE					
Peromyscus maniculatus	6	7	Alameda Co., Calif.	30+	see Eisenberg (1962a, 1963a)
californicus	5	6	Alameda Co., Calif.	22+	"
eremicus	2	4	San Diego Co., Calif.	9	"
crinitus	2	3	San Bernardino Co., Calif.	8	"
HETEROMYIDAE					
Heteromys lepturus	0	2	Cintapec in Veracruz, Mexico	–	see Eisenberg (1963b)
anomalus	2	2	Trinidad, B.W.I.	0	"
desmarestianus	2	1	Costa Rica	0	as *anomalus*
Liomys pictus	3	6	Mazatlan in Sinaloa, Mexico	7	see Eisenberg (1963b)
Perognathus californicus	4	2	Santa Cruz and San Benito Cos., Calif.	3	"
inornatus	1	2	San Benito and San Joaquin Cos., Calif.	0	"
parvus	8	4	Oliver, B.C., Canada	2	as *inornatus*
Microdiopodops pallidus	7	4	Mineral and Churchill Cos., Nev.	0	see Eisenberg (1963b)
Dipodomys merriami	3	4	San Diego and Kern Cos., Calif.	3	"
nitratoides	4	3	San Benito and Kern Cos., Calif.	12	"
panamintinus	3	2	Kern Co., Calif.	2	"
GERBILLINAE					
Gerbillus gerbillus	2	1	Abu Rawash, Egypt	0	as *Perognathus*
(*Dipodillus*) *nanus*	5	7	West Pakistan	1	"
Meriones unguiculatus	10	10	laboratory stock	5	as *Peromyscus*
hurrianae	2	2	West Pakistan	7	"
Pachyuromys duprassi	1	0	North Africa	–	as *Perognathus*
Tatera indica	3	2	West Pakistan	11	as *Peromyscus*
DIPODIDAE					
Allactaga elator	5	2	West Pakistan	0	as *Dipodomys*
Jaculus jaculus	2	0	Abu Rawash, Egypt	–	"
orientalis	1	1	Amariya, Egypt	1	"

TABLE 2.—*Comparisons of reproduction*

Species	Gestation (days)	Age at eye opening (days)	Litter size	Authority
CRICETINAE				
Peromyscus maniculatus	22–24	11–16	2–9	present study
crinitus	24	12–15	3–5	" "
eremicus	21	12–14	2–4	" "
californicus	21–25	14–16	1–3	" "
GERBILLINAE				
Gerbillus nanus	23	14–15	3	" "
Tatera indica	26	17–19	3–8	" "
Meriones unguiculatus	25	17–19	3–6	" "
hurrianae	25	14–15	5–7	" "
Pachyuromys duprassi	21	20–21	–	Petter (1961)
HETEROMYIDAE				
Heteromys melanoleucus	?	20–21	ca. 4	Rood (1963)
desmarestianus	?	?	3–4	Eisenberg (1963b)
Liomys pictus	24–26	18–21	2–5	"
Perognathus californicus	25	14–16	2–5	"
parvus	24–25	14–15	2–8	present study
Dipodomys merriami	33	11–12	av. 2	Eisenberg (1963b)
nitratoides	32	10–11	av. 2	"
panamintinus	29	17–18	3–4	"
DIPODIDAE				
Allactaga elator	?	–	2–6	Ognev (1963)
Jaculus orientalis	28–30	35–36	3–7	present study and Kirmiz (1962)

Table 3.—*Comparisons of morphology*

Species	Adult weights (gms)[1]	Ratio of hind foot length to body length[2]
Cricetinae		
Peromyscus maniculatus	18–34	.23
crinitus	14–23	.25
eremicus	18–24	.24
californicus	35–40	.24
Gerbillinae		
Gerbillus gerbillus	25–49	.35
nanus	15–36	.30
Tetera indica	70–150	.23[3]
Meriones unguiculatus	76–95	.25[3]
hurrianae	60–95	.25[3]
Pachyuromys duprassi	30–65	–
Heteromyidae		
Heteromys anomalus	45–60	–
desmarestianus	61–78	.26–.28
Liomys pictus	35–51	.21–.24
Perognathus californicus	18–25	.31
parvus	17–26	.27
inornatus	10–18	.27
Microdipodops pallidus	10–16	.37
Dipodomys nitratoides	28–43	.36
merriami	30–40	.36
panamintinus	44–68	.32–.33
Dipodidae		
Allactaga elator	45–71	≥.50[3]
Jaculus jaculus	50–80	≥.50[3]
orientalis	130–225	≥.50[3]

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[1] Based on captive weights, which average higher than field weights.

[2] Computed from measurements in Petter (1961), Eisenberg (1963b), Hall and Kelson (1959).

[3] Taken from Hatt (1932).

TABLE 4.—*Comparisons of habitat*

Species	Habitat type	Authority
CRICETINAE		
Peromyscus maniculatus gambelii	Oak-woodland, chaparral	Eisenberg, 1962a
crinitus stephensi	High altitude desert	Eisenberg, 1963a
eremicus eremicus	Low altitude desert	" "
californicus parasiticus	Oak-woodland, chaparral	Eisenberg, 1962a
GERBILLINAE		
Gerbillus gerbillus	Sand desert	Zahavi and Wahrman, 1957
nanus	Soil desert	"
Tatera indica	Semidesert, near water sources	Petter, 1961
Meriones unguiculatus	Semidesert	Deduced from range maps
hurrianae	Semidesert	Petter, 1961
Pachyuromys duprassi	Sand and soil desert	" "
HETEROMYIDAE		
Heteromys (all species)	Tropical evergreen forest	Eisenberg, 1963b
Liomys pictus	Subtropical thorn forest	" "
Perognathus californicus	Semiarid to arid brush	" "
inornatus	Seasonally arid grassland	" "
parvus	Semidesert	" "
Microdipodops pallidus	High altitude, sand desert	" "
Dipodomys merriami	Seasonally arid grassland to sand desert	" "
nitratoides	Seasonally arid grassland to sand desert	" "
panamintinus	High altitude pebble desert	" "
DIPODIDAE		
Allactaga elator	Pebble desert	Ognev, 1963
Jaculus jaculus	Desert	Kirmiz, 1962
orientalis	Desert	" "

Table 5.—*General comparisons of behavior and ecology*

Species	Activity period	Food preference	Water source	Hibernation
CRICETINAE				
Peromyscus (all species)	Nocturnal	Seeds	Needs free water or succulents	No[1]
GERBILLINAE				
Gerbillus gerbillus	"	Seeds	Metabolic water	No
nanus	"	Seeds and insects	" "	No
Tatera indica	"	Seeds	Succulent plants	No
Meriones unguiculatus	Semidiurnal	Seeds and insects	" "	No
hurrianae	"	" " "	" "	No
Pachyuromys duprassi	Nocturnal	" " "	Metabolic water(?)	(?)
HETEROMYIDAE				
Heteromys (all species)	"	Seeds and green plants	Needs free water	No
Liomys pictus	"	"	Free water or succulents	No
Perognathus californicus	"	Seeds and insects	Can live on metabolic water	Periods of torpor
parvus	"	" " "	"	Yes
inornatus	"	" " "	"	Periods of torpor
Microdipodops pallidus	"	" " "	"	Yes
Dipodomys merriami	"	Seeds	"	No
nitratoides	"	"	"	No
panamintinus	"	"	"	No
DIPODIDAE				
Allactaga elator	"	"	Metabolic water	Yes
Jaculus jaculus	"	"	" "	Periods of torpor
orientalis	"	"	" "	"

[1] *P. eremicus* can exhibit seasonal torpor (see Macmillan, 1965).

Table 6.—*Comparisons of sandbathing movements*

Species	Number of subjects	Number of observation periods	Average time of observation period (seconds)	Total number of acts	Proportion of total	
					Side rubs	Ventral rubs
DIPODIDAE						
Allactaga elator	3	62	249	274	.920	.080
HETEROMYIDAE						
Dipodomys deserti	2	38	340	425	.675	.325
nitratoides	2	11	456	261	.61	.39
Perognathus californicus	4	51	308	305	.55	.45
parvus	14	45	263	112	.77	.23
GERBILLINAE						
Meriones unguiculatus	11	37	372	44	1.00	.00
Gerbillus nanus	4	51	270	189	.99	.01

TABLE 7.—*Integration of sandbathing movements*

Species	Number of couplets beginning with a side rub	Proportion of total		
		Side rub followed by—		
		Opposite side	Same side	Ventrum
DIPODIDAE				
Allactaga elator	113	.49	.42	.09
HETEROMYIDAE				
Dipodomys				
deserti	133	.35	.20	.44
nitratoides	96	.21	.60	.19
Perognathus				
californicus	126	.37	.21	.42
parvus	71	.45	.18	.36
GERBILLINAE				
Meriones unguiculatus	13	1.00	0	0
Gerbillus nanus	55	.88	.12	0

TABLE 8.—*Similarities in maintenance behavior* (O=not observed, X=occasionally observed, XX=typical behavior)

Species	Incisor and snout tamping in borrow construction	Chopping of foodstuffs	Caching	Bipedal locomotion
CRICETINAE				
Peromyscus[1]	0	0	XX	0
GERBILLINAE				
Meriones unguiculatus	X	XX	X	0
hurrianae	X	XX	X	0
Tatera indica	X	XX	X	0
Gerbillus nanus	0	0	X	0
gerbillus	0	0	XX	0
Pachyuromys duprassi	0	0	X	0
DIPODIDAE				
Jaculus jaculus	XX	0	0	XX
orientalus	XX	0	0	XX
Allactaga elator	XX	0	X	XX
HETEROMYIDAE				
Heteromys[1]	0	0	XX	0
Liomys[1]	0	0	XX	0
Perognathus[1]	0	0	XX	0
Microdipodops pallidus	0	0	XX	XX
Dipodomys[1]	0	0	XX	XX

---

[1] All species studied.

TABLE 9.—*Similarities in marking and sandbathing* (all components are shown by all species when fur is wet, a phenomenon not considered in the present comparison; O=not noted, X=occasional, XX=typical of most sequences)

Species	Integrated components in functional pelage dressing with a secondary marking function			Marking movements which are generally independent of pelage dressing		
	Ventrum rub	Side rub	Rolling over	Ventrum rub	Side rub	Perineal drag
CRICETINAE						
Peromyscus maniculatus	0	0	0	0	0	XX
californicus	0	0	0	0	0	XX
eremicus	0	0	0	0	0	XX
crinitus	0	XX	0	0	0	XX
GERBILLINAE						
Meriones unguiculatus	0	XX	X	XX	0	XX
hurrianae	0	XX	X	XX	0	XX
Gerbillus gerbillus	0	XX	0	0	0	XX
nanus	0	XX	0	0	0	XX
Tatera indica	X	XX	X	0	0	XX
Pachyuromys duprassi	0	XX	X	0	0	XX
DIPODIDAE						
Allactaga elator	X	XX	0	0	0	XX
Jaculus jaculus	X	XX	0	0	0	XX
orientalis	X	XX	0	0	0	XX
HETEROMYIDAE						
Heteromys anomalus	0	0	0	X	0	XX
lepturus	0	0	0	X	0	XX
Liomys pictus	0	0	0	X	X	XX
Perognathus[1]	XX	XX	0	0	0	XX
Microdipodops[1]	XX	XX	0	0	0	XX
Dipodomys[1]	XX	XX	0	0	0	XX

[1] All species studied.

TABLE 10.—*Response totals for male-anestrous female encounters in a neutral arena* (parentheses enclose the average number of bouts per encounter)

Species	Number of encounters	Duration of encounter	Total and average frequency of behavior pattern			
			Grooming	Uprights	Chase	Fight
Peromysus maniculatus[1]	18	30 min.	17(.9)	34(1.9)	15(.8)	4(.2)
Liomys pictus	21	“	2(.1)	7(.3)	85(4.0)	7(.3)
Dipodomys panamintinus	19	“	2(.1)	15(.8)	43(2.3)	2(.1)
Microdipodops pallidus	14	“	2(.1)	13(.9)	19(1.3)	2(.1)

[1] Territorial encounter only, which accounts for the rather high level of chasing that occurred prior to the grooming relationship.

TABLE 11.—*Response totals for males in a male-anestrous female encounter* (counts made for the first 200 seconds of the encounter only; all data from a neutral arena; parentheses enclose the average number of bouts per encounter)

Species	Number of encounters	Range and average frequency of behavior pattern				
		Naso-nasal	Naso-anal	Grooming	Chase-flight	Fight
Meriones unguiculatus	16	3-10(6.4)	0-9(3.2)	1-7(2.9)	0-2(.3)	0
Gerbillus gerbillus	2	6-7(6.5)	1-5(3.0)	1(1.0)	0(0)	0-2(1.0)
nanus	20	1-14(4.4)	0-2(.2)	0-3(.5)	0-2(.7)	0
Dipodomys panamintinus	6	0-2(.5)	0-10(2.5)	0	0-9(2.0)	0

TABLE 12.—*Response totals for males in a male-anestrous female encounter* (counts made for the first 200 seconds of the encounter only; all data from a territorial encounter box; parentheses enclose the average number of bouts per encounter)

Species	Number of encounters	Range and average frequency of behavior pattern				
		Naso-nasal	Naso-anal	Grooming	Chase-flight	Fight
Gerbillus nanus	9	1-3(.8)	0	0-1(.1)	0-4(1.4)	0-4(.4)
Allactaga elator	9	0-7(2.7)	0-6(1.1)	0-3(1.0)	0-1(.1)	0
Perognathus californicus	15	0-1(.07)	0-2(.26)	0	0-6(2.4)	0-19(5.6)
Meriones unguiculatus	3	1-2(1.3)	1-2(1.3)	1-2(1.3)	0	0

TABLE 13.—*Behavioral changes exhibited by the male* Dipodomys panamintus *through estrus in male-female encounters* (NN=Naso-nasal, NA=Naso-anal, H/H=Head over head under, NAm=Mutual naso-anal, Cu=Crawling under, Gr=Grooming, Dr=Driving, Mnt=Mounting, Thr=Mounts with thrusting, Ch=Chase and attack leaps, Fi=Fight, Fl=Flight and escape leaps, Up=Upright, SB=Sandbathing, DK=Digging and kick back, W=Washing (exclusive of postcopulatory wash), M=Marking, Si=Sitting, Ex=Exploring)

Date	Total number of acts	Duration of encounter (secs)	Percent of total for each pattern								
			Contact promoting						Sexual		
			NN	NA	H/H	NAm	Cu	Gr [2]	Dr [3]	Mnt	Thr
VI/25/63	55	360	1.8	1.8	0	0	0	-	10.9	0	0
VI/26/63 [1]	171	780	.58	14.6	11.1	0	29.8	-	27.5	0	0
VI/27/63	42	350	0	0	0	0	0	-	2.4	0	0
VII/9/63	50	330	0	0	4.0	0	0	-	12.0	0	0
VII/10/63 [1]	201	1260	0	4.5	11.9	0	6.9	-	16.4	.99	25.4
VII/10/63 [1]	70	1966	0	0	4.3	0	0	-	1.4	20.0	61.4
VII/11/63	14	22	0	0	0	0	0	-	0	0	0

Date	Total number of acts	Duration of encounter (secs)	Percent of total for each pattern									
			Agonistic				Individual					
			Ch [3]	Fl	Fl [3]	Up	SB [3]	DK [3]	W [3]	M	Si [3]	Ex [3]
VI/25/63	55	360	37.8	0	4.7	0	1.82	14.5	1.82	3.6	9.1	10.9
VI/26/63 [1]	171	780	9.9	1.2	0	0	0	14.0	0	2.3	.58	0
VI/27/63	42	350	38.0	0	0	0	2.4	33.4	0	0	11.9	11.9
VII/9/63	50	330	34.0	2.0	4.0	0	2.0	14.0	0	2.0	26.0	0
VII/10/63 [1]	201	1260	6.3	.5	1.5	0	0	7.0	0	.5	13.4	2.0
VII/10/63 [1]	70	1966	8.5	0	0	0	0	0	0	0	2.9	0
VII/11/63	14	22	50.0	0	0	0	7.2	21.4	7.2	7.2	0	7.2

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[1] Date of estrus.

[2] Grooming during head over head under and mount.

[3] Ten seconds or less in duration was counted as one bout (see Methods).

Table 14.—*Behavioral changes exhibited by male of* Perognathus parvus *through estrus in a male-female encounter* (see table 13 for abbreviations)

Date	Total number of acts	Duration of encounter (secs)	Percent of total for each pattern								
			Contact promoting						Sexual		
			NN	NA	H/H	NAm	Cu	Gr	Dr [2]	Mnt	Thr
II/3/63	117	940	7.7	0	0	0	0	1.7	7.7	2.6	0
II/5/63 [1]	102	770	9.8	0	0	0	0	1.0	14.7	8.8	5.9
II/7/63	53	400	9.4	0	0	0	0	0	5.7	0	0
II/14/63	30	270	10.0	0	0	0	0	0	3.3	13.3	0
II/15/63	23	210	0	0	0	0	0	0	13.0	17.3	0
II/18/63 [1]	84	660	8.3	0	0	0	0	5.9	9.5	7.1	4.8
II/21/63	79	630	16.5	0	0	0	0	5.0	22.8	10.2	0

Date	Total number of acts	Duration of encounter (secs)	Percent of total for each pattern									
			Agonistic				Individual					
			Ch [2]	Fi	Fl [2]	Up	SB [2]	DK [2]	W [2]	M	Si [2]	Ex [2]
II/3/63	117	940	4.3	0	0	2.6	10.3	4.3	7.7	.9	50.4	0
II/5/63 [1]	102	770	3.9	0	0	6.9	2.9	1.9	1.9	1.0	37.3	0
II/7/63	53	400	15.1	0	0	11.3	11.3	11.3	11.3	3.8	20.8	0
II/14/63	30	270	0	3.3	10.0	0	0	0	0	0	56.8	3.3
II/15/63	23	210	0	4.3	8.7	0	0	4.4	0	0	43.5	8.8
II/18/63 [1]	84	660	15.5	0	0	2.4	1.2	2.4	7.1	0	34.6	7.1
II/21/63	79	630	0	2.5	7.6	11.4	0	3.8	1.3	0	19.0	0

[1] Date of estrus.

[2] Ten seconds or less in duration was counted as one bout (see Methods).

Table 15.—*Behavioral changes exhibited by male of* Gerbillus nanus *through estrus in a male-female encounter* [2] (see table 13 for abbreviations)

Date	Total number of acts	Duration of encounter (secs)	Percent of total for each pattern								
			Contact promoting						Sexual		
			NN	NA	H/H	NAm	Cu	Gr	Dr [2]	Mnt	Thr
XII/19/63	10	290	0	0	0	0	0	0	0	0	0
I/9/64 [1]	211	890	17.5	0	0	0	0	0	36.0	13.3	1.9
I/11/64	10	75	0	0	0	0	0	0	0	0	0

Date	Total number of acts	Duration of encounter (secs)	Percent of total for each pattern							
			Agonistic				Individual			
			Ch [2]	Fi	Fl [2]	Up	SB [2]	DK [2]	W [2]	M
XII/19/63	10	290	20.0	0	60	0	20.0	0	0	0
I/9/64 [1]	211	890	.47	1.0	.47	3.3	.47	2.4	11.4	.47
I/11/64	10	75	0	100	0	0	0	0	0	0

[1] Date of estrus.

[2] Ten seconds or less in duration was counted as one bout (see Methods).

TABLE 16.—*Tendency to sandbathe at same locus during a male-female encounter*[1]

Species	Number of encounters with sandbathing	Average number of male loci	Average number of female loci	Percent of overlap
Gerbillus nanus	10	1.3	1.2	50
Allactaga elator[2]	3	1.0	–	–
Meriones unguiculatus[3]	9	1.0	1.25	0

[1] For similar data from the Heteromyidae, see Eisenberg, 1963c.

[2] These species have been known to exchange sandbathing loci, but this tendency is of infrequent occurrence.

[3] Side rubbing only.

TABLE 17.—*Comparisons of male contact-promoting and sexual behaviors for selected species of rodents* (Data from male-female encounters when female in pro-estrus or estrus; see table 12 for abbreviations)

Species	Number of encounters	Total acts recorded	Relative proportion of each behavior pattern for all bouts of contact-promoting and sexual behavior recorded							
			NN	NA	H/H	NAm	Cu	Gr[1]	Dr	Mnt
Liomys pictus	5	107	.02	.11	.05	.01	.02	.44	.14	.21
Perognathus californicus	9	165	.07	.07	.01	.02	.01	.21	.53	.09
parvus	6	142	.29	0[2]	0[2]	0	0	.08	.38	.24
Dipodomys panamintinus	8	211	.01	.06	.12	.11	.11	.02	.30	.25
Meriones unguiculatus	5	133	.19	.22	.03	0[2]	.02	.11	.19	.25
Gerbillus nanus	3	302	.14	0[2]	0[2]	.03	0	.16	.51	.19
gerbillus	1	61	.39	.10	.07	.03	0	.08	.21	.11
Allactaga elator	1	47	.21	.17	.17	0	0	.17	.17	.11

[1] Grooming generally occurs during mounting but was not scored separately.

[2] Noted in other series with anestrous females but of infrequent occurrence.

Table 18.—*Comparison of copulation patterns for selected rodents* (N=number of separate observation periods)

Species	N	Number of mounts in one series	Mount durations (secs)		Interval durations in series of mounts (secs)		Series duration (mins and secs)	Special characteristics
			Range	Average	Range	Average		
HETEROMYIDAE								
Perognathus californicus	5	5-14	1-5	2.3	1-16	4.7	70″-96″	Male falls to one side at conclusion of mount with ejaculation
Perognathus parvus	3	5-7	1-10	2.7	2-64	12	58″-82″	Female and often male falls to one side at conclusion of mount with intromission as does *P. inornatus*
Dipodomys panamintinus	3	2-3	30-513	-	1-20	-	8′12″-8′33″	Long mount with terminal ejaculation
nitratoides	1	3	60-150	-	30-120	-	8′30″	Long mount with terminal ejaculation
GERBILLINAE								
Gerbillus nanus	1	1-10	1-3	1.5	6-20	14	60″-70″	No special attributes
Meriones unguiculatus	1	1-9	.5-3.5	1.1	1-15	4.3	170″-200″	No special attributes

TABLE 20. *Pairing tendencies of tolerant to semitolerant rodents*

Species	Number of experiments	Cage size (sq. in.)	Sq. in. per gm.	Sq. in. per animal	Pairing tendency	Remarks
Peromyscus maniculatus	3	328	8	164	Nest together	♂ tolerated at partus
"	3	776	18.5	388	"	"
crinitus	3	328	11	164	"	No breeding
"	1	772	25.8	388	"	♂ separate at partus
"	2	1110	37	555	"	"
eremicus	2	328	8	164	"	♂ tolerated at partus
"	2	776	18.5	388	"	"
"	1	1120	28	555	"	"
californicus	2	328	3.5	164	"	"
"	6	776	8.5	388	"	"
Meriones unguiculatus	2	550	5.5	275	"	♂ must be removed at partus
	1	1728	17	864	"	"
"	1	2304	23	1152	"	♀ nests alone at partus
hurrianae	4	180	1.8	90	"	"
Tatera indica	2	180	1.3	90	"	"
"	2	1728	12.3	864	"	"
"	1	2304	17	1152	"	"
Jaculus orientalis	1	2304	14.1	1152	"	♀ builds separate nest at partus

TABLE 21. *Pairing tolerance without the production of young*

Species	Number of experiments	Cage size (sq. in.)	Sq. in. per gm.	Sq. in. per animal	Pairing tendency	Remarks
Heteromys anomalus	1	180	2.0	90	Nest together	No young
Perognathus parvus [1]	2	550	21	275	"	"
Dipodomys nitratoides [1]	3	776	10	388	"	"
merriami [1]	3	1110	15	555	"	"
Meriones unguiculatus [1]	5	180	1.8	90	"	"
Gerbillus gerbillus	1	180	4.5	90	"	"
"	1	2304	58	1152	"	"
nanus [1]	2	550	21	275	"	"
Allactaga elater	2	1728	21	864	"	"
"	2	2304	32	1152	Some tendency to nest separately	"

[1] Species that were bred in either a greater space or by an encounter technique. Reproductive failure appears to result from either an inhibition of the female cycle or failure to implant.

TABLE 22.—*Colony growth experiments*

Species	Founding number	Number of experiments	Number animals at termination	Cage size (Sq. in.)	Range of terminal density		Ultimate cause of colony failure
					Sq. in./Gm.	Sq. in./animal	
Peromyscus							
a) *maniculatus*	2	3	26, 19, 19	776	2.0-1.5	30-40	Failure of ♀ cycle and some loss of young
crinitus	2	1	8	776	6.5	97.5	Failure of ♀ cycle (in part)
eremicus	2	2	19, 10	776	1.5-3.8	76-30	Failure of ♀ cycle with adult fighting
californicus	2	6	11, 11, 7, 10, 4,2	776	1.5-4.1	67.5-184.5	Failure of ♀ estrous cycle
b) *crinitus*	2	2	7, 6	1110	10.5-12.2	158-183	Mortality by adult fighting plus a failure of the ♀ cycle
eremicus	2	1	7	1110	7.9	158	Mortality by adult fighting plus a failure of the ♀ cycle
Dipodomys nitratoides	2	1	14	5010	10(9.9)	360	Extended fighting among the adults and abandonment of the young by the mother
Tatera indica	6	1	11	1728	1.5	106	Abandonment of the young by mothers; some fighting among males only
“	8	1	24	1728	.8	53	
“	17	1	23	1728	.8	50	

TABLE 23.—*Relative differences in the thresholds of four behavioral pathologies associated with crowding (hypothetical)* (A=extended proximity of adult male causes female to stop estrous periods; B=in confinement the agonistic tendencies result in high mortalities; C=proximity of adults causes female to neglect or destroy young; D=proximity of adult male inhibits growth and maturation of young males)

Type of social system	Thresholds for exhibition of pathological behavior			
	A	B	C	D
Social group				
Communal (extended family group)	High	High	High	Intermediate
Pair unit only	High	Intermediate	Intermediate	Low
Loose social system	Intermediate	Intermediate	Low	Low
Solitary (dispersed)	Low	Low	Low	Low

TABLE 24.—*Field and laboratory correlates for the three testing situations*

Distribution in field	Encounter behavior (male female)		Pairing tendencies	Reproduction in confined populations
	Neutral arena	Territorial box		
Communal	Contact-promoting	Brief defense; then contact-promoting	Sustained pair tolerance through parturition and rearing	Sustained with later curtailment
Pair association	Avoidance; then contact-promoting	Brief defense; then contact-promoting	Pairing up to parturition; female will tolerate male through rearing phase	Early curtailment
Solitary (dispersed)	Agonistic or avoidance	Agonistic and avoidance	Pairing only through estrus (normal); sustained pairing with no reproduction (pathological)	None, if area is small

TABLE 25.—*Social trends for selected species*

Social tendencies	HETEROMYIDAE	GERBILLINAE	CRICETIDAE	DIPODIDAE
Social group				
Communal		*Tatera indica*		
Pair tolerance			*Peromyscus californicus* *Peromyscus maniculatus* *Peromyscus eremicus*	
Intermediate tolerance	*Heteromys anomalus*	*Meriones hurrianae* *Meriones unguiculatus* *Gerbillus gerbillus*	*Peromyscus crinitus*	*Jaculus orientalis* *Allactaga elater*
Solitary (dispersed)	*Heteromys desmarestianus* *Liomys pictus* *Dipodomys panamintinus* *Microdipodops pallidus* *Perognathus californicus* *Perognathus parvus* *Dipodomys merriami* *Dipodomys nitratoides*	*Gerbillus nanus*		

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A New Genus and New Species Of Zoarcid Fish From the North Pacific Ocean

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Dr. Teodor Nalbant (Institutul de Cercitari Piscicole, Bucharest, Rumania) has kindly sent to me for examination two specimens of a zoarcid fish that represent an undescribed new genus and new species in the family Zoarcidae. I appreciate Dr. Nalbant's kindness in giving me permission to report on these unique specimens.

Nalbantichthys, new genus

Type-species: *Nalbantichthys elongatus*, new species.

This new genus is characterized by the slender elongate scaleless body with loose skin; pelvic fins absent; small elongate gill opening situated completely dorsal to base of very small pectoral fin; next to last vertebra (fig. 3) with rudiments of three neural and three (possibly four) hemal spines (otherwise there is a single neural and single hemal spine for each anteriorly placed vertebra), and one fin ray for each vertebra except the penultimate vertebra and hypural plate; single median interorbital pore; nasal openings represented by a pair of tubular nostrils; vomer and palatines toothless; jaws, especially at the tips, with strong conical teeth; branchiostegal rays seven; vertebrae 25+119 to 125, totaling 144 to 150.

Nalbantichthys is more closely related to *Melanostigma* Günther than to any other genus of zoarcid fishes because both genera have the gill opening restricted to a pore entirely above the base of the pectoral fin in combination with scaleless loose skin and pelvic fins absent. These characters exclude the more or less related genera *Gymnelus* Reinhardt, *Lyocara* Gill, *Oidiphorus* McAllister and Rees, and *Maynea* Cunningham, all with the gill opening extending downward below the dorsal edge of the pectoral fin base.

Nalbantichthys differs from *Melanostigma* by lacking teeth on vomer and palatines and a much greater number of vertebrae—144 to 150 instead of 83 to 99 vertebrae (McAllister and Rees, 1964, Nat. Mus. Canada, Bull. 199, appendix table p. 110 [p. 88 gives 83 to 93 vertebrae]).

This genus is named *Nalbantichthys* in honor of my ichthyological colleague Dr. Teodor Nalbant.

***Nalbantichthys elongatus*, new species**

Figures 1, 2, 3

Holotype: USNM 200671, collected in the south-central Bering Sea, May 1964, by Mr. Constantine Bădică, from the bottom at a depth of 300 meters, by the trawler *Galatzi*, total length 138.3 mm, standard length 136 mm, sex male.

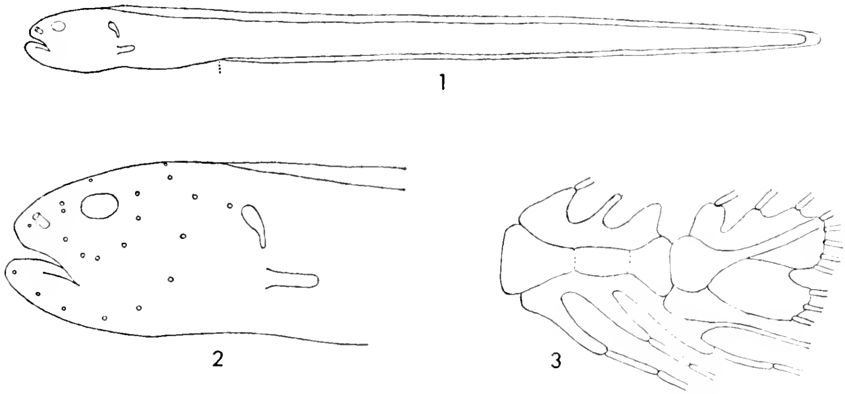
Paratype: No number in Institutul de Cercitari Piscicole, Bucharest, taken with holotype and bearing same locality data, total length 110.3 mm, standard length 108 mm.

Dr. Nalbant in a letter dated February 16, 1967, states that this new genus and new species were taken "together with *Sebastodes* sp., *Sarritor frenatus frenatus* Gilbert, *Percis japonicus* Pallas, and *Careproctus cameliae* Nalbant."

Description.—No dorsal fin ray is associated with the first vertebra; however, in the radiograph one free predorsal pterygiophore shows up clearly just in front of the tip of the neural spine of the first vertebra; dorsal and anal fin rays are equal in number to the vertebrae with which they are associated except for the penultimate vertebra and the hypural plate; radiographs show three rays dorsally and five terminal ones on the dorsal part of the hypural plate so that the dorsal fin ray counts are 148+3+5=156 for the holotype and 142+3+5=150 for the paratype. The first 25 vertebrae are abdominal, followed by the caudal vertebrae, each bearing one anal ray except the penultimate vertebra, which has four anal rays followed by three rays on the caudal part of the hypural plate. Thus the holotype has 123+4+3=130 anal rays and the paratype 117+4+3=124.

The penultimate vertebra appears to be composed of the elements of at least three caudal vertebrae (fig. 2) since three degenerate neural spines are represented with only the first bearing a dorsal fin ray. The degenerate hemal spines are definitely three with the last divided distally into two elements, each bearing an anal ray, possibly the posterior hemal branch representing a fourth vertebra. The penultimate vertebra was counted as one vertebra. I do not consider the penultimate vertebra of *Nalbantichthys* as abnormal since both specimens are alike in that character.

The somewhat rudimentary fleshy pectoral fin as seen in one of the radiographs has six rays; no lateral line was observed; peritoneum blackish; mouth terminal, lower jaw slightly shorter than upper jaw; teeth on jaws conical, uniserial on sides and a patch of canines at tip of both jaws; margin of eye not free; eye covered with a dermal membrane; by dipping the head of the holotype in a solution of alizarin the pores on the head became visible as shown in figure 2.



FIGURES 1–3.—*Nalbantichthys elongatus*, new species: 1, outline of holotype; 2, arrangement of pores on head; 3, penultimate vertebra and hypural plate. (Drawings by Dorothea B. Schultz.)

The following counts were made, first for the holotype, then for the paratype, respectively: Dorsal rays (including those in middle of caudal) 156 and 150; anal rays to midcaudal 130 and 124; vertebrae $25+125=150$ and $25+119=144$; branchiostegals 7 and ?; pectoral rays 6 and ?.

Measurements (made on the holotype and paratype and expressed in thousandths of the total length, first for the holotype, then the paratype): Total lengths 138.3 and 110.3 mm; length of head from snout tip to upper edge of gill opening 100 and 105; depth of head at gill opening 77 and 75; diameter of eye 14 and 16; distance from tip of snout to rear of maxillary 44 and 54; longest diameter of gill opening 16 and 16; tip of snout to front edge of eye 25 and 27; width of fleshy interorbital space 19 and 15; snout tip to anus 245 and 263; snout tip to dorsal origin 105 and 103; length of pectoral fin 22 and 21; distance from lower edge of gill opening to upper edge of base of pectoral fin 14 and 15; length of nasal tube 7 and 7; length of caudal fin 17 and 21.

REMARKS.—This new species has two unique characters for the family Zoarcidae. The first is the anatomical nature of the penultimate vertebra, described above and diagrammed in figure 2. One might cast doubt on the uniqueness of the penultimate vertebrae were they unlike in both specimens. Since they are basically identical, both show rudiments of three vertebrae, each supporting a neural spine and three, or possibly four, hemal spines. The second character is the large number of vertebrae 144 to 150, more than I have noted for any other genus in the family Zoarcidae.

For comparison purposes with the new species, radiographs of type specimens of zoarcids in the United States National Museum (USNM) collection have been prepared by Mrs. Dorothy Ann Hubbs (except for those specimens too brittle or too soft to remove from the jars).

An examination of these radiographs definitely did not show any modification of the penultimate vertebra like that observed for *Nalbantichthys*.

The scientific name of each species as published in the original description is listed alphabetically (along with my counts of the abdominal and caudal vertebrae) as follows:

Aprodon corteziana Gilbert, 1890, Proc. U.S. Nat. Mus., vol. 13, p. 107 (holotype 46457: vertebrae 24+90=114; paratypes 47056, 47057, and 47180: vertebrae, respectively, 24+?; 24+90=114; 23+89=112).

Bothrocara remigera Gilbert, 1915, Proc. U.S. Nat. Mus., vol. 48, p. 366, pl. 20, fig. 19 (holotype 75820: vertebrae 23+93=116).

B. zesta Jordan and Fowler, 1902, Proc. U.S. Nat. Mus., vol. 25, p. 749, fig. 3 (holotype 50576: vertebrae 21+98=119).

Embryx parallelus Gilbert, 1915, Proc. U.S. Nat. Mus., vol. 48, p. 360, pl. 19, fig. 16 (holotype 75818: vertebrae 23+108=131).

Leurynnis paucidens Lockington, 1880, Proc. U.S. Nat. Mus., vol. 2, p. 326 (holotype 23502: vertebrae 21+81=102; paratype 22+82=104).

Lycenchelys bullisi Cohen, 1964, Proc. Biol. Soc. Washington, vol. 77, p. 113, figs. 1–3 (holotype 188232: vertebrae 24+82=106).

L. spilotus Fowler, 1943, U.S. Nat. Mus. Bull. 100, vol. 14, no. 2, p. 89, fig. 24 (holotype 99511: vertebrae 23+90=113).

L. poecilimon Jordan and Fowler, 1902, Proc. U.S. Nat. Mus., vol. 25, no. 1313, p. 748, fig. 2 (holotype USNM 50578: vertebrae 23+90=113).

Lycodapus attenuatus Gilbert, 1915, Proc. U.S. Nat. Mus., vol. 48, p. 372, pl. 21, fig. 22 (holotype 75821: vertebrae 17+76=93).

L. dermatinus Gilbert, 1893, Rept. U.S. Fish Comm., vol 19, p. 471, pl. 35 (holotype 53035: vertebrae 14+66=80).

L. lycodon Gilbert, 1915, Proc. U.S. Nat. Mus., vol. 48, p. 371, pl. 21, fig. 21 (holotype 75822: vertebrae 16+74=90).

L. mandibularis Gilbert, 1915, Proc. U.S. Nat. Mus., vol. 48, p. 369, pl. 20, fig. 20 (holotype 78523: vertebrae 16+77=93).

Lycodes brevipes Bean, 1890, Proc. U.S. Nat. Mus., vol. 13, p. 38 (holotype 45362: vertebrae 20+82=102; paratypes 162712: vertebrae 22+81=103; 21+80=101; 20+82=102).

L. camchaticus Gilbert and Burke, 1910 (1912), U.S. Bur. Fish. Bull., vol. 30, p. 89, fig. 34 (holotype 74396: vertebrae 22+100=122).

L. concolor Gill and Townsend, 1897, Proc. Biol. Soc. Washington, vol. 11, p. 233 (holotype 48764: vertebrae 22+93=115).

L. diapterus Gilbert, 1891, Proc. U.S. Nat. Mus., vol 14, p. 564 (holotype 44385: vertebrae 21+100=121; paratypes 46716 and 125538: vertebrae, respectively, 21+100=121; 23+?93).

L. frigidus Collett, 1878, Forh. Ved.-Selsk. Christiana, no. 14, p. 45 (holotype 22977: vertebrae 24+82=106).

L. paxillus Goode and Bean, 1879, Proc. U.S. Nat. Mus., vol. 2, p. 44 (holotype 22177: vertebrae 24+107=131).

L. turneri Bean, 1879, Proc. U.S. Nat. Mus., vol. 1, p. 463 (holotype 21529: vertebrae 26+71=97).

L. verillii Goode and Bean, 1877, Amer. Journ. Sci. Arts, vol. 14, p. 474 (holotype 21013: vertebrae 24+88=112).

L. zoarchus Goode and Bean, 1895, Oceanic Ichthyology, U.S. Nat. Mus. Spec. Bull., vol. 2, p. 308, figs. 276, 276a, 283c (holotype 39398: vertebrae 24+96=120; paratype 39298: vertebrae 24+99=123).

Lycodopsis crassilabrus Gilbert, 1890, Proc. U.S. Nat. Mus., vol. 13, p. 106 (holotype 44280: vertebrae 24+105=129).

L. crotalinus Gilbert, 1890, Proc. U.S. Nat. Mus., vol. 13, p. 105 (holotype 44297: vertebrae 24+102=126).

Lyconema barbatum Gilbert, 1893 (1895), Rept. U.S. Fish Comm., vol. 19, p. 471, pl. 35 (holotype 48582: vertebrae 21+93=114; paratype 53036: vertebrae 22+90=112).

Maynea brunnea Bean, 1890, Proc. U.S. Nat. Mus., vol. 13, p. 39 (holotype 119446: vertebrae 23+89=112; paratype 119447: vertebrae 22+94=116).

M. californica Gilbert, 1915, Proc. U.S. Nat. Mus., vol. 48, p. 362, pl. 19, fig. 17 (holotype 75819: vertebrae 27+86=113).

Rhigophila dearborni DeWitt, 1962, Copeia, no. 4, p. 821, figs. 1–4 (paratypes 196979: vertebrae 24+69=93; 24+73=97; 24+69=92; 24+67=91).

Zoarces gilli Jordan and Starks, 1905, Proc. U.S. Nat. Mus., vol. 28, p. 212, fig. 11 (holotype 45355: vertebrae 24+107=131).

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Portunid Crabs from the International Indian Ocean Expedition In the Smithsonian Collections (Crustacea: Portunidae)

By W. Stephenson and May Rees[1]

The present material, mostly collected by the *Anton Bruun* on Cruises 1 and 4B, comprises 35 recognisable species that are present in very unequal numbers. Of the total of 3444 specimens, 2250 were of one species (*Portunus argentatus*). Of the remaining 1194, 442 specimens were of one species (*Charybdis hoplites*) and 550 of the other four (*C. callianassa*, *C. edwardsi*, *C. rostrata*, and *P. pulchrieristatus*). At the other extreme, 18 species were represented by less than five specimens. Several of these are common inshore or shallow water species in the Indo-West Pacific area, including *C. feriatus*, *C. natator*, *P. pelagicus*, *P. sanguinolentus*, *Scylla serrata*, and *Thalamita crenata*. Their small numbers indicate merely that during the cruises these environments usually were neglected in preference for offshore situations.

There is comparable heterogeneity in the numbers of species recorded from the different stations; thus, five species were recorded from 1 station (202A), four species from 7 stations, three from 10, two from 16, and one species from 34 stations. Stations 201A, 202A,

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and 202B were the richest trio of stations with respect to number of species recorded (4, 5, 4, respectively) and number of individuals (434, 1760, 289, respectively).

Throughout, synonymy has been abbreviated in most cases to a few recent references that permit ready identification. Fuller listings are given in cases where the synonymy has presented problems.

Dimensions are those of breadths and are given in millimeters. Measurements were by dial calipers to the nearest 0.1 mm, but these are given below only to the nearest 0.5mm.

Genus *Charybdis* de Haan, 1833

Charybdis callianassa (Herbst)

Cancer callianassa Herbst, 1789, pl. 54, fig. 7 (fide Leene, 1938).

Charybdis (*Charybdis*) *callianassa* (Herbst).—Leene, 1938, pp. 81–4, figs. 41–43.—Stephenson, Hudson, and Campbell, 1957, pp. 493–5, figs. 1B–D, 2C, 3D, pl. 1 (fig. 2); pl. 44.—Stephenson and Rees, 1967, p. 8.

Material examined.—1 ovig. female (30 mm), Sta. No. AB 40–63. 4 males (22.5–27 mm), Sta. No. 203B. 53 males (16.5–30.5 mm), 91 females (20–29 mm), Sta. No. 203C. 1 male (32 mm), 1 female (29 mm), Sta. No. 204A. 1 female (18.5 mm), Sta. No. 222A. 5 males (20–25.5 mm), 16 females (19–31.5 mm), 2 ovig. females (20.5–23.5 mm), 3 *Sacculina*-infested specimens (20–22 mm), Sta. No. 223A. 5 males (19.5–25 mm), 1 female (18 mm), Sta. No. 224A. 1 ovig. female (23 mm soft, without appendages), Sta. No. 9682.

All trawled in shallow water (12.5–33 m); all notings on nature of bottom mention mud.

Remarks.—In many specimens the ridge on the cardiac region of the carapace is very indistinct, and these specimens are difficult to key out from Leene (1938). The last listed specimen probably belongs to this species, but, in absence of chelipeds, there is some uncertainty.

C. ihlei Leene and Buitendijk (1949, pp. 291–3; figs. 1, 4a), closely resembles the present species but differs in having a bifid first anterolateral tooth and a different male pleopod. This species apparently is known only from the holotype.

Distribution.—Karachi to northern Australia.

Charybdis feriatus (Linnaeus)

Cancer feriatus Linnaeus, 1758, p. 625.

Charybdis (*Charybdis*) *cruciata* (Herbst).—Leene, 1938, pp. 24–7, figs. 1, 2.—Stephenson, Hudson, and Campbell, 1957, pp. 495, 497, figs. 2E, 3F, pl. 1 (fig. 3), pl. 4B.—Crosnier, 1962, pp. 75–7, figs. 130–2.

Charybdis cruciata (Herbst).—Sakai, 1939, pp. 403–4, pl. 82 (fig. 3); 1965, pp. 123–4, pls. 62, 63 (fig. 1).

Charybdis (*Charybdis*) *feriatus* (L.).—Stephenson and Rees, 1967, p. 10.

MATERIAL EXAMINED.—1 male (77.5 mm), Sta. No. AB 47B–63. 1 female (34 mm), Sta. No. 201A. 1 female (76.5 mm, no trace of pigment), Sta. No. 9682.

All trawled, in depths of from 12.5 to 30 m.

DISTRIBUTION.—East coast of South Africa to Japan and Australia.

***Charybdis hongkongensis* Shen**

Charybdis (*Goniohellenus*) *hongkongensis* Shen, 1934, p. 46, figs. 11, 12.—Leene, 1938, pp. 110–113, figs. 61, 62.

MATERIAL EXAMINED.—9 males (18–54 mm), 1 *Sacculina*-infested male (34.5 mm), 2 females (27.5–37.5 mm), Sta. No. AB–20. 3 males (29.5–34.5 mm), 1 female (18.5 mm), Sta. No. AB–41A. 1 male (38.5 mm), Sta. No. AB42–63.

All trawled, depths from 29 to 60 m.

DISTRIBUTION.—Hong Kong (Shen, 1934); Banda Sea; Diamantpunt, Sumatra (Leene, 1938).

***Charybdis hoplites* (Wood-Mason)**

FIGURE 1

Goniosoma hoplites Wood-Mason, 1877, p. 422.—Alcock and Anderson, 1894, p. 184; 1896, pl. 23 (fig. 6).

Charybdis (*Goniohellenus*) *hoplites* (Wood-Mason).—Alcock, 1899a, p. 67; 1899b, p. 66.—Nobili, 1906, p. 119.—Gordon, 1931, pp. 534–5, figs. 12b, b′ [under *C. sinensis*].—Leene, 1938, pp. 99–102, figs. 53, 54a–c.

Charybdis (*Goniohellenus*) *hoplites* var. *pusilla* Alcock, 1899b, p. 67.—Leene, 1938, pp. 102–4, figs. 55, 56a, b.

MATERIAL EXAMINED.—171 males (18–43 mm), 95 females (18–30.5 mm), 49 ovig. females (20–33.5 mm), 1 *Sacculina*-infested specimen (27 mm), 1 unsexable specimen (25.5 mm), 4 fragmented specimens, Sta. No. 201A. 3 males (18–24.5 mm), 3 females (23–43 mm), 1 ovig. female (33.5 mm), Sta. No. 202A. 3 males (20–22.5 mm), 4 females (18.5–33.5, 1 fragmented), 9 ovig. females (16.5–24 mm), 1 *Sacculina*-infested male (24.5 mm), Sta. No. 202B. 2 males (23, 23.5 mm), 1 ovig. female (22.5 mm), Sta. No. 202C. 23 males (16–22.5 mm), 12 females (15.5–21 mm), Sta. No. 212A. 2 males (20, 23.5 mm), Sta. No. 213A. 2 males (17.5, 22 mm), 1 ovig. female (19 mm), Sta. No. 218A. 1 male (17.5 mm), 1 ovig. female (19.5 mm), Sta. No. 221A. 1 ovig. female (20.5 mm), Sta. No. 228A. 1 ovig. female (21 mm), Sta. No. 237A. 29 males (17.5–31 mm), 8 females (19–23 mm), 8 ovig. females (18.5–23.5 mm), Sta. No. 241A. 1 male (20.5 mm), 1 female (21.5 mm), Sta. No. 248A. 4 males (22.5–30.5 mm), Sta. No. 249A. 1 female (27 mm), Sta. No. 252A. 1 female (23.5 mm), Sta. No. 253A. 1 male (27.5 mm), Sta. No. 255A. 1 male (ca. 22.5 mm), 1 female (ca. 29.5 mm), (both cephalothorax only), Sta. No. 263A. 3 males (17–28.5 mm), 3 females (21–28.5 mm), Sta. No. 264A. 1 male (25 mm), 3 females (23–25.5 mm), Sta. No. 265A. 1 female (40 mm), Sta. No. 268A. 1 female (41 mm), Sta. No. 270A.

All trawled, depths from 35 to 368 m, bottoms mostly mud, but one station (202B) of coral and sand.

Remarks.—The above specimens differ from Leene's (1938) description of the forma typica only in the following minor particulars:

1. On the anterior border of the arm of the cheliped, Leene describes two spines and a tubercle. In most of the present specimens, three spines are present, but in the larger specimens there are often four.

2. The upper border of the carpus of the second pair of walking legs bears either no armature or microscopic spinules. Leene describes the forma typica as bearing either three spinulessor being unarmed and the var. *pusilla* as bearing microscopic spinule.

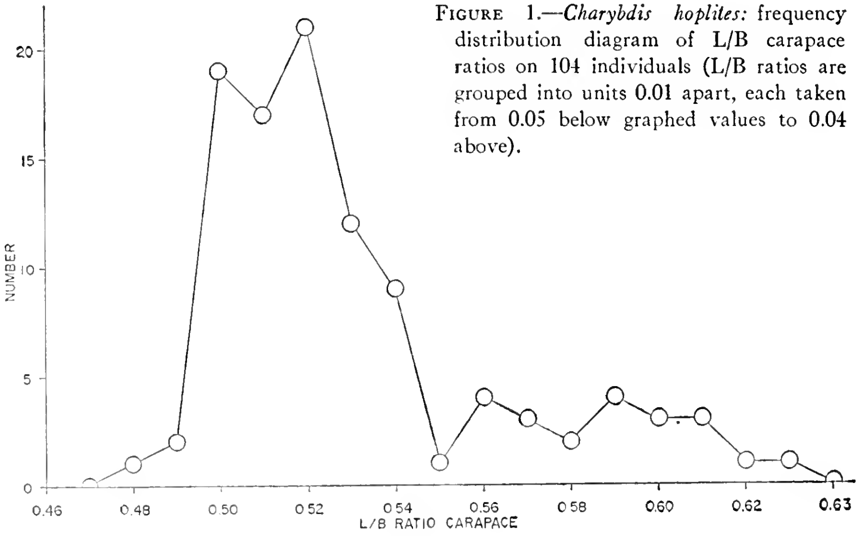

Figure 1.—*Charybdis hoplites:* frequency distribution diagram of L/B carapace ratios on 104 individuals (L/B ratios are grouped into units 0.01 apart, each taken from 0.05 below graphed values to 0.04 above).

3. These specimens usually have a very small cluster of granules on the carapace posterior to each mesobranchial area.

Sixteen individuals were noted with carapaces narrower than the remainder, and two more appeared when samples were measured. These were from eight stations, and in six cases these were stations from which typical *C. hoplites* were recorded. Apart from carapace proportions the specimens did not appear to differ in any way from the remainder.

Measurements made upon the original 16 narrower specimens and upon randomly selected specimens from the remainder showed that the differences in proportions were not primarily due to different lengths of the last anterolateral teeth; thereafter only lengths and breadths of carapaces were measured. L/B ratios were variable and were not obviously related to the size or sex of the specimens. Data on 104 specimens are given as a frequency distribution diagram on figure 1. The specimens include the 16 narrow individuals, randomly chosen small individuals from several collections, and the larger individuals from several collections. Because the figure shows only a slight hint of bimodality, the narrower specimens do not merit separation from the remainder.

Alcock's var. *pusilla* appears to be within the range of variation of the one taxonomic entity and, following Leene's suggestion, is added to the synonymy of the present species. On the other hand, Leene's (1938) var. *omanensis* merits specific status, although there are problems of synonymy with *C. smithii* Mc Leay 1838. Meanwhile Leene's var. *longicollis* clearly has specific status (see below).

Charybdis longicollis Leene

Charybdis hoplites Balss, 1924, p. 2 [specimens from Ras Abu Somer].
Charybdis (*Goniohellenus*) *hoplites* var. *longicollis* Leene, 1938, pp. 107–110, figs. 59, 60a–c.—Stephensen, 1945, pp. 118–9, figs. 24 F–G, 25.—Crosnier, 1962, pp. 86–7, figs. 140, 147, 148, pl. 7 (fig. 2).
Charybdis (*Goniohellenus*) *longicollis* Leene.—Holthuis, 1961, pp. 47–50, figs. 14, 15.
Charybdis longicollis Leene.—Lewinsohn and Holthuis, 1964, pp. 57–8.
Not *Charybdis hoplites* Wood-Mason, 1877, p. 422.

Material examined.—1 male (40.5 mm), Sta. No. 258A. 3 males (24.5–28 mm), 1 female (21 mm), Sta. No. 266A. 1 ovig. female (29 mm), Sta. No. 268A.

All trawled, depths from 30 to 368 m, bottoms all muddy.

Remarks.—*Charybdis hoplites* and *C. longicollis* resemble each other in possessing (1) relatively short and slightly curved anterolateral borders, (2) last anterolateral teeth of moderate length and directed laterally or slightly forwards, (3) anterolateral teeth generally somewhat square-cut, but with forwardly directed anterior spines, (4) mesobranchial area of carapace swollen, (5) no longitudinal line of granules on carapace running from mesogastric to metagastric region, (6) metagastric region of carapace with short granular ridges, (7) median frontal lobes protruding beyond submedians and narrowly rounded.

Charybdis longicollis is distinguished from *C. hoplites* by having (1) cardiac and mesobranchial areas of carapace with ridgelike elevations, as against granular patches; (2) sides of antepenultimate segment of male abdomen strongly as against slightly concave; (3) first pleopod of male relatively straight and thin as against sinuous and thick, outer side with relatively few subterminal bristles, inner side with large subterminal bristles as against spinules or small bristles.

DISTRIBUTION.—Eastern Mediterranean, Red Sea, Ras Abu Somer, Ravayah, Persian Gulf, Gulf of Oman, Malgache [Madagascar], and Seychelles.

Charybdis miles (de Haan)

Portunus (*Charybdis*) *miles* de Haan, 1835, p. 41, pl. 11 (fig. 1).

Charybdis miles (de Haan).—Stimpson, 1858, p. 39.—Doflein, 1902, p. 659.—Rathbun, 1902, p. 27.—Stimpson, 1907, p. 82.—Parisi, 1916, p. 175.—Balss, 1922, p. 104.—Yokoya, 1933, p. 175.—Sakai, 1939, p. 405, pl. 46 (fig. 2); 1965, p. 123, pl. 61.

Goniosoma miles (de Haan).—A. Milne Edwards, 1861, pp. 378, 385.—Ortmann, 1893, p. 81.

Charybdis (*Goniosoma*) *miles* (de Haan).—Alcock, 1899a, pp. 62–3.—Chopra, 1935, p. 486, fig. 9.—Shen, 1937, p. 123, fig. 13.

Charybdis (*Charybdis*) *miles* (de Haan).—Leene, 1938, pp. 38–43, figs. 10, 11, 12, 13.—Stephenson, Hudson, and Campbell, 1957, pp. 500–1, figs. 2H, 3I, pl. 2 (fig. 3), pl. 4F.—Rees and Stephenson, 1966, p. 37.—Stephenson and Rees, 1967, p. 11.

MATERIAL EXAMINED.—1 male (52.5 mm), 1 ovig. female (47.5 mm), Sta. No. AB–20. 1 male (51.5 mm), Sta. No. AB21–63. 1 male (26.5 mm), 1 female (28 mm), Sta. No. 255A. 4 males (21.5–54 mm), 1 ovig. female (47.5 mm), Sta. No. 256A. 1 female (54.5 mm), Sta. No. 261A. 1 male (81.5 mm), 1 female (30.5 mm), Sta. No. 262A.

All trawled, depths 55–99 m, muddy bottoms (in cases where records made).

REMARKS.—See *C. riversandersoni*.

DISTRIBUTION.—Previously from Ganjam Coast of India to Hong Kong, Japan, and eastern Australia. Now eastward to Gulf of Oman.

Charybdis natator (Herbst)

Cancer natator Herbst, 1789, pl. 40 (fig. 1) [fide Leene, 1938].

Charybdis (*Charybdis*) *natator* (Herbst).—Leene, 1938, pp. 93–7, figs. 50, 51.—Stephenson, Hudson, and Campbell, 1957, pp. 501–2, figs. 2G, 3H, pl. 2 (fig. 4), pl. 4J.—Crosnier, 1962, pp. 82–3, figs. 143–4, pl. 13 (fig. 2).—Stephenson and Rees, 1967, p. 11.

Charybdis natator (Herbst).—Sakai, 1939, p. 407.—Barnard, 1950, pp. 169–70.

MATERIAL EXAMINED.—1 male (64 mm), Sta. No. AB46–63. 2 females (20–26.5 mm), Sta. No. 201A.

Both probably trawled, depths 23–55 m, muddy bottom (Sta. 201A only).

REMARKS.—The small specimens from Station 201A differ from large specimens in having (1) much more conspicuous carapace areas,

(2) relatively larger first anterolateral teeth, (3) short granular ridges on the postfrontal areas of the carapace, and (4) longer wrist spines. These small specimens are close to *C. moretonensis* Rees and Stephenson (1966), who list the distinguishing features.

DISTRIBUTION.—East coast of Africa to Japan and Australia.

Charybdis orientalis Dana

Charybdis orientalis Dana, 1852a, p. 285, pl. 17 (fig. 10); 1852b, p. 85.—Sakai, 1939, pp. 407–8, pl. 53 (fig. 2).

Charybdis (*Charybdis*) *orientalis* Dana.—Leene, 1938, pp. 68–72, figs. 32–34 [excluding some synonymy].—Stephenson, Hudson, and Campbell, 1957, pp. 502–3, figs. 2B, 3B, pl. 3, (fig. 1), pl. 4G.—Crosnier, 1962, pp. 80–1.—Stephenson and Rees, 1967, p. 11.

Not *Charybdis orientalis* Edmondson, 1946, p. 281, fig. 173e (= *C. hawaiiensis*).

MATERIAL EXAMINED.—1 male (38.5 mm), India, north side Okah Point, Port Okah, Mar. 9, 1963. 7 males (ca. 23–58 mm), 7 females (34–ca. 67 mm), Sta. No. LW–1. 3 males (18.5–73.5 mm), 3 females (21–34.5 mm), Sta. No. RF–2.

Shore collections, rocky and sandy bottoms.

REMARKS.—This species resembles *C. hellerii* (A. Milne Edwards), particularly the larger individuals in which the second anterolateral tooth is barely smaller than the first. Both species possess an extension of the posterior border of the carpus of the natatory leg, but, whereas that in *C. orientalis* is a blunt tubercle, in *C. hellerii* there is a sharp spine.

Rees and Stephenson (1966) have shown that Leene (1938) was incorrect in synonymizing *C. incisa* Rathbun, 1923, with *C. orientalis*, and Edmondson (1954) has also shown that *C. hawaiiensis* is a separate species.

DISTRIBUTION.—Malgache [Madagascar] and East Africa to Japan and Australia.

Charybdis riversandersoni Alcock

Charybdis (*Goniosoma*) *riversandersoni* Alcock, 1899a, p. 53.—Alcock and McArdle, 1902, pl. 40 (fig. 3).

Charybdis sagamiensis Parisi, 1916, p. 175, pl. 11 (fig. 1).

Charybdis riversandersoni Alcock.—Balss, 1922, p. 105.—Gordon, 1931, pp. 537–8, fig. 13c.—Sakai, 1939, pp. 404–5, pl. 46 (fig. 1); 1965, pp. 122–3, pl. 60 (fig. 2).

Charybdis (*Charybdis*) *riversandersoni* Alcock.—Leene, 1938, pp. 28–30, figs. 3, 4a, 4b.

MATERIAL EXAMINED.—1 female (26 mm), Sta. No. 202A. 2 males (65.5, 75.5 mm), Sta. No. 263A. 1 male (18.5 mm), 2 females (26, 34.5 mm), 1 additional cheliped, Sta. No. 264A.

All trawled, depths from 46 to 291 m, muddy bottoms.

REMARKS.—The largest specimen has four spines on the anterior borders of the arms of the chelipeds; all of the remaining chelipeds bear three spines on these borders. All specimens have the characteristically swollen branchial regions of the carapace.

This species, which is close to *C. miles*, has the undersurface of the immovable finger smooth and rounded, whereas in *C. miles* it is deeply grooved. There are also differences in the last anterolateral teeth, which are longer and more laterally directed in *C. riversandersoni*.

The two species were also distinguishable by the pigmentation of the present recently preserved specimens. In *C. riversandersoni* the red pigment on the under side of the immovable finger of the cheliped did not extend along its entire length, while in *C. miles* it extended to the distal part of the palm. In the larger males of *C. riversandersoni* there was a pale circle in each postlateral area of the carapace, bordered by deeper pink. This had no counterpart in *C. miles*.

Sakai's (1939) colored plates of fresh material of the two species clearly show the differences in the last anterolateral teeth and in the pigmentation under the immovable finger, but they show *C. riversandersoni* with three pale areas in the postlateral portion of the carapace (pl. 46: fig. 1) and *C. miles* with one pale area (pl. 46: fig. 2). Sakai's (1965) plates again show the differences in last anterolateral teeth, show even more clearly the differences between the colors of the immovable fingers, but show one indistinct light postlateral patch in *C. riversandersoni* (pl. 60: fig. 2), against a very distinct patch in *C. miles* (pl. 61).

DISTRIBUTION.—Previously Konkak Coast, Bay of Sagami, South China Sea, and now Arabian Sea and Gulf of Oman.

***Charybdis rostrata* (A. Milne Edwards)**

Goniosoma rostratum A. Milne Edwards, 1861, p. 379, pl. 35 (figs. 2, 2b).—Henderson, 1893, p. 377.

Charybdis (Goniosoma) rostrata (A. Milne Edwards).—Alcock, 1899a, p. 59.—de Man, 1925, p. 326, fig. 2.—Chopra, 1935, p. 491, fig. 12.

Charybdis (Charybdis) rostrata (A. Milne Edwards).—Leene, 1938, pp. 78–81, figs. 39, 40.

MATERIAL EXAMINED.—1 female (24 mm), Sta. No. AB–37. 12 males (17–25.5 mm), 50 females (16.5–25 mm), 1 ovig. female (21 mm) (many specimens cephalothorax only), Sta. No. AB–40. 18 males (12–27 mm), 12 females (16.5–25.5 mm), 1 *Sacculina*-infested specimen (22.5 mm), Sta. No. AB 44–63. 1 male (16.5 mm), 6 females (18.5–22.5 mm), Sta. No. AB 44a–63. 1 male (21.5 mm), 1 yg. (5 mm), Sta. No. AB 45–63.

All trawled, depths from 15 to 81 m.

Remarks.—One of the males (23 mm), from Station AB–40, has the left branchial cavity swollen from containing a parasite. The young specimen from Station AB 45–63, almost certainly belonging to this species, has an almost continuous front with a barely detectable median notch.

Several specimens have three spines on the anterior border of the arm, and these key out to *C. callianassa* from Leene (1938). The present species is immediately recognizable from the prominent frontal teeth.

As Leene has noted, the last anterolateral teeth are longer in females than in males and longer in smaller specimens than in larger ones.

Distribution.—Indian region (Ceylon, Calcutta, Andamans) to Indo-Malayan Archipelago.

Charybdis smithii McLeay

Charybdis smithii McLeay, 1838, p. 61.—Krauss, 1843, p. 24.—Stebbing, 1910, p. 37.

Goniosoma truncata (Fabricius).—A. Milne Edwards, 1861, p. 380, pl. 34 (fig. 4).

Charybdis (*Goniohellenus*) *edwardsi* Leene and Buitendijk, 1949, p. 296, figs. 3, 4c.—Della Croce and Holthuis, 1965, pp. 33–7 [with pl.].

Gonioneptunus smithii (McLeay).—Barnard, 1950, pp. 163–4, 818, fig. 37j.

?*Charybdis* (*Goniohellenus*) *hoplites* var *omanensis*, Leene, 1938, pp. 104–7, figs. 57, 58.

Not *Portunus truncatus* Fabricius, 1798, p. 365 (=*Charybdis truncata*).

Stephenson and Rees (in ms.) have examined the type of *C. smithii* and will report more extensively on the synonymy.

Material examined.—3 males (59.5–70.5 mm), Sta. No. AB 3–63. 1 female (56 mm), Sta. No. 172 (dipnet at surface). 1 male (63 mm), Sta No. 202A. 1 female (63 mm), Sta. No. 207A. 2 males (both 58.5 mm), Sta. No. 231A. 14 males (61.5–75 mm), 1 female (56.5 mm), Sta. No. 249A. 51 males (56.5–73.5 mm), 10 females (52–61.5 mm), Sta. No. 252A. 3 males (62–67 mm), Sta. No. 253A. 4 males (62–73 mm), Sta. No. 263A. 1 male (59.5 mm), 3 females (50–59.5 mm), Sta. No. 264A. 5 males (49.5–71 mm), 13 females (40.5–60 mm), Sta. No. 268A.

Apart from the first two listed stations, all trawled, in depths of from 70 to 368 m on mud and/or clay bottoms.

Distribution.—From a large area of the Indian Ocean, as will be shown in later publications by Stephenson and by Stephenson and Rees.

Charybdis vadorum Alcock

Charybdis (*Goniohellenus*) *hoplites* var. *vadorum* Alcock, 1899a, p. 67.

Charybdis (*Goniohellenus*) *sinensis* Gordon, 1930, p. 522; 1931, p. 534, figs. 11, 12c, d, d′.—Shen, 1934, p. 44, figs. 9, 10.

Charybdis (*Goniohellenus*) *vadorum* (Alcock).—Chopra, 1935, p. 493, text-fig. 13, pl. 9 (fig. 2).—Leene, 1938, pp. 114–7, figs. 63–5.—Stephenson and Rees, 1967, p. 12.

?*Archias sexdentatus* Paulson, 1875, p. 56, pl. 8 (fig. 3–3b).—Nobili, 1906, p. 198 (fide Leene, 1938).

Material examined.—2 ovig. females (ca. 21.5, ca. 24 mm) (cephalothorax only), Sta. No. AB 41–63. 4 males (22–23.5 mm), 2 females (21, 24 mm), Sta. No. AB 41–A. 3 males (21–25.5 mm), 1 ovig. female (24 mm), Sta. No. AB 42–63.

All trawled, depths from 29 to 46 m.

Remarks.—Certain differences between Leene's (1938) description and figures have been noted by Stephenson and Rees (1967). In addition, the frontal teeth are more rounded than Leene figured.

Distribution.—Red Sea and Persian Gulf to Hong Kong.

Charybdis variegata (Fabricius)

Portunus variegatus Fabricius, 1798, p. 364.

Charybdis (*Charybdis*) *variegata* (Fabricius).—Leene, 1938, pp. 84–8, figs. 44, 45.—Stephenson, Hudson, and Campbell, 1957, p. 503, fig. 3C, pl. 3 (fig. 2).—Sakai, 1939, p. 406, fig. 9a, pl. 47 (fig. 4); 1965, p. 121, pl. 59 (fig. 2).—Rees and Stephenson, 1966, pp. 39–40.

Material examined.—1 male (31.5 mm), Sta. No. AB 46–63.

Probably trawled, depth 23–25 m.

Distribution.—Persian Gulf to northern Australia.

Charybdis species

Material examined.—Female 15.5 mm, Sta. No. 218–A.

Trawled, depth 79–84 m, bottom sandy.

Remarks.—This specimen, which is a soft, possibly badly preserved female, has an eared postlateral junction and a basal antennal joint that permits the flagellum to lie in the orbit. These are the diagnostic features of the subgenus *Gonioneptunus*, but the specimen does not resemble any of the known forms within this subgenus and possibly is *C. hoplites*.

Charybdis species

The following specimens were not identifiable beyond generic level:

1 yg. (ca. 3.5 mm), Sta. No. 251B. 1 badly fragmented specimen, Sta. No. 268A.

Genus *Lupocyclus* Adams and White, 1849

Lupocyclus philippinensis Semper

Lupocyclus philippinensis Semper, *in* Nauck, 1880, p. 68.—Leene, 1940, pp. 174–6, fig. 5, pl. 3.—Stephenson and Campbell, 1960, p. 109 [in key].—Crosnier, 1962, pp. 40–1, figs. 49, 51, 53, 56, 57, pl. 2 (fig. 1).

Material examined.—3 males (14–19.5 mm), additional larger male (fragmented), Sta. No. 21–63. 4 males (12–13.5 mm), 2 females (13, 16 mm), 1 ovig. female (17 mm) (many specimens fragmented), Sta. No. 202A.

Trawled, depths from 70 to 106 m.

Remarks.—Crosnier (1962, fig. 53) has accurately shown the curved junction, concave distally, between the ultimate and penultimate segments of the male abdomen. Leene (1940, pl. 3) shows a straight junction.

Distribution.—Laccadives, Ceylon, Philippines, Japan.

Genus *Portunus* Weber, 1795

Portunus argentatus (A. Milne Edwards)

Figures 2*a–c*, *e–g*

Amphitrite argentata White, 1847, p. 146 [descriptio nulla].

Neptunus argentatus A. Milne Edwards, 1861, pp. 332, 339, pl. 31 (figs. 4, 4a, 4b).

Neptunus (*Amphitrite*) *argentatus* A. Milne Edwards.—Alcock, 1899a, pp. 36–7.—Sakai, 1939, p. 391, fig. 5b, pl. 81 (fig. 1).

Portunus (*Achelous*) *argentatus* (A. Milne Edwards).—Rathbun, 1906, p. 871.—Edmundson, 1954, pp. 238–9, figs. 14, 15.

Monomia argentata (White, A. M. Edwards).—Barnard, 1950, pp. 156–8, figs. 27c, 30a–d.

Portunus argentatus (A. Milne Edwards).—Stephenson, 1961, pp. 105–6, figs. 1F, 3D, pl. 2 (fig. 2), pls. 4D, 5A.—Crosnier, 1962, pp. 50–1, figs. 71, 75, 77, 80, 81, pl. 3 (fig. 1).—Stephenson and Rees, 1967, p. 16.

Material examined.—52 males (25.5–34.5 mm), 47 females (23–35 mm), 29 ovig. females (27.5–36.5 mm), 2 *Sacculina*-infested males (32.5, 33 mm), 1 *Sacculina*-infested specimen (29.5 mm), 1 unsexable specimen with both branchial cavities swollen with parasites (22 mm), Sta. No. AB 21–63. 3 males (24–32 mm), Sta. No. AB–22. 7 males (26.5–32 mm), 12 females (24.5–31 mm), 1 *Sacculina*-infested specimen (30.5 mm), Sta. No. AB–22A. 2 females (19, 22.5 mm), Sta. No. AB 28A. 1 fragmented specimen, Sta. No. AB–47B. 1 male (42 mm), Sta. No. AB–49. 1238 males (15–27 mm), 232 females (17.5–44.5 mm), 272 ovig. females (19–26 mm), Sta. No. 202A. 153 males (18.5–32.5 mm), 46 females (16.5–46 mm), 72 ovig. females (21.5–34.5 mm), Sta. No. 202B. 16 males (18.5–40 mm), 11 females (18–23 mm), 7 ovig. females (21.5–34.5 mm), Sta. No. 202C. 2 males (16.5, 19 mm), 4 females (16–17 mm), 1 ovig. female (27 mm), Sta. No. 203A. 1 female (23 mm), Sta. No. 206A. 21 males (23.5–30 mm), 4 females (21.5–25 mm), 11 ovig. females (21–29 mm), Sta. No. 266A.

All trawled, depths from 22 to 196 m, bottoms (where noted) sand with mud, clay, or coral.

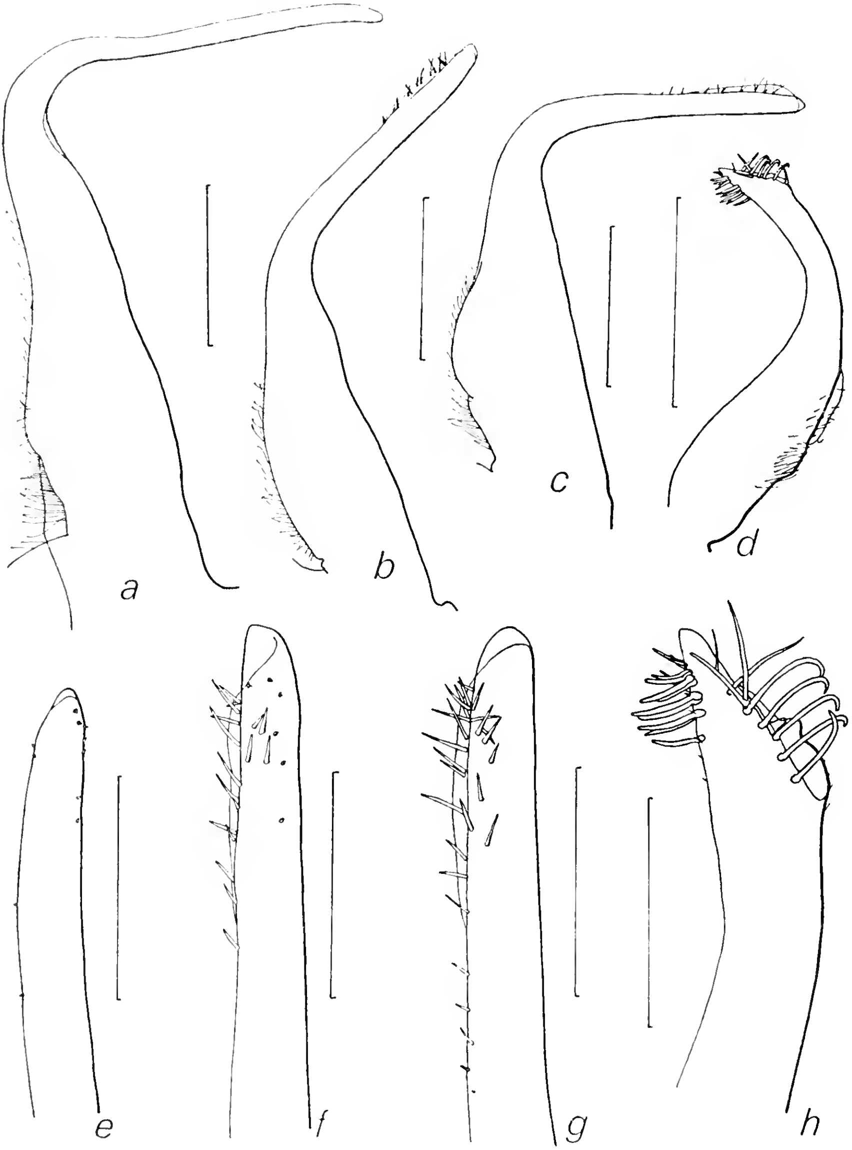

FIGURE 2.—First male pleopods: *a*, *Portunus argentatus* (205 mm, Sta. 202B), pleopod close to form b; *b*, *P. argentatus* (20 mm, Sta. 202B), relatively straight pleopod; *c*, *P. argentatus* (20.5 mm, Sta. 202A), pleopod approaching form a; *d*, *Thalamita gracilipes* (10.5 mm, Sta. B–16) whole pleopod. Tips of pleopods *a–d*, respectively: *e–h*. (Scales: *a–d*, 0.5 mm; *e–h*, 0.1 mm.)

REMARKS.—Because two forms of male pleopods have been described for this species (Stephenson and Rees, 1967, p. 16), pleopods of all the males in the present collection were examined. The number involved (almost 1500) no doubt greatly exceeds the numbers examined in any other species of portunid and possibly any other brachyuran.

All males were concluded to belong to form B, which typically possesses a pleopod with a right-angled bend. The range of the present material clearly links the shapes figured by Crosnier (1962, fig. 77) and by Stephenson and Rees (1967, fig. 2), with the bulk being intermediate.

A very small number of individuals (not more than five) possessed pleopods with considerable curvature near their right-angled bends (fig. 2*a*, this paper). A greater number (33) possessed relatively straight pleopods (fig. 2*b*). The latter were relatively small specimens (breadths 15–ca. 21.5 mm) although they overlapped considerably the sizes of those with normal pleopods (breadths 17.5–40 mm). It is assumed that the small specimens were immature males, which would have developed curved pleopods on later moults.

In addition to variations in curvature, there were variations in the form and spinulation of the tips of the pleopods (see figs. 2*c*–*g*). While none showed the bulbous shape of form A (Stephenson, 1961, figs 1F, 3D), one specimen showed slight swelling and reasonably dense spinulation (figs. 2*c*, *g*).

A single specimen from Station AB 21–63 was unsexable because of presumed parasitic castration caused by parasites in both branchial cavities. Three specimens with parasites in a single branchial cavity were noted (two with left cavities, one with right, all from Station AB 21–63). In none of these specimens was the sex indeterminable (two females, one male). Four *Sacculina*-infested specimens were noted. Two of these were clearly males, with normal pleopods, while two were most probably females. *Sacculina* infestation had less obvious effects upon secondary sexual characteristics than had the double branchial infestation.

DISTRIBUTION.—East coast of Africa to Japan, Australia, and Hawaii.

Portunus emarginatus **Stephenson and Campbell**

Portunus emarginatus Stephenson and Campbell, 1959, pp. 107–8, figs. 2H, 3H, pl. 2 (fig. 4), pls. 4H, 5H.—Crosnier, 1962, pp. 66–8, figs. 108, 112–4, 116, 120, 121.—Stephenson and Rees, 1967, p. 30.

?*Portunus longispinosus* Rathbun.—Stephenson and Campbell, 1959, pp. 104–6, figs. 2F, 3F, pl. 2 (fig. 2), pls. 4F, 5F.

MATERIAL EXAMINED.—1 male (10.5 mm), Sta. No. B9. Dredged, 18–24 ft., fine white sand.

REMARKS.—See *Portunus* cf. *longispinosus*.

DISTRIBUTION.—Malgache [Madagascar], Australia, and Palau.

Portunus gladiator (Alcock)

Neptunus (*Amphitrite*) *gladiator* Alcock, 1899a, pp. 35–6.—Shen, 1937, pp. 101–3, figs. 2a–c.

Monomia gladiator (Fabricius).—Barnard, 1950, p. 156.

Portunus gladiator Fabricius.—Crosnier, 1962, pp. 51–4, figs. 72, 76, 78, 82, 83, pl. 3 (fig. 2).

?*Portunus gladiator*.—Fabricius, 1798, p. 368.

Not *Portunus gladiator* Fabricius.—Stephenson and Campbell, 1959, pp. 110–111, figs. 2J, 3J, pl. 3 (fig. 2), pls. 4I, 5J.

MATERIAL EXAMINED.—2 females (50.5, 51.5 mm), Sta. No. AB–20. 1 male (31.5 mm), Sta. No. 202 B.

Trawled, depths from 58 to 90 m.

REMARKS.—As indicated by Stephenson and Rees (1967, p. 24), further work is required to clarify the confused synonymy of the *Portunus gladiator* complex. The present specimens were compared with Crosnier's material.

DISTRIBUTION.—Eastern South Africa, Malgache [Madagascar], India, and Hong Kong, and now near Mergui.

Portunus hastatoides Fabricius

Portunus hastatoides Fabricius, 1798, p. 368.—Stephenson and Campbell, 1959, pp. 101–2, figs. 2D, 3D, pl. 1 (fig. 4), pls. 4D, 5D.—Crosnier, 1962, pp. 68–9, figs. 98, 109, 117, 122, 123.—Sakai, 1965, p. 119, pl. 58 (fig. 2).—Stephenson and Rees, 1967, p. 27.

Neptunus (*Hellenus*) *hastatoides* (Fabricius).—Alcock, 1899a, pp. 38–9.—Sakai, 1939, pp. 391–2, pl. 47 (fig. 1).

Hellenus hastatoides (Fabricius).—Barnard, 1950, pp. 158–9.

MATERIAL EXAMINED.—2 males (26.5, 33.5 mm), Sta. No. AB 42–63. 1 male (33 mm), Sta. No. 47B–63. 8 males (15–29.5 mm), 2 females (ca. 24.5, 27 mm), Sta. No. 48–63. 2 males (37, 40.5 mm), 2 females (40.5, 42 mm), 1 ovig. female (35 mm), Sta. No. 203C. 1 male (36.5 mm), Sta. No. 218A. 1 male (31.5 mm), Sta. No. 224A 1 male (ca. 27.5 mm), Sta. No. 228A. 4 males (30.5–39.5 mm), 4 females (27–34 mm), Sta. No. 9682.

Trawled (except Sta. No. 48–63 dredged), depths from 22 to 84 m, bottom (when noted) from silty sand through mud to clay.

DISTRIBUTION.—East Coast of Africa to Japan, Australia, and Philippines, but not from the Red Sea.

Portunus cf. *longispinosus* (Rathbun)

cf. *Portunus* (*Xiphonectes*) *longispinosus* (Dana).—Rathbun, 1906, p. 871, fig. 30, pl. 12 (fig. 6).

MATERIAL EXAMINED.—1 male (14 mm), Sta. No. B 16.

Dredged, 12-18 ft sand, shell, and coral rubble.

REMARKS.—As indicated by Stephenson and Rees (1967, p. 28), there is confusion over the different species in the *Portunus longispinosus* complex. The present specimen keys out in Stephenson and Rees as *P. longispinosus* Rathbun but differs from Rathbun's illustration (1906, pl. 12: fig. 6), in possessing a less strongly embossed carapace.

A brief examination (at the Smithsonian Institution by the senior author) of the material identified by Rathbun as *P. longispinosus* showed that there is variation in a number of features; it is hoped that this and other material in the complex can be dealt with in a later publication.

Portunus minutus (Shen)

Neptunus (Lupocycloporus) minutus Shen, 1937, p. 115, fig. 9a–c.
Portunus minutus (Shen).—Stephenson and Campbell, 1959, p. 89 (in key).

MATERIAL EXAMINED.—1 female (19 mm), Sta. No. AB 41A.

Trawled, 29–33 m.

REMARKS.—This specimen has fine spines on the anterior border of the arm of the cheliped. Stephenson, in a later publication, will deal with a new species very close to *P. minutus*.

DISTRIBUTION.—Previously from Hong Kong and Gulf of Siam. Now off the Gulf of Martaban.

Portunus orbicularis (Richters)

Achelous orbicularis Richters, 1880, p. 153, pl. 16 (figs. 14, 15).—Henderson, 1893, p. 371.—Stebbing, 1920, p. 236.—Barnard, 1950, pp. 159–60, fig. 31a
Neptunus (Achelous) orbicularis (Richters).—Alcock, 1899a, p. 47.
Portunus (Achelous) orbicularis (Richters).—Rathbun, 1906, p. 871, pl. 12 (fig. 4).—Edmondson, 1946, p. 280; 1954, pp. 239–41, figs. 16c–e, 17b.
Cycloachelous orbicularis (Richters).—Ward, 1942, p. 51.
Portunus orbicularis (Richters).—Crosnier, 1962, pp. 58–61, figs. 95, 99–102.

MATERIAL EXAMINED.—3 females (12–16 mm), Sta. No. B 16.

Dredged, 12–18 ft, sand, shell, and coral rubble.

REMARKS.—The descriptions by Richters, Alcock, and Crosnier mention a carapace that is almost smooth. Crosnier (1962, p. 60), who gives the most recent detailed description, states: "*Carapace* glabre, subcirculaire, avec des granules surtout à la périphérie et sur les régions cardiaque et intestinale." His figure 99 shows this granulation and indicates that it is very fine. Meanwhile Barnard (1950, p. 159) had stated: "Carapace . . . feebly granulate in places, with patches of distinct granules mostly near the periphery and on the gastric and cardiac regions." His figure 31a shows a much more distinct and coarsely granular form than Crosnier's. The present specimens have distinctly granular carapaces, with fine granules near the periphery, with diffuse patches of moderate-sized granules in the protogastric region, with even larger granules in the mesogastric region, and with moderate-sized granules again in the cardiac region. In these respects, they resemble Barnard's material.

Barnard also shows a single elevation in the cardiac region tapering away posteriorly, which is visible on the present specimens but not on Crosnier's figure. Edmonson (1954, fig. 17b) shows a similar embossing of the carapace on a Hawaiian specimen, but in Rathbun's plate (1906, pl. 12: fig. 4) a different shape of the cardiac region is shown and also conspicuous metagastric ridges. Thus, merely on the basis of carapace ornamentation, three forms could all have been called *P. orbicularis:* (1) Richters' and Crosnier's, and presumably Alcock's (2) Barnard's, Edmondson's, and the present specimens, and (3) Rathbun's.

The male pleopod figured by Crosnier (fig. 101) also differs from that of Edmondson (1954, fig. 16d), but the extent to which this is due to Edmondson's draftsmanship is unknown.

It is evident that a careful re-examination of all available material of the present "species" should be made. The authors are reluctant to erect a new species without a male specimen being available.

Portunus pelagicus **(Linnaeus)**

Cancer pelagicus Linnaeus, 1766, p. 1042.
Neptunus pelagicus (L.).—Sakai, 1939, pp. 387–8, pl. 49.
Portunus pelagicus (L.).—Stephenson and Campbell, 1959, pp. 96–8, figs. 2A, 3A, pl. 1 (fig. 1), pls. 4A, 5A.—Crosnier, 1962, pp. 43–5, figs. 58, 61, 67.—Sakai, 1965, p. 117, pls. 55, 56.—Stephenson and Rees, 1967, p. 34.

Material examined.—2 females (33.5, ca. 40 mm) (cephalothorax only, specimens soft), *Anton Bruun* Cr. 1, Thailand, Patong Phuket; Mar. 22, 1963; coll. Taylor, Tyler, Sterling, and Rogers.

Either shore or dipnet collection.

Distribution.—East Africa to Tahiti, also Mediterranean.

Portunus pulchricristatus **(Gordon)**

Neptunus (Hellenus) spinipes Alcock, 1899a, pp. 31–2, 39–40.
Neptunus (Hellenus) pulchricristatus Gordon, 1931, p. 534, figs. 8, 10A.
Portunus pulchricristatus (Gordon).—Stephenson and Rees, 1967, p. 35.
Not *Neptunus (Amphitrite) spinipes* Miers, 1886, p. 178, pl. 25 (fig. 1).

Material examined.—6 males (18.5–23.5 mm), 1 female (20 mm), 5 ovig. females (19.5–ca. 23 mm), Sta. No. AB 41–63. 4 males (24–26 mm), 1 female (23.5 mm), 1 ovig. female (20.5 mm), Sta. No. 41A. 3 males (ca. 21–22.5 mm), Sta. No. AB 48–63. 95 males (21–28.5 mm), 2 females (20, 26 mm), 13 ovig. females (20.5–25 mm), Sta. No. 201A. 1 male (19.5 mm), 1 female (ca. 19 mm), Sta. No. 213A. 8 males (21.5–29 mm), 2 females (21.5, 25 mm), 2 ovig. females (20, 24.5 mm), Sta. No. 221A. 1 male (22.5 mm), Sta. No. 255A. 1 male (19 mm), Sta. No. 262A. 1 male (27.5 mm), Sta. No. 264A.

Trawled (except Sta. No. AB 48–63 dredged), depths from 29 to 291 m, muddy bottoms.

Remarks.—A single male (25.5 mm, Sta. No. 201A) has one parasitized branchial cavity.

Distribution.—Oman to Philippines, but not Australia.

Portunus sanguinolentus (Herbst)

Cancer sanguinolentus Herbst, 1796, p. 161, pl. 8 (figs. 56, 57).

Portunus sanguinolentus (Herbst).—Fabricius, 1798, p. 367.—Stephenson and Campbell, 1959, pp. 98–9, figs. 2B, 3B, pl. 1 (fig. 2), pls. 4B, 5B.—Crosnier, 1962, pp. 45–7, figs. 59, 62, 63, 68.—Sakai, 1965, p. 116, pl. 53.—Stephenson and Rees, 1967, p. 45.

Neptunus sanguinolentus (Herbst).—Sakai, 1939, p. 387, pl. 47 (fig. 1).

Material examined.—1 male (42 mm), Can 26. 1 male (42 mm), Sta. No. AB 28d–63. 1 male (40 mm), Sta. No. 32.

Dipnet.

Distribution.—East Africa to Australia. Current work shows that Hawaiian specimens are pigmented differently from Japanese and Australian material, but the precise status of the Hawaiian form has not yet been determined.

Portunus trituberculatus (Miers)

Portunus pelagicus De Haan 1835, p. 37, pls. 9, 10.

Neptunus trituberculatus Miers, 1876, p. 222; 1886, p. 172.—Sakai, 1934, p. 303; 1936, p. 129, pl. 37.

Portunus trituberculatus (Miers).—Rathbun, 1902, p. 26.—Stephenson and Campbell, 1959, p. 90 [in key].—Sakai, 1965, pp. 116–7, pl. 54.—Stephenson and Rees, 1967, p. 50.

Neptunus (*Neptunus*) *trituberculatus* (Miers).—Sakai, 1939, p. 388, pl. 50.

Material examined.—1 female (ca. 97 mm), *Anton Bruun* Cr. 1, India, north side Okah Point, Port Okah; Mar. 9, 1963. 2 males (ca. 160, 170 mm), Sta. No. 46–63.

Sta. No. 46–63 probably trawled, depth 23–25 m.

Distribution.—Red Sea, China, and Japan, and now India and Bay of Bengal.

Genus *Scylla* de Haan, 1833

Scylla serrata (Forskål)

Cancer serratts Forskål, 1775, p. 90.
Scylla serrata (Forskål).—Stephenson and Campbell, 1960, pp. 111–5, fig. 2N, pl. 4 (fig. 4), pls. 5N, 6C.—Crosnier, 1962, pp. 72–3, figs. 128, 129.—Stephenson and Rees, 1967, p. 55.

Material examined.—1 ovig. female (ca. 86 mm), *Anton Bruun* Cr. 1, India, Visakhapatanan Port, July 31, 1963.

Habitat uncertain.

Distribution.—East Africa to Tahiti including Japan, Australia, and New Zealand.

Genus *Thalamita* Latreille, 1829

Thalamita admete (Herbst)

Cancer admete Herbst, 1803, pp. 40–1, pl. 57 (fig. 1).
Thalamita admete (Herbst).—Sakai, 1939, pp. 414, 421–2, pl. 85 (fig. 1).—Stephenson and Hudson, 1957, pp. 320, 324–6, figs. 2I, 3I, pl. 1 (fig. 1), pls. 7A, 10A.—Crosnier, 1962, pp. 96–7, figs. 154, 157, 162–4, 168.—Stephenson and Rees, 1967, p. 56.
Thalamita edwardsi Borradaile.—Crosnier, 1962, p. 98, fig. 158.
Thalamita dispar Rathbun, 1914, p. 657, pl. 1 (fig. 4).

Material examined.—3 males (ca. 5–26 mm), Sta. No. B9. 2 males (9, 13 mm), 1 ovig. female (10 mm), Sta. No. B16.

Dredged, 12–24 ft, sandy bottoms, lagoons at Cocos Keeling I.

Remarks.—Stephenson and Rees (1967, pp. 56–57) have detailed the synonymy of this species. Examination of Rathbun's (1914) type of *T. dispar* by the senior author confirms that it belongs to *T. admete*. Stephenson made the following notes:

> Resembles *T. edwardsi* in (1) cardiac ridges of carapace just recognisable, (2) posterior mesobranchial ridges represented by a small pimple, (3) hands of chelipeds smooth, no granules on outer surface. Uppermost carina of outer surface coarsely beaded, middle and lowermost smooth, (4) no trace of fourth anterolateral tooth on right, at most a rudiment on left. Male pleopods—resembling Fig. 20d in Stephenson and Rees MS.

Distribution.—Red Sea and East Africa to Tahiti.

Thalamita chaptalii (Audouin)

Portunus chaptalii Audouin, 1826, p. 83 [figs. *in* Savigny, 1809, pl. 4 (fig. 1)].
Thalamita chaptali (Audouin).—Stephenson and Hudson, 1957, pp. 327–8. figs. 2F, 3F, pl. 1 (fig. 3), pls. 7C, 10B.—Forest and Guinot, 1961, p. 34, figs. 21A, B.—Sankarankutty, 1961a, p. 106.—Crosnier, 1962, pp. 111, 113, figs. 184, 189, 191.—Stephenson and Rees, 1967, p. 64.

Material examined.—1 ovig. female (8 mm), *Anton Bruun* Cr. 1, Thailand, Patong Phuket; Feb. 22, 1963; coll. Taylor, Tyler, Sterling, and Rogers.

Probably shore collection.

Remarks.—Without accompanying males, there is some uncertainty in the above identification.

Distribution.—Malgache [Madagascar] and the Red Sea to Australia and Tahiti.

Thalamita crenata (Latreille)

Portunus crenatus Latreille, 1829 [fide Milne Edwards, H., 1834, p. 461].

Thalamita crenata (Latreille).—Alcock, 1899a, pp. 76–7.—Sakai, 1939, pp. 413–15, pl. 84 (fig. 3).—Edmondson, 1954, pp. 267–9, figs. 39b, 40a–f.—Stephenson and Hudson, 1957, pp. 332–4, figs. 2Q, 3Q, pl. 2 (fig. 3), pls. 7F, 9C.—Sankarankutty, 1961a, pp. 106–7.—Crosnier, 1962, pp. 130–2, figs. 220, 226, 227, 232, 233.—Stephenson and Rees, 1967, p. 66.

Material examined.—1 male (14.5 mm), 1 female (53.5 mm), *Anton Bruun* Cr. 1, Thailand, Patong Phuket; Feb. 22, 1963; coll. Taylor, Tyler, Sterling, and Rogers.

Probably shore collection.

Remarks.—Both specimens are without their chelipeds, which are of diagnostic importance.

Distribution.—East Africa and Red Sea to Japan, Australia, Hawaii, Society Is., and Tuamotus.

Thalamita demani Nobili

Thalamita demani Nobili, 1905, p. 402; 1906, pp. 209–10.—Crosnier, 1962, pp. 124–5, figs. 200, 208–9.—Stephenson and Rees, 1967, p. 74.

Thalamita invicta de Man, 1895, p. 565, pl. 13 (figs. 11, 11a).

Thalamita cooperi Stephenson and Hudson, 1957, pp. 331–2 [in part].

Thalamita trilineata Stephenson and Hudson, 1957, pp. 359–60, figs. 2E, 3E, pl. 6 (fig. 4), pls. 8S, 10L.—Stephenson, 1961, p. 124, pl. 4 (fig. 2I).

?*Thalamita invicta*.—Thallwitz, 1891, pp. 46–7, fig. 11.

Not *Thalamita cooperi* Borradaile, 1902, pp. 206–7, fig. 37.—Sankarankutty, 1961b, p. 122, fig. 113.

Material examined.—1 female (12.5mm), Sta. No. B 17.

Dredged, 6 ft., in weed, lagoon at Cocos Keeling I.

Remarks.—If the small fourth anterolateral teeth are overlooked, females of this species are confused easily with *T. cooperi* Borradaile.

Distribution.—Red Sea and Malgache [Madagascar] to Australia and Philippines.

Thalamita prymna (Herbst)

Cancer prymna Herbst, 1803, pp. 41–2, pl. 57 (fig. 2).

Thalamita prymna (Herbst).—Alcock, 1899a, pp. 78–9.—Sakai, 1939, pp. 413, 416, pl. 51 (fig. 1); 1965, p. 125, pl. 64 (fig. 2).—Stephenson and Hudson, 1957, pp. 346–9, figs. 2R, 3R, pl. 4 (fig. 3), pls. 8L, 9E.—Crosnier, 1962, pp. 136–8, figs. 234–6.—Stephenson and Rees, 1967, p. 89.

Material examined.—4 males (38.5–63.5 mm), 2 females (40.5–62 mm), *Anton Bruun* Cr. 1, India, north side Okah Point, Port Okah; Mar. 9, 1963. 2 males (32.5- ca. 48.5 mm) (both without chelae), *Anton Bruun* Cr. 1, Thailand, Patong Phuket; Mar. 22, 1963; coll. Taylor, Tyler, Sterling, and Rogers.

Both probably shore collections.

Remarks.—In the larger specimens the spines on the ridge of the basal antennal joint are largely worn away, with resultant problems in identification (see Stephenson and Rees, 1967, p. 90).

Distribution.—East Africa and Red Sea to Marshalls and Samoa, including Australia and Japan.

Thalamita gracilipes (A. Milne Edwards)

Figures 2*d*, *h*

Thalamonyx gracilipes A. Milne Edwards, 1873, pp. 169–71, pl. 4 (figs. 3, 3a–d).—Alcock, 1899a, pp. 71–2.—Rathbun, 1906, p. 873.—Edmondson, 1954, pp. 251–2, figs. 26a, b.—Crosnier, 1962, pp. 91–3, fig. 153 bis a–d.

Thalamonyx danae var. *gracilipes* A. Milne Edwards.—Miers, 1886, pp. 192–3.

Thalamita gracilipes (A. Milne Edwards).—Stephenson and Hudson, 1957, pp. 318, 361.

? *Goniosoma* (*Thalamonyx*) *danae* A. Milne Edwards.—Ortmann, 1894, p. 83.

Material examined.—Male (10.5mm), Sta. No. B–16. Male (6 mm), ovig. female (11.5 mm), Sta. No. B–34.

Dredged, 12–24 ft, sandy bottom, lagoons at Cocos Keeling I.

Remarks.—A. Milne Edwards in 1873 listed the diagnostic differences between this species and *Goniosoma danae* A. Milne Edwards (1869, pp. 153–5, pl. 7: figs. 6, 7): *T. gracilipes* has an almost entire front, a narrower carapace, and longer legs. None of these differences do appear to have diagnostic value and the entirety of the front and carapace breadth appear to depend on the size of the specimen—compare Crosnier (1962, fig. 153 bis a) with A. Milne Edwards (1873, pl. 4: fig. 3). Milne Edwards' descriptions and figures indicate that there is an apparently important difference in the ornamentation of the posterior part of the carapace. In *G. danae* there are ovoid elevations in the mesobranchial area but apparently none in the cardiac region. In *T. gracilipes* there are four ridges forming an arc, one in each mesobranchial and one in each cardiac region.

Miers' specimens appear identical to the largest of the present specimens, being pubescent to the point of hirsuteness. Ortmann (1894) considered that *G. danae* and *T. gracilipes* were synonymous, presumably working from Milne Edwards' (1873) diagnostic features.

Forest (*in* Crosnier, 1962, p. 93) wondered whether *T. gracilipes* of Edmondson (1954) was a different species because of its less prominent front and because it had a different male abdomen. The form of the abdomen of the larger male in the present collections greatly resembles that figured by Edmondson (1954, fig. 26b). Edmondson, however, shows a continuous ridge in the posterior part of the carapace; possibly this is due to inaccurate draftsmanship.

Crosnier's figure of a male pleopod (1962, fig. 153 bis d) is obviously from an immature specimen. That of the larger male in the present collection is short, curved, with a slightly swollen tip ending obliquely. Subterminally on the outer side, there are stout bristles, mostly in pairs, with nine visible in profile view followed by thinner bristles; a sparse row of spinules is also present. On the inner side, in profile view, there are five elongate hook-shaped bristles followed by four almost straight bristles.

Edmondson has noted that *Thalamonyx* has been regarded variously as a subgenus of *Charybdis*, a separate genus, or as part of the genus *Thalamita*. Because of the increasing indefiniteness of the boundaries of the genus *Thalamita* (see Stephenson and Rees, 1967a, pp. 59–61), the present authors follow Stephenson and Hudson (1957) and regard the present species as belonging to *Thalamita*.

DISTRIBUTION.—Madagascar, Andaman Is., New Caledonia, Tongo Is., Hawaii.

***Thalamita spinifera* Borradaile**

Thalamita exetastica var. B. *spinifera* Borradaile, 1902, p. 203.

Thalamita spinifera Borradaile.—Rathbun, 1906, pp. 874–5.—Edmondson, 1951, p. 221; 1954, pp. 269–70, figs. 41a–d, 42a.—Crosnier, 1962, pp. 125–7, figs. 210, 211, 214, 215, pl. 11 (fig. 1).—Stephenson and Rees, 1967, p. 93.

MATERIAL EXAMINED.—1 male (18.5 mm), Sta. No. 262A. Trawled, 79 m, sandy bottom.

DISTRIBUTION.—Malgache [Madagascar], Maldives, Philippines, and Hawaii.

***Thalamita* species**

This specimen could not be identified beyond the genus.

MATERIAL EXAMINED.—1 yg. male (6 mm), Sta. No. 28A. Trawled, 66 m.

TABLE 1.—*Data on International Indian Ocean Expedition Stations* (GMT=Gulf of Mexico Shrimp Trawl; depth=meters unless otherwise stated; generic abbreviations: *C.*=*Charybdis*, *L.*=*Lupocyclus*, *P.*=*Portunus*, *S.*=*Scylla*, *T.*=*Thalamita*)

Sta. No.	Anton Bruun Cruise No.	Position	Gear	Depth	Bottom, other notes	Date	Portunid species
AB3–63							*C. smithii* (3)
Can 26	A	31°58′ N, 49°17′ E	dipnet	surface		31/i/1963	*P. sanguinolentus* (1)
AB–20	1	09°13′ N, 95°51′ E	GMT	60–58		23/iii/1963	*C. hongkongensis* (12) *C. miles* (2) *P. gladiator* (2)
AB21–63	1	09°54′ N, 97°42′ E	GMT	70		24/iii/1963	*C. miles* (1) *L. philippinensis* (3) *P. argentatus* (132)
22	1	10°37′ N, 97°34′ E	?	?		24/iii/1963	*P. argentatus* (3)
AB–22A	1	10°39′ N, 97°06′ E	GMT	290		24/iii/1963	*P. argentatus* (20)
AB28a–63	1	11°52′ N, 92°49′ E	GMT	66		27/iii/1963	*P. argentatus* (2) *Thalamita* sp.
AB28d–63	1	11°37′ N, 92°56′ E	dipnet?	surface?		27/iii/1963	*P. sanguinolentus* (1)
AB32	1	12°52′ N, 94°13′ E	dipnet	surface		28/iii/1963	*P. sanguinolentus* (1)
AB–37	1	13°28′ N, 97°19′ E	GMT	73–81		30/iii/1963	*C. rostrata* (1)
AB–40–63	1	15°21′ N, 96°24′ E	GMT	26–27		31/iii/1963	*C. callianassa* (1) *C. rostrata* (63)
AB–41	1	15°04′ N, 95°51′ E	GMT	44–46		31/iii/1963	*C. vadorum* (2) *P. pulchriocristatus* (12)
AB–41A	1	15°04′ N, 95°51′ E	GMT	29–33		31/iii/1963	*C. hongkongensis* (4) *C. vadorum* (6) *P. minutus* (1) *P. pulchricristatus* (6)

AB-42	1	15°08′N, 94°54′E	GMT	35		1/iv/1963	*C. hongkongensis* (1) *C. vadorum* (4) *P. hastatoides* (2)
AB-44	1	21°52′N, 91°36′E	GMT	15		4/iv/1963	*C. rostrata* (31)
AB-44a	1	21°43′N, 91°33′E	GMT	15		4/iv/1963	*C. rostrata* (7)
AB-45	1	21°32′N, 91°29′E	GMT	17		4/iv/1963	*C. rostrata* (2)
AB46-63	1	21°00′N, 91°59′E	GMT?	23-25?		5/iv/1963	*C. natator* (1) *C. variegata* (1) *P. trituberculatus* (2)
AB-47B-63	1	19°50′N, 92°55′E	GMT	30-22		5/iv/1963	*C. feriatus* (1) *P. argentatus* (1) *P. hastatoides* (1)
AB48-63	1	19°41′N, 93°08′E	dredge	37		5/iv/1963	*P. hastatoides* (10) *P. pulchricristatus* (3)
AB49-63	1	19°32′N, 92°52′E	GMT	53		6/iv/1963	*P. argentatus* (1)
–	1	17°42′N, 83°17′E (Visakhapatnam)				12-14/iv/1963	*S. serrata* (1)
201A	4B	17°54′N, 72°27′E–17°57′N, 72°23′E	GMT	46-55	Green mud and shells	13/xi/1963	*C. feriatus* (1) *C. hoplites* (321) *C. natator* (2) *P. pulchricristatus* (110)
202A	4B	17°25′N, 71°39′E–17°21′N, 71°41′E	GMT	96-106	Greenish sand and mud	13/xi/1963	*C. hoplites* (9) *C. riversandersoni* (1) *C. smithii* (1) *L. philippinensis* (7) *P. argentatus* (1742)
202B	4B	17°41′N, 71°33′E–17°45′N, 71°32′E	GMT	90		14/xi/1963	*C. hoplites* (17) *P. argentatus* (271) *P. gladiator* (1)
202C	4B	18°27′N, 71°13′E–18°28′N, 71°09′E	GMT	84-97	Coral, sand	14/xi/1963	*P. argentatus* (34)

TABLE 1.—*Data on International Indian Ocean Expedition Stations*—Continued

Sta. No.	Anton Bruun Cruise No.	Position	Gear	Depth	Bottom, other notes	Date	Portunid species
203A	4B	19°07′N, 71°41′E–19°08′N, 71°42′E	GMT	69–68	Sand, green mud, shells	14/xi/1963	*P. argentatus* (7)
203B	4B	19°47′N, 72°04′E–19°50′N, 72°05′E	GMT	27–29	Soft green clay, mud	14/xi/1963	*C. callianassa* (4)
203C	4B	20°22′ N, 71°47′ E–20°22′ N, 71°44′ E	GMT	26	Brown mud	15/xi/1963	*C. callianassa* (144) *P. hastatoides* (3)
204A	4B	20°30′ N, 70°54′ E–20°30′N, 70°50′E	GMT	33	Brown, sticky mud	15/xi/1963	*C. callianassa* (2)
206A	4B	20°23′ N, 70°00′ E–20°20′ N, 69°55′ E	GMT	71–79	Green clay, shells, sand	15/xi/1963	*P. argentatus* (1)
207A	4B	19°56′ N, 69°24′ E–19°51′ N, 69°24′ E	GMT	280	Light organic chunks, green clay	16/xi/1963	*C. smithii* (1)
212A	4B	21°29′ N, 69°27′ E–21°27′ N, 69°25′ E	GMT	35–36	Soft green clay, mud	16/xi/1963	*C. hoplites* (35)
213A	4B	21°11′ N, 69°16′ E–21°08′ N, 69°13′ E	GMT	70–72	Green mud, sand, shell	17/xi/1963	*C. hoplites* (2) *P. pulchricristatus* (2)
218A	4B	22°03′ N, 68°19′ E–22°02′ N, 68°17′ E	GMT	79–84	Greenish silty sand	18/xi/1963	*C. hoplites* (3) *P. hastatoides* (1)
221A	4B	22°32′ N, 68°07′ E–22°31′ N, 68°05′ E	GMT	57	Sandy green clay (mud)	18/xi/1963	*C. hoplites* (2) *P. pulchricristatus* (12)
222A	4B	22°45′ N, 68°24′ E–22°43′ N, 68°22′ E	GMT	26–27	Soft, sticky, green clay, mud	18/xi/1963	*C. callianassa* (1) *C. hoplites* (1)

223A	4B	22°54′ N, 68°36′ E–22°52′ N, 68°34′ E	GMT	15	Soft mud	19/xi/1963	*C. callianassa* (26)
224A	4B	23°00′ N, 68°10′ E–23°01′ N, 68°08′ E	GMT	24	Soft mud	19/xi/1963	*C. callianassa* (6) *P. hastatoides* (1)
228A	4B	23°45′ N, 67°26′ E–23°43′ N, 67°23′ E	GMT	23–24	Greenish brown clay	20/xi/1963	*P. hastatoides* (1)
231A	4B	23°13′ N, 66°40′ E–23°18′ N, 66°39′ E	GMT	183–155	Sands, shells, mud	20/xi/1963	*C. smithii* (2)
237A	4B	25°04′ N, 65°26′ E–25°04′ N, 65°24′ E	GMT	26	Hard packed mud	22/xi/1963	*C. hoplites* (1)
241A	4B	24°54′ N, 63°52′ E–24°56′ N, 63°53′ E	GMT	101–90	Mud, shell fragments	22/xi/1963	*C. hoplites* (45)
RF–2	4B?	25°06′35′′N, 63°48′65′′E [sic]	Hand collecting	Shore	Rocks and sand	27/xi/1963	*C. orientalis* (6)
LW–1	4B?	25°06′35′′N, 63°48′65′′E [sic]	Rotenone and dip net	0–8 ft	Rocks, sand, and scanty scattered coral	27/xi/1963	*C. orientalis* (14)
248A	4B	25°10′N, 60°27′E–25°08′N, 60°23′E	GMT	65–82	Clay, mud, shell	29/xi/1963	*C. hoplites* (2)
249A	4B	25°16′N, 59°40′E–25°16′N, 59°35′E	GMT	115–94	Sticky clay, shell	20/xi/1963	*C. hoplites* (5) *C. smithii* (15)
251B	4B	25′17′N, 59°05′E	dredge	35	Green-brown mud, clay, broken shell	29/xi/1963	*Charybdis* sp. (1 yg.)
252A	4B	25°20′N, 58°27′E–25°20′N, 58°30′E	GMT	101	Green mud, sand	29/xi/1963	*C. hoplites* (1) *C. smithii* (61)
253A	4B	25°25′N, 58°20′E–25°23′N, 58°24′E	GMT	82–90	Green mud, clay	29/xi/1963	*C. hoplites* (1) *C. smithii* (3)

TABLE 1.—*Data on International Indian Ocean Expedition Stations*—Continued

Sta. No.	Anton Bruun Cruise No.	Position	Gear	Depth	Bottom, other notes	Date	Portunid species
255A	4B	25°50′N, 57°07′E–25°45′N, 57°07′E	GMT	92–95	Clay, mud, sand, minute gastropod shells	30/xi/1963	*C. hoplites* (1) *C. miles* (2) *P. pulchricristatus* (1)
256A	4B	26°10′N, 57°02′E–26°13′N, 57°02′E	GMT	64–55	Green mud	30/xi/1963	*C. miles* (5)
258A	4B	26°58′N, 56°43′E–26°56′N, 56°42′E	GMT	33–35	Soft clay, mud, shell fragments	1/xii/1963	*C. longicollis* (1)
261A	4B	25°52′N, 56°53′E–25°53′N, 56°53′E	GMT	99	Green mud, few small shells	1/xii/1963	*C. miles* (1)
262A	4B	25°37′N, 56°34′E–25°39′N, 56°34′E	GMT	79	Green muddy sand	1/xii/1963	*C. miles* (2) *P. pulchricristatus* (1) *T. spinifera* (1)
263A	4B	25°12′N, 56°47′E–25°12′N, 56°51′E	GMT	206	Grey soft mud	2/xii/1963	*C. hoplites* (20) *C. riversandersoni* (2) *C. smithii* (4)
264A	4B	25°02′N, 56°52′E–25°08′N, 56°52′E	GMT	291–272	Sticky grey clay, and mud	2/xii/1963	*C. hoplites* (7) *C. riversandersoni* (4) *C. smithii* (4) *P. pulchricristatus* (1)
265A	4B	24°32′N, 56°53′E–24°34′N, 56°52′E	GMT	84–90	Black mud	2/xii/1963	*C. hoplites* (5)

266A	4B	24°27′ N, 56°50′ E–24°30′ N, 56°47′ E	GMT	47–49	Dark green sandy mud	2/xii/1963	*C. longicollis* (1) *P. argentatus* (36)
268A	4B	24°12′ N, 57°27′ E–24°13′ N, 57°22′ E	GMT	364–368	Grey clay, mud, shell fragments	2/xii/1963	*C. hoplites* (1) *C. longicollis* (1) *C. smithii* (18) *Charybdis* sp. (fragmented)
270A	4B	22°05′ N, 59°47′ E–22°08′ N, 59°48′ E	GMT	55	Sand, some clay	4/xii/1963	*C. hoplites* (1)
172	4A	14°44′ N, 51°02′ E	Dipnet	surface		15/x/1963	*C. smithii* (1)
B9		Cocos-Keeling, lagoon ½ mile SW of Wharf, Central Direction I	dredge	18–24 ft	Fine white sand; coll. Virginia Orr	18/i/1963	*P. emarginatus* (1) *T. admete* (3)
B16		Cocos-Keeling lagoon 1½ miles S by E of Possession Pt, Horsburgh I	dredge	12–18 ft	Sand, shell and coral rubble; coll. Virginia Orr.	21/i/1963	*P.* cf *longispinosus* (1) *P.* cf. *orbicularis* (3) *T. admete* (3) *T. gracilipes* (1)
B17		Cocos-Keeling lagoon 300 yds off West I, just N of North Lagoon	dredge	6 ft	Heavy sea-weed, (mostly *Thalassia*); coll. Virginia Orr	21/i/1963	*T. demani* (1)
B34		Cocos-Keeling lagoon, 2 miles E of northern end of West I	dredge	24 ft	Hard fine sand and weed; coll. Virginia Orr	11/ii/1963	*T. gracilipes* (2)

Table 1.—*Data on International Indian Ocean Expedition Stations*—Continued

Sta. No.	Anton Bruun Cruise No.	Position	Gear	Depth	Bottom, other notes	Date	Portunid species
–	1	Thailand, Patong Phuket	dipnet?	shore?	Coll. Taylor, Tyler Sterling and Rogers	22/ii/1963	*P. pelagicus* (2) *T. chaptali* (1) *T. crenata* (2) *T. prymna* (2)
–	1	India, north side Okah Point, Port Okah				9/iii/1963	*P. trituberculatus* (1) *T. prymna* (6)
9682	?	18°48′ N, 72°37′ E	M.U.F. Janjira Bottom Trawl	12.5–14 fm		12/v/1964	*C. callianassa* (1) *C. feriatus* (1) *P. hastatoides* (8)

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Genus Gloiopotes and a New Species With Notes on Host Specificity And Intraspecific Variation (Copepoda: Caligoida)

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Examination of 94 recent collections of the genus *Gloiopotes* have made possible a reevaluation of the species and certain conclusions regarding host specificity and intraspecific variation. In 1964 Hewitt published an account of *Gloiopotes huttoni* with notes on the other species. In his paper he placed *G. watsoni* in synonymy with *G. huttoni* and attributed the differences to variation within the species. I have been able to show that the two are actually distinct and should be considered separate species. In addition a new species from the Gulf of Mexico is described below.

I am indebted to the following persons who generously donated material to me for inclusion in this study: Dr. Bruce Collette, Bureau of Commercial Fisheries; Dr. Robert Gibbs, Smithsonian Institution; Dr. Richard Gooding, University of Singapore; and Dr. Alan Lewis, University of British Columbia. A portion of the field work was supported by the National Science Foundation, U.S. Program in Biology.

All drawings were made with the aid of a camera lucida.

All material has been desposited in the Museum of Natural History, Smithsonian Institution.

Gloiopotes Steenstrup and Lutken, 1861

Gloiopotes Steenstrup and Lutken, 1861, p. 363. [Type-species=*G. hygomianus*.]
Lepeophtheirus, Thomson, 1889, p. 354 [refers to *L. huttoni* only].
Caligus, Marukawa, 1925, p. 1243 [refers to *C. longicaudatus* only].

Euryphoridae. First 3 thoracic segments fused with head. Fourth thoracic segment with winglike dorsal plate. Genital segment with posterior outer corners produced in female. Fifth legs conspicuous in both sexes. Abdomen 2-segmented. Caudal rami filiform. First antenna 2-segmented. Second antenna with strong claw. Second antenna claw of male with median accessory process. Postantennal and postoral processes present. Sternal furca present. Legs 1–3 biramose (Yamaguti, 1963, p. 103, erroneously cites leg 1 as uniramose). Leg 4 uniramose. Egg strings uniseriate.

Key to Females of *Gloiopotes*

1. Dorsal body surface without conspicuous ornamentation, posterior process of sternal furca with single point, distal posterior lobe of genital segment extending beyond end of 5th leg . . . . **hygomianus**
   Dorsal body surface with conspicuous ornamentation, posterior process of sternal furca bifid, distal lobe of genital segment not extending beyond end of 5th leg 2
2. Lateral margins of dorsal thoracic plate nearly parallel to anterior-posterior body axis, lateral margins of genital segment with conspicuous bulge bearing stout spines 3
   Lateral margins of dorsal thoracic plate at nearly 45° angle to anterior-posterior body axis, lateral margins of genital segment uniformly rounded, bearing small spines 4
3. Middle of 2nd abdominal segment with bulbous swelling, 5th leg extending to end of abdomen . . . . **ornatus**
   Middle of 2nd abdominal segment swollen but not bulbous, 5th leg not extending to end of abdomen . . . . **americanus**, new species
4. Genital segment longer than wide, tip of 5th leg not extending to end of abdomen . . . . **huttoni**
   Genital segment wider than long, tip of 5th leg extending to end of abdomen . . . . **watsoni**

Gloiopotes americanus, new species

FIGURES 1–24

SPECIMENS STUDIED.—Eight collections from *Istiophorus americanus* in the southwestern portion of the Gulf of Mexico made by various cruises of the Oregon at stations 1051, 1069, 1071, 1075, and 1145. Holotype ♀, USNM 120189, allotype ♂, USNM 120190, and 12 paratypes (4♀♀, 8 ♂♂) USNM 120191, from the collection made at station 1145 (28°17′ N, 87°52′ W). Also the following collections in the USNM labelled *Gloiopotes ornatus:* USNM 78600 from sailfish caught at Stuart, Fla.; USNM 102036 from sailfish caught at Pass-a-Grille, Fla.

FEMALE.—Total length (including caudal rami) 10.90 mm (10.05–11.70 mm); greatest width (measured at widest part of cephalon) 4.95 mm (4.50–5.25 mm) based on an average of 136 specimens.

Body form as in figure 1. Dorsal surface of cephalon with rows of hairs and spinules as indicated in the figure. Most hairs bifurcate. Dorsal thoracic plate of segment bearing leg 4 winglike, inner posterior corner extending slightly over genital segment. Lateral edges of plates held nearly parallel to body axis. Genital segment (fig. 2) about as long as wide, narrowest anteriorly with posterior corners projecting posteriorly. Lateral margin of genital segment with slightly bulbous area bearing a row of spinules. Dorsal surface of segment with prominent spines (usually 3) on either side of midpoint. Abdomen (see fig. 2) 2-segmented; 1st segment about one-half as long as second segment; both segments with prominent spines on dorsal surface as in the figure; 2 prominent spines on ventral surface near posterior end of second segment. Abdomen comprises about 18.5 percent of total length. Caudal ramus (fig. 3) long and slender, bearing a notch on outer edge of anterior quarter. Each ramus with 5 plumose setae (2 at notch and 3 terminal) and several prominent spines (usually 8) on both surfaces.

Oral area with well-developed postantennal and postoral processes (fig. 4). Postantennal process usually with 3 tines; innermost tine occasionally bifurcate producing a 4-pointed process (fig. 5). Postoral process with 2 tines directed posteriorly. Both processes heavily pigmented.

First antenna (fig. 6) 2-segmented; basal segment with a process on anterior border and 23 stout plumose setae along anterior edge of distal half; 2nd segment with distal half sclerotized bearing 1 subterminal and 13 terminal naked setae. Second antenna (fig. 7) with well-developed claw, heavily pigmented at tip. Mouth tube (fig. 8) of usual caligoid type. Mandible a styliform process projecting within tube bearing 12 teeth at tip. First maxilla reduced to a group of 2 setae anterior to postoral process (see fig. 4). Second maxilla (fig. 9) long and slender, terminating in 2 weakly developed fringed spines. Maxilliped (fig. 10) with a well-developed claw usually pigmented at tip; adhesion area near distal end of basal segment. Sternal furca (fig. 11) with innermost tine bifurcate and heavily pigmented. Lateral to furca on each side is an accessory lobe, often bearing a process on outer corner.

Legs 1–3 biramose. Leg 1 (fig. 12) exopod 2-segmented. Last segment with 3 terminal spines and 4 inner setae. Two innermost spines bifurcate, each bearing a delicate median seta (fig. 13). Endopod (fig. 14) small, 2-segmented; 2nd segment with 3 setae. Leg 2 (fig. 15) exopod 3-segmented; each segment with a well-developed pigmented spine on outer distal corner; inner margin bearing a strongly recurved seta armed with stout plumosities. Endopod 3-segmented, armed as in the figure. Leg 3 (fig. 16) exopod 3-segmented with well-developed bifurcate spine representing 1st segment. Endopod 3-segmented. Basal segment fused with coxopod and difficult to distinguish. Fourth leg (fig. 17) uniramose, armed as in figure. Fifth leg projecting beyond outer distal corner of genital segment to end of abdomen, bearing 3 plumose setae (1 basal, 2 terminal). Terminus of leg 5 (fig. 18) with strong spines.

Egg strings uniseriate, 3.7 mm (3.3–4.2 mm) long, based on an average of 7 specimens.

Color in life bluish purple.

Male.—Total length (including caudal rami) 9.28 mm (8.85–10.05 mm); greatest width (measured at widest part of cephalon) 3.75 mm (3.45–4.05 mm) based on an average of 25 specimens. Body form as in figure 19. Cephalon and thoracic segments ornamented dorsally as in female. Thoracic segment bearing legs 4 with dorsal plates as in female. Genital segment (fig. 20) rounded, 1.5 x 1.7 mm, slightly longer than wide with 5th legs projecting from outer distal corners to about middle of abdomen. Spinules on dorsal surface as indicated in figure. Abdomen 2-segmented; 2nd segment twice as long as 1st, both segments with dorsal spinules. Caudal rami as in female.

Oral area in general as in female. Second antenna (fig. 21) with terminal claw and accessory subterminal claw. Inner distal corner of basal segment with adhesion area. Maxilliped basal segment (fig. 22) with sclerotized knobs as indicated in figure. Other cephalic appendages as in female.

Legs 1–4 as in female.

Leg 5 (fig. 23) projecting posteriorly from genital segment, armed with 1 plumose seta near base and heavy spines along inner edge to tip as in figure. Leg about 2.2 mm long measured along inner edge from origin to tip, extending to about middle of abdomen. Leg 6 (fig. 24) represented by an outer plumose seta and 2 inner spines near junction of genital segment and abdomen.

Remarks.—*Gloiopotes americanus* can be separated from *G. watsoni* and *G. huttoni* by the presence of a spinose bulge along the lateral margins of the genital segment of *G. americanus*. Also the outer margins of the winglike plates of *G. americanus* are nearly parallel to the anterior-posterior axis of the body while those of *G. watsoni* and *G. huttoni* are at an angle of nearly 45°.

This new species can be separated from *G. ornatus* by the nature of the spinose bulge along the margins of the abdomen of the female.

In *G. ornatus* the bulge is conspicuous, whereas in *G. americanus* it is only slight (see pl. 1). The males of these two species can be separated on the basis of leg 5 extending nearly to the end of the abdomen in *G. ornatus* whereas it extends only slightly beyond the middle of the abdomen in *G. americanus* (see pl. 2).

So far *G. americanus* has only been recorded from the sailfish *Istiophorus americanus* with all collections from the Gulf of Mexico except one collection from Stuart, Fla. It may be that this species is restricted to this host.

Gloipotes ornatus Wilson

Figures 25–26

Gloiopotes ornatus Wilson, 1905, p. 127; 1907, p. 699; 1919, p. 315; 1932, p. 415; 1936, p. 32.—Rathbun, 1905, p. 93.—Yamaguti, 1936, p. 5; 1963, p. 104.—Rao, 1951, p. 254.—Shiino, 1954, p. 277; 1959, p. 349.—Heegaard, 1963, p. 174.—Hewitt, 1964, p. 95.

Specimens studied.—Twenty-one collections from *Tetrapturus albidus* and 6 collections from *Makaira nigricans* from various M/V *Delaware* cruises in the western North Atlantic, 1 collection from *M. nigricans* caught off Beaufort, N.C., and 7 collections in the USNM (including types) from both hosts cited above (5 collections off east coast of U.S. and 2 from Caribbean).

Body form and ornamentation as in *G. americanus.*

The adult females of *G. ornatus* tend to be larger than those of *G. americanus.* Total length 11.72 mm (10.50–12.90 mm); greatest width 5.23 mm (4.50–5.70 mm) based on an average of 136 specimens.

Adult males total length 9.75 mm (9.00–11.10 mm); greatest width 3.93 mm (3.45–4.50 mm) based on an average of 128 specimens. The 5th legs of males extend posteriorly well beyond middle of abdomen (see fig. 26 and pl. 2).

Since *G. ornatus* and *G. americanus* cannot be separated on appendage characters, a description of the appendages of *G. ornatus* is not given here. The descriptions and figures of *G. americanus* appendages apply to *G. ornatus* as well.

Remarks.—This species cannot be distinguished from *G. americanus* on the basis of the appendages. However, the adult females can be separated by certain characters of the genital segment and abdomen. In *G. ornatus* there is a distinct lateral bulbous expansion of the second abdominal segment that is not present in *G. americanus.* Also, the lateral swollen areas of the genital segment are more pronounced in *G. ornatus* (see pl. 1). The 5th legs of the female *G. ornatus* extend to the end of the abdomen or slightly beyond, whereas the 5th legs of *G. americanus* do not (compare figs. 2 and 25, and see pl. 1). The only specimens of this species studied by the author were collected from the northwestern Atlantic Ocean and Caribbean Sea. So far, it has not been collected from the sailfish *Istiophorus americanus* but has been found on all other species of billfish examined.

Gloiopotes huttoni (Thompson)

Figures 27–37

Lepeophtheirus huttoni Thompson, 1889, p. 354.—Wilson, 1907, p. 701.

Gloiopotes huttoni Bassett-Smith, 1899, p. 440.—Rao, 1951, p. 254.—Shiino, 1954, p. 278.—Yamaguti, 1963, p. 104.—Hewitt, 1964, p. 86.

Caligus longicaudatus Marukawa, 1925, p. 1243; 1949, p. 927.

Gloiopotes longicaudatus Shiino, 1954, p. 273; 1957, p. 364; 1958, p. 105; 1959, p. 348; 1963, p. 343.—Heegaard, 1963, p. 174.—Ho, 1963, p. 87.—Yamaguti, 1963, p. 104.—Hewitt, 1964, p. 94.

Gloiopotes species Yamaguti, 1936, p. 4.

Gloiopotes costatus Wilson, 1919, p. 313.—Yamaguti, 1936, p. 5 [spelled *constatus*].—Shiino, 1954, p. 277.—Heegaard, 1963, p. 174 [spelled *constatus*].—Yamaguti, 1963, p. 103.—Hewitt, 1964, p. 94.

Gloiopotes zeugopteri Rao, 1951, p. 248.—Shiino, 1959, p. 349.—Yamaguti, 1963, p. 104.—Hewitt, 1964, p. 95.

Specimens studied.—Nine collections from *Tetrapturus audax*, 1 collection from *Makaira indicus*, 2 collections from *Istiophorus orientalis*, all from various sites in the Indian Ocean collected during the International Indian Ocean Expedition; 2 collections from *T. audax* collected off Peru during the Southeastern Pacific Biological Oceanographic Program; 5 collections in the USNM labeled as *G. costatus* from billfishes (labeled "swordfish" or "marlin") from the eastern Pacific; 1 collection in the USNM from *M. audax* from Hawaii.

Female.—Body form as in figure 27. Total length 13.75 mm (11.70–15.15 mm); greatest width 6.20 mm (5.10–7.20 mm) based on an average of 65 specimens. Specimens from *I. orientalis* tend to be smaller (12.15 x 5.40 mm average) based on an average of 10 specimens.

Dorsal surface of cephalon with rows of bifurcate hairs and spinules arranged as indicated in figure. Dorsal thoracic segment bearing leg 4 with winglike plates. Lateral edges of plates held at an angle to anterior-posterior axis of body. Genital segment (fig. 28) longer than wide (length from anterior shoulder to end of posterior lobe not including leg 5). Lateral edges of genital segment with small spinules. Dorsal surface of segment with 2 rows of prominent spines as in *G. ornatus* and *G. americanus*. Posterior lobe of genital segment well developed and projecting well beyond middle of leg 5. Abdomen 2-segmented with spinules as in figure 28. Caudal rami (fig. 29) as in *G. ornatus* and *G. americanus*. Sternal furca as in figure 30.

Appendages as in *G. ornatus* and *G. americanus*.

Male.—Body form and dorsal ornamentation in general like *G. ornatus* and *G. americanus*. Total length 10.84 mm (10.05–12.75

mm); greatest width 4.29 mm (3.75–4.95 mm) based on an average of 28 specimens. The specimens from *I. orientalis* tend to be smaller than those from other hosts (10.16 x 4.13 mm), average of 10 specimens. Genital segment (fig. 33) longer than wide (2.55 x 2.17 mm). Fifth legs extend posteriorly to about middle of abdomen. Dorsal surface of genital segment and abdomen with spines usually arranged as in figure. This arrangement may vary from specimen to specimen even within the same collection.

Appendages as in *G. ornatus* and *G. americanus*.

REMARKS.—I have examined the type specimens of *G. costatus* Wilson and determined this species to be synonymous with *G. huttoni*. Lewis (1967) points out that the tripartite spine of leg 3 is actually bipartite and does not differ from *G. ornatus* as claimed by Wilson. My own examination of the type specimens confirms Lewis' conclusions.

***Gloiopotes watsoni* Kirtisinghe**

FIGURES 38–39

Gloiopotes watsoni Kirtisinghe, 1934, p. 167.—Rao, 1951, p. 254.—Shiino, 1959, p. 348.—Yamaguti, 1963, p. 104.—Hewitt 1964, p. 95.
Gloiopotes auriculatus Barnard, 1957, p. 11.—Hewitt, 1964, p. 95.

SPECIMENS STUDIED.—Eight collections from *Makaira nigricans*, 4 collections from *Tetrapterus audax*, 4 collections from *Makaira indicus*, 6 collections from *Istiophorus orientalis*, all from the Indian Ocean; 1 collection from *Makaira nigricans*, collected off Peru during the Southeastern Pacific Biological Oceanographic Program; 5 USNM collections from *Makaira nigricans* from Taiwan, Hawaii, and Panama Bay; 2 USNM collections from *Istiophorus orientalis* off the Pacific coast of Mexico; and 2 USNM collections from "marlin" caught off Tahiti.

FEMALE.—Body form in general as in *G. huttoni* except for differences noted below. Total length 12.16 mm (10.80–13.80 mm). Greatest width 5.56 mm (4.480–6.45 mm) based on an average of 91 specimens. The average length and width measurements varied from one host group to the next, those copepods on *I. orientalis* having the smallest average size and those on *T. audax* largest (see p. 12).

Dorsal plates of 4th thoracic segment with lateral margins held at an angle to long axis of the body as in *G. huttoni*.

Genital segment (fig. 38) wider than long (3.0 x 3.2 mm), average of 91 specimens from 4 hosts. Lateral margins rounded, without conspicuous bulge, ornamented with row of small spinules. Dorsal surface ornamented as in *G. huttoni*. Posterior lobe shorter than in *G. huttoni* (see pl. 3). Abdomen and caudal ramus as in *G. huttoni*.

The appendages of *G. watsoni* cannot be distinguished from *G. ornatus*, *G. americanus*, or *G. huttoni* with the result that descriptions of appendages of those species apply to *G. watsoni* as well.

MALE.—Body form in general as in *G. huttoni*. Total length 11.45 mm (10.45–12.75 mm) based on an average of 36 specimens from all 4 hosts in the Indian Ocean. As in the female those specimens from *I. orientalis* tend to be smaller (10.65 mm. average) than other hosts. Dorsal surface ornamented with hairs and spinules as in *G. huttoni*.

Genital segment (fig. 39) about as wide as long (2.6 x 2.6 mm). Fifth leg usually extends posteriorly beyond middle of abdomen. Abdomen and caudal rami as in *G. huttoni*.

Appendages as in *G. huttoni*.

REMARKS.—Females of this species can be separated from *G. huttoni* by the nature of the genital segment. In *G. watsoni* the genital segment is wider than long whereas it is longer than wide in *G. huttoni*. The posterior lobe is shorter in *G. watsoni*. In *G. huttoni* the posterior lobe of the genital segment extends nearly as far as the 5th leg (see pl. 3). In *G. huttoni* the tip of the 5th leg extends only to about the posterior three-fourths of the abdomen, whereas in *G. watsoni* it extends to the end of the abdomen. Males of the two species differ in the nature of the genital segment. In *G. huttoni* the segment is longer than wide, whereas in *G. watsoni* it is nearly square.

***Gloiopotes hygomianus* Steenstrup and Lütken**

FIGURES 40–42

Gloiopotes hygomianus Steenstrup and Lütken, 1861, p. 363.—Bassett-Smith, 1899, p. 458.—Stebbing, 1900, p. 670.—Wilson, 1907, p. 702.—Rao, 1951, p. 254.—Shiino, 1954, p. 278; 1960, p. 533.—Yamaguti, 1963, p. 103.—Hewitt, 1964, p. 95.—Lewis, 1966, p. 11.

SPECIMENS STUDIED.—Two collections from the western North Atlantic, 1 collection from Socorro Island (eastern Pacific), 1 collection from the Indian Ocean, and 4 collections in the USNM (3 Hawaii, 1 Puerto Rico), all from *Acanthocybium solandri*.

FEMALE.—Body form as in figure 40. Total length 16.7 mm (15.9–17.7 mm); greatest width 6.2 mm (6.0–6.5 mm) based on an average of 8 specimens from 4 collections.

Shiino (1960) has provided a good description of both sexes of this species except for the changes recommended below. Shiino considers the first antenna as 3-segmented. The distal segment is heavily sclerotized on its outer half and appears 3-segmented, but I could find no evidence of segmentation at the midpoint of the distal segment. Consequently, the 1st antenna should be considered 2-segmented in all species of the genus. The process referred to as the "second maxilla" by Shiino should be called the 1st maxilla, "first maxilliped" as 2nd maxilla, and "second maxilliped" as maxilliped, to be consistent with more recent literature. The process referred to as the "first maxilla" is now considered to be the postantennal process.

The appendages of female and male are generally as in other species of the genus. The sternal furca (fig. 41) with the large posterior process with only a single point rather than bifid as in other species of the genus.

Male.—Body form as in figure 42. Total length 12.1 mm (11.7–12.5 mm); greatest width 4.8 mm (4.2–5.7 mm) based on an average of 6 specimens from 3 collections.

Remarks.—This species is cosmopolitan in distribution and is restricted to *Acanthocybium solandri*. Both sexes can be separated easily from the other species of the genus on the basis of the following points: the shape of the dorsal plate of the segment bearing legs 4, the nature of the sternal furca, the dorsal surface of *G. hygomianus* lacking the spinules and hairs found on the other species, the innermost distal spine of leg 4 of *G. hygomianus* being only slightly longer than the other 2 spines (in the other species this spine is nearly twice the length of either of the other 2).

Host Specificity

It has been almost impossible to make positive statements on the relationships between copepods parasitic on fish and their hosts owing to lack of understanding of the systematics and ecology of both groups. It is hoped that revisionary work by systematists in both groups will reveal the relationships that exist between these animals. Large collections of material are desirable and usually necessary for this kind of work. The 94 collections of the genus *Gloiopotes* forming the basis of this study have brought to light certain features of host specificity heretofore unrecorded. Since the phylogeny and ecology of parasites often reflect that of their hosts, this aspect of the study of parasitic copepods should be a useful tool to the ichthyologist.

For purposes of determining host specificity in the genus *Gloiopotes*, only those collections seen by the author have been considered. Collections with dubious host names and literature records have not been used. The genus *Gloiopotes* apparently is restricted to the Istiophoridae, Xiphidae, and to the scombrid genus *Acanthocybium*. The exact taxonomic position of *Acanthocybium* is in doubt, but studies of larval development of *Acanthocybium* by Walter Matsumoto (Bureau of Commercial Fisheries, Honolulu) suggest affinities between *Acanthocybium* and billfishes (R. H. Gibbs, pers. comm.). If one accepts the premise that a phylogenetic relationship to billfishes may exist, then the fact that it is the only known host for *G. hygomianus* supports this point of view (all other species of *Gloiopotes* are found on billfishes). *A. solandri* is cosmopolitan in distribution and *G. hygomianus* has been collected from it (8 collections) in the Atlantic and Indo-Pacific Oceans.

The remaining 4 species of *Gloiopotes* are related more closely to each other than to *G. hygomianus.* Two species (*G. ornatus* and *G. americanus*) are found only in the Atlantic, and the other 2 (*G. huttoni* and *G. watsoni*) are restricted to the Indo-Pacific. The istiophorids from which these collections were made are also divided into Atlantic and Indo-Pacific species. In the Atlantic, *G. americanus* has been found only on *I. americanus* (10 collections) and it is the only species of *Gloiopotes* so far collected from that host. *G. ornatus* is found on *T. albidus* (22 collections) and on *M. nigricans* (10 collections) and is the only species of *Gloiopotes* from those hosts. In the Indo-Pacific, both *G. huttoni* and *G. watsoni* have been collected from *T. audax* and *I. orientalis.* In 22 collections from *T. audax,* 14 of these were *G. huttoni* and 8 *G. watsoni,* indicating about a 2:1 prevalence of *G. huttoni.* In 16 collections from *I. orientalis* only 4 were *G. huttoni* while 12 were *G. watsoni,* indicating a 3:1 prevalence of *G. watsoni.* All 18 collections from the genus *Makaira* (14 *M. mazara* and 4 *M. indicus*) were *G. watsoni.*

A single collection of *G. huttoni* in the USNM from *Xiphius gladius* collected off California is insufficient on which to base any conclusions regarding relationships with this host. I hope that future collections from this host will fill the gap. So far, no copepods have been collected from *Tetrapturus brevirostris.*

A summary of number of collections of the 5 species of *Gloiopotes* and their distribution among the host species is as follows:

	Indo-Pacific		Atlantic		Cosmopolitan
	huttoni	*watsoni*	*ornatus*	*americanus*	*hygomianus*
Makaira nigricans		14	10		
” *indicus*	1	3			
Tetrapturus albidus			22		
” *audax*	14	8			
Istiophorus americanus				10	
” *orientalis*	4	12			
Acanthocybium solandri					8

Variation

Recent papers by Hewitt (1964) and Lewis (1967) have alluded to the wide range of intraspecific variation in the genus *Gloiopotes.* Both of these authors have considered *G. huttoni* and *G. watsoni* as synonymous species. Analysis of the 50 collections from the Indo-

Pacific reported herein clearly shows them to be distinct species. This would account for some of the variation cited by these authors. I have critically examined collections of each of these two species in order to determine the extent of intraspecific variation.

In one particularly large sample of *G. huttoni* taken from *T. audax* off Chile (Cruise 14, R. V. *Anton Bruun*, sta. 565), 50 adult females were randomly selected. The distribution of individuals throughout the size range is as follows:

length (in mm.)	*no. of indiv.*	*length (in mm.)*	*no. of indiv.*
13.80–13.95	1	15.30–15.45	21
14.10–14.25	1	15.60–15.75	4
14.40–14.55	3	15.90–16.05	3
14.70–14.85	6	16.20–16.35	1
15.00–15.15	9	16.50–16.65	1

The body of the animal was divided into 5 regions; cephalon, leg 4 segment, genital segment, abdomen, and caudal ramus. Each of these regions was measured along its dorsal anterior-posterior median axis, and the percentage of the total body length that each comprised was determined. The results of these measurements are as follows:

	cephalon	*leg 4 seg.*	*gen. seg.*	*abdomen*	*caudal ramus*
percent of total length	48.4	7.5	15.6	20.0	8.5
range	44.5–51.0	5.4–9.8	10.8–22.3	17.4–25.0	7.2–10.0

These same proportions in individuals in the lower, middle, and upper thirds of the total length range were considered separately to determine the correlation, if any, between the total length and the relative component lengths. These results are as follows:

length and range (in mm)	*cephalon*	*leg 4 seg.*	*gen. seg.*	*abdomen*	*caudal ramus*
13.80–14.70	49.1	7.2	14.9	20.1	8.7
(9 spec.)	45.5–50.5	6.5–8.7	10.8–19.0	17.4–25.0	7.6–10.0
14.85–15.45	48.7	7.2	15.6	20.0	8.5
(32 spec.)	47.6–51.0	5.9–9.8	12.8–17.6	19.2–22.9	7.2–9.4
15.75–16.50	47.7	7.4	16.2	20.2	8.5
(9 spec.)	44.5–49.1	6.4–8.9	14.4–22.3	18.2–21.0	8.0–9.4

The figures above indicate that the cephalon becomes proportionately shorter with increased total length and the genital segment proportionately longer. This change may have some relationship to the production and development of eggs within the body of the animal. Eggs are produced within the cephalon and migrate via the oviducts to the genital segment, where they are stored prior to release as egg strings. It is not known how many times a single female will produce egg strings, but it is apparently more than once; I have often observed developing eggs within the oviducts in females already carrying egg strings. The decrease in proportion of the cephalon in larger (older?) adults may reflect a reduction in their egg-producing organs. Egg strings were present on most individuals in all size groups.

In order to determine possible host influence on these same characters, adult females of *G. watsoni* from 4 hosts in the Indian Ocean were examined. These results are as follows:

		percent of total length				
host	*avg. tot. length (in mm)*	*cephalon*	*leg 4 seg.*	*gen. seg.*	*abdomen*	*c. ramus*
I. orientalis	11.6	50.2	7.1	14.8	18.0	9.9
3 colls.	(11.3–12.0)	(47.4–52.5)	(4.5–9.3)	(12.0–19.4)	(16.7–19.1)	(8.0–12.2)
M. nigricans	11.6	50.5	7.1	14.6	17.4	10.4
4 colls.	(10.5–12.6)	(46.5–52.4)	(4.3–8.9)	(11.9–19.7)	(15.0–19.7)	(8.6–11.5)
M. indica	12.7	49.8	6.9	14.7	18.0	10.6
4 colls.	(11.9–13.4)	(47.6–52.4)	(4.5–9.3)	(11.5–19.8)	(16.3–20.8)	(8.4–13.9)
T. audax	13.1	50.2	7.5	14.6	18.0	9.7
1 coll.	(12.6–13.5)	(49.5–51.2)	(6.7–8.9)	(13.7–15.5)	(16.1–19.5)	(8.9–11.1)

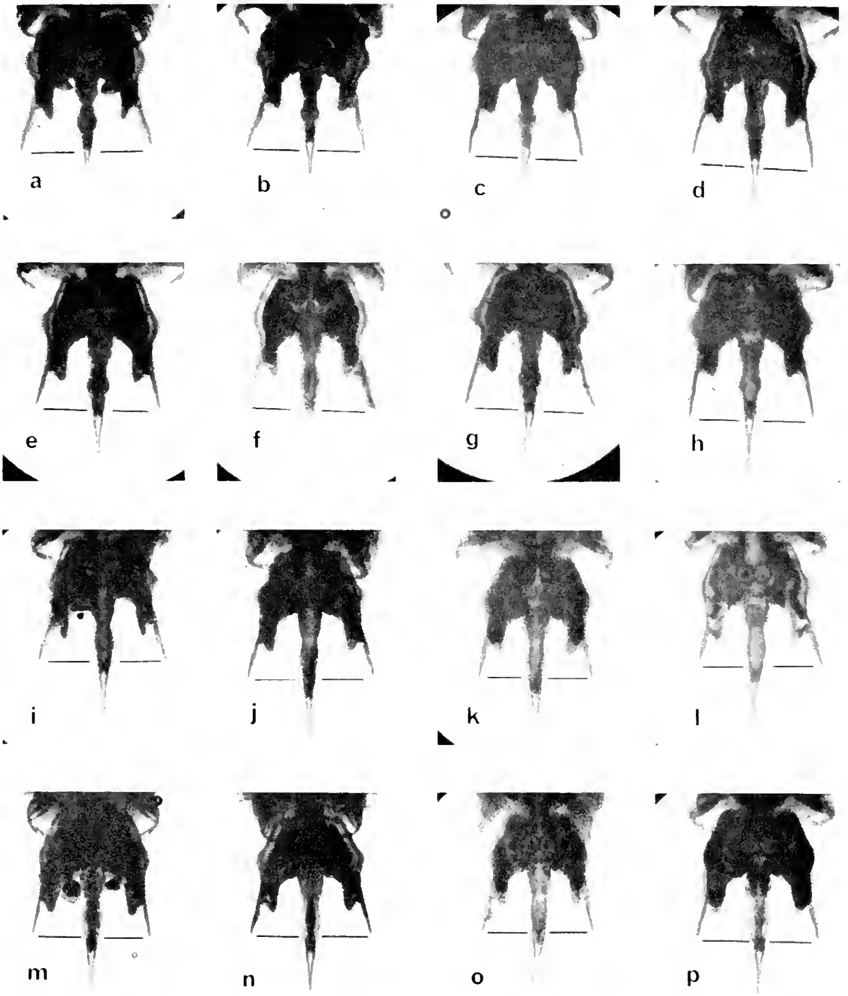
Although the average sizes of the adult females of *G. watsoni* vary depending on the host (shortest on *I. orientalis* and longest on *T. audax*), the components seem to remain in about the same proportion and no correlation can be drawn.

There was no single sample of *G. watsoni* large enough to permit a meaningful study of a single population.

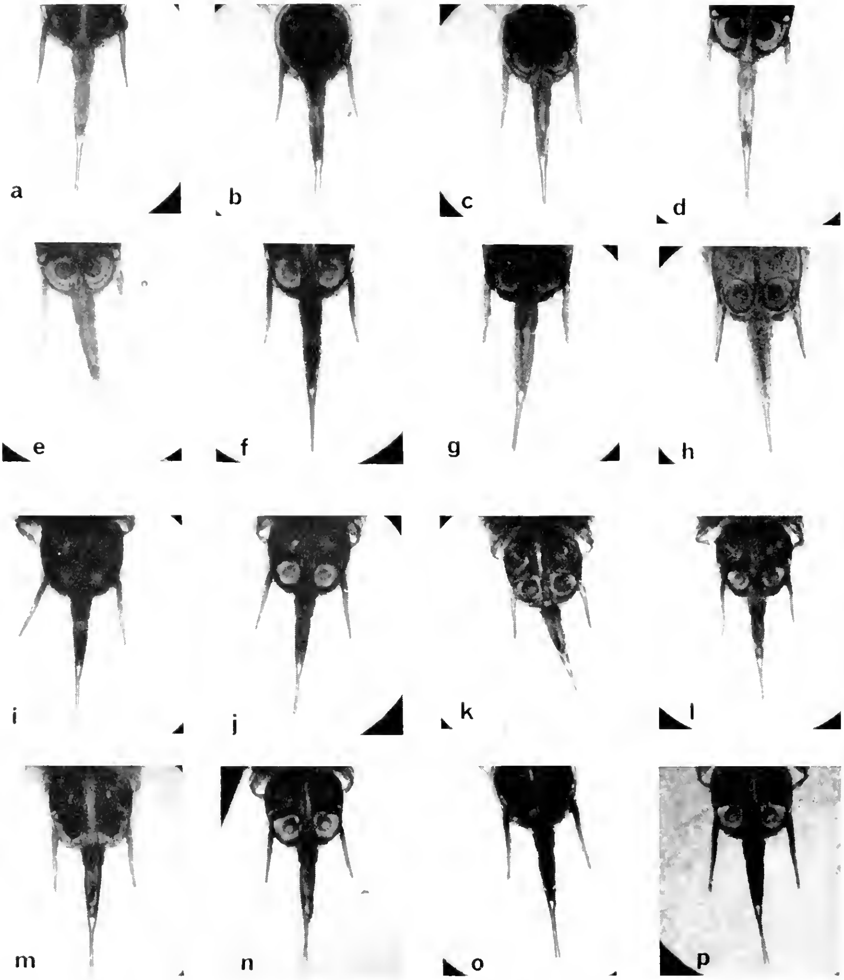
The use of the dorsal thoracic plate as a means of separating species has been used by some authors (Wilson 1907, 1919, and Hewitt 1964). There is considerable variation in the shape of this structure and it cannot be relied on as a good taxonomic character (see figs. 43–47). The Atlantic species can be separated from the Indo-Pacific ones by the angle of inclination at which the outer edges of these plates are held to the anterior-posterior body axis. The Atlantic species have the edges held nearly parallel whereas the Indo-Pacific ones are at a much greater angle (compare figs. 1, 27, and 38). This character is of no further value in separating species.

Lewis (1967, p. 63) points out the variation in the postantennal process of *G. huttoni* (?). I found the same variation in the number of points (3 or 4) on the process (see figs. 4 and 5) in all species. As Lewis also points out, this variation may be present in the same individual (right side differing from left). Twenty-one female specimens of *G. watsoni* in 3 collection from *M. indica* in the Indian Ocean were examined. Ten showed 4 points on both sides, 9 had 3 on both, and 2 had 3 on one side and 4 on the other.

Another character selected for study was the 2 rows of stout spines on the dorsal surface of the female genital segment. Typically each



Gloiopotes ornatus, female: *a–d*, from *Tetrapturus albidus; e–h*, from *Makaira nigricans*. *Gloiopotes americanus*, female: *i–p*, from *Istiophorus americanus*.



Gloiopotes huttoni, male: *a–f*, from *Tetrapturus audax; g, h*, from *Makaira indica. Gloiopotes watsoni*, male: *i–l, from Makaira nigricans; m, n*, from *Istiophorus orientalis; o*, from *M. indica; p*, from *Tetrapturus audax.*

row consists of 3 spines but occasional variation was noted (some rows have 1, 2, or 4 spines). In the large sample of 50 adult females of *G. huttoni* from a single population, 12 (24 percent) varied from the usual 3–3 arrangement. In this sample there was a higher incidence (33 percent) of variation in the lower third length range (shortest); a somewhat lower incidence (25 percent) in the middle third group; and lowest incidence (11 percent) in the upper third group (longest). In addition, 123 females from other collections of both *G. huttoni* and *G. watsoni* were examined, and 30 (24 percent) of these varied from the 3–3 formula. The actual distribution of specimens from this last group is as follows:

spine formula	2–2	2–3	3–3	3–4	4–4	3–1
no. of specimens	2	13	93	12	1	2

This variation seems to occur with similar frequency in the other species of the genus except *G. hygomianus* (genital segment of this species has no spines).

There is considerable variation in the configuration of the female genital segment within each species (see figs. 48–55). In spite of this variation, the genital segment is of major importance as a taxonomic character for separating females of the genus.

Similar variation in the characters discussed above also occurs in the Atlantic species (*G. ornatus* and *G. americanus*) and it was felt that no purpose would be served in repeating the same analysis on them. Preliminary investigation showed that the results would be essentially the same.

Males also showed some variation in the aforementioned characters but to a lesser degree.

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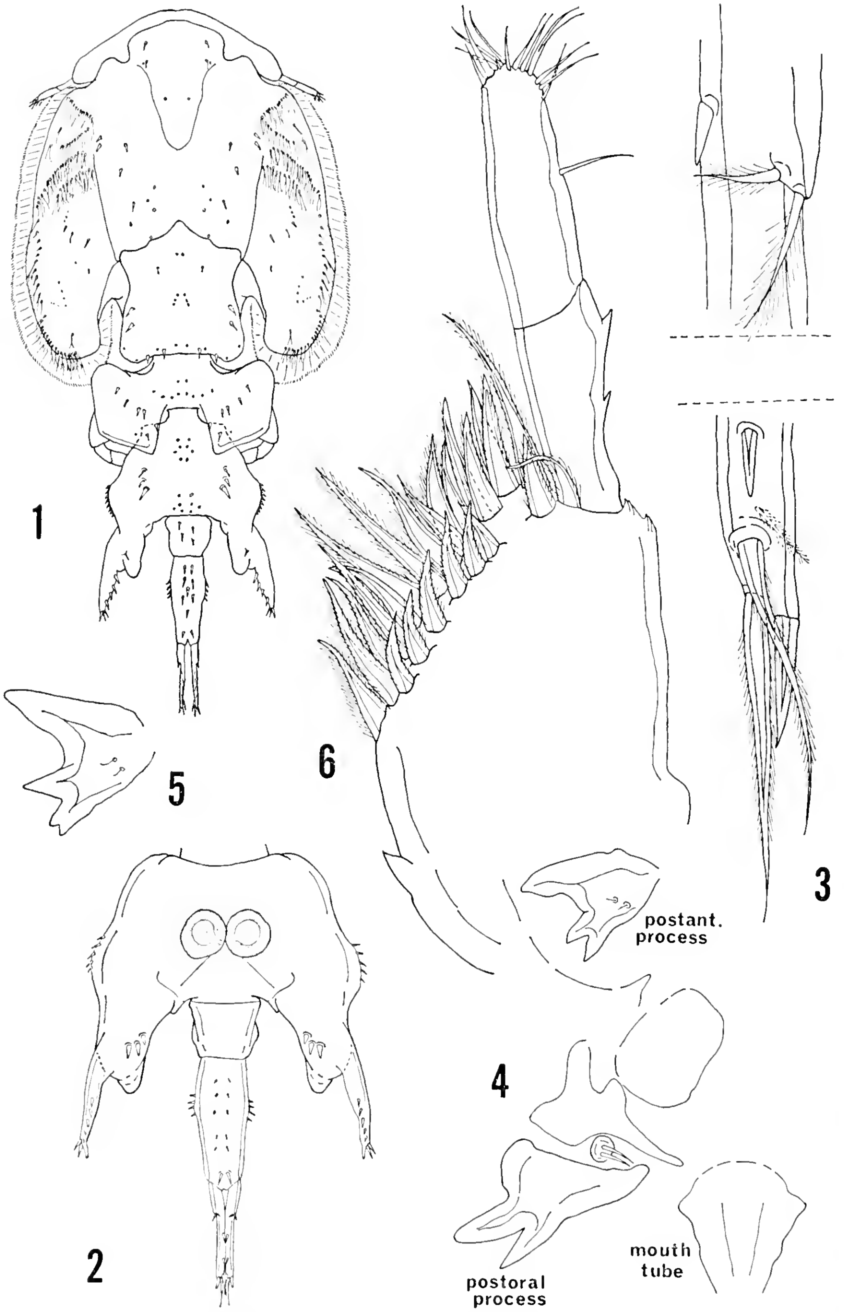
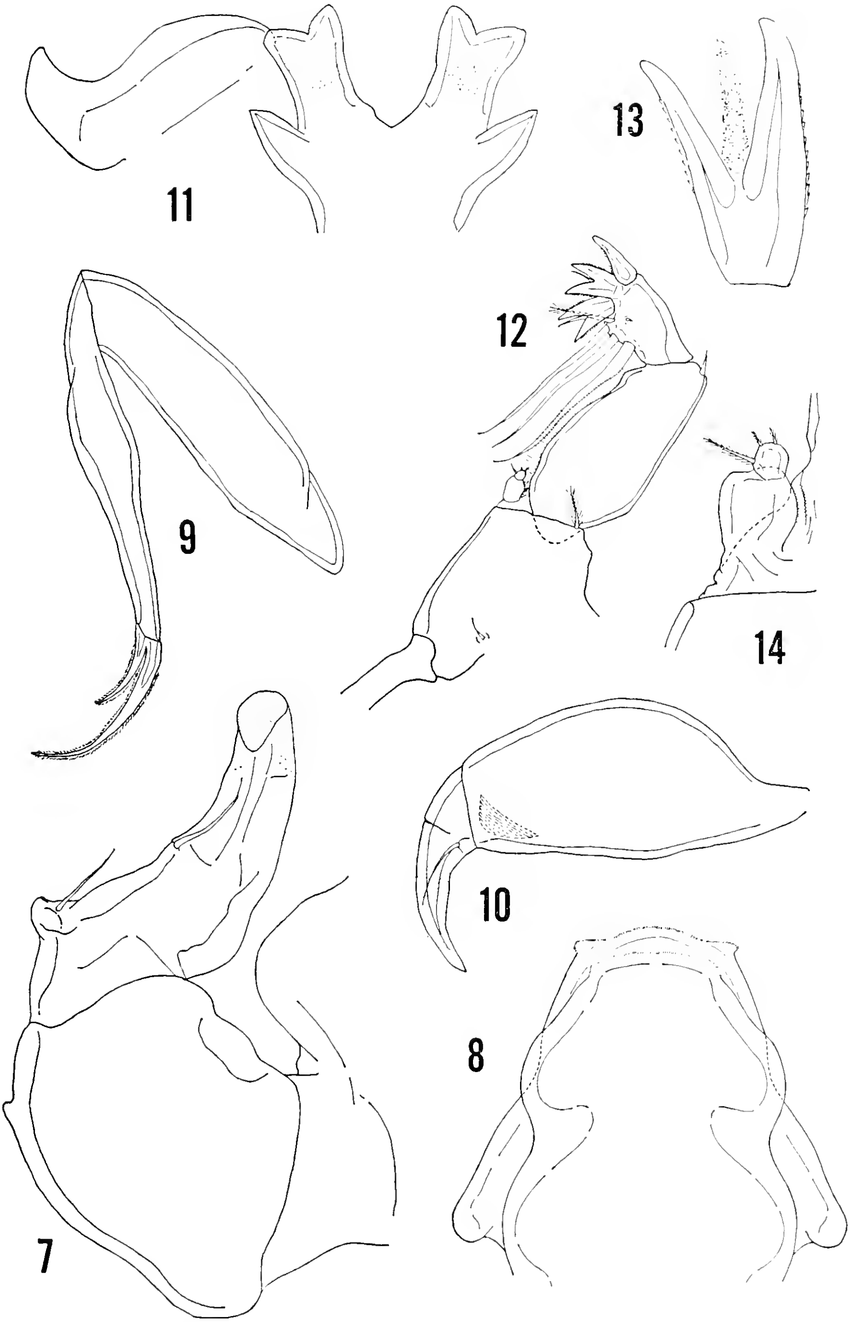
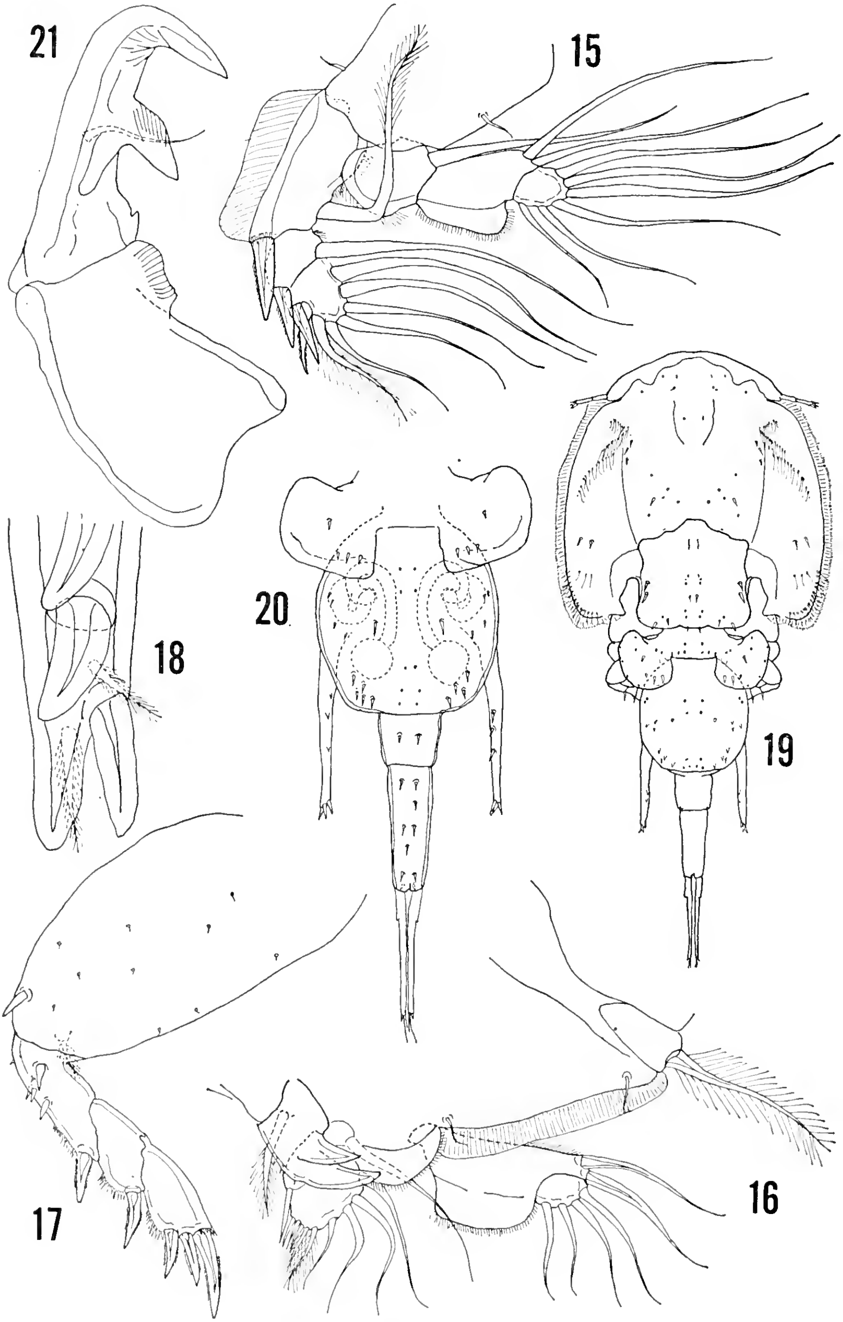


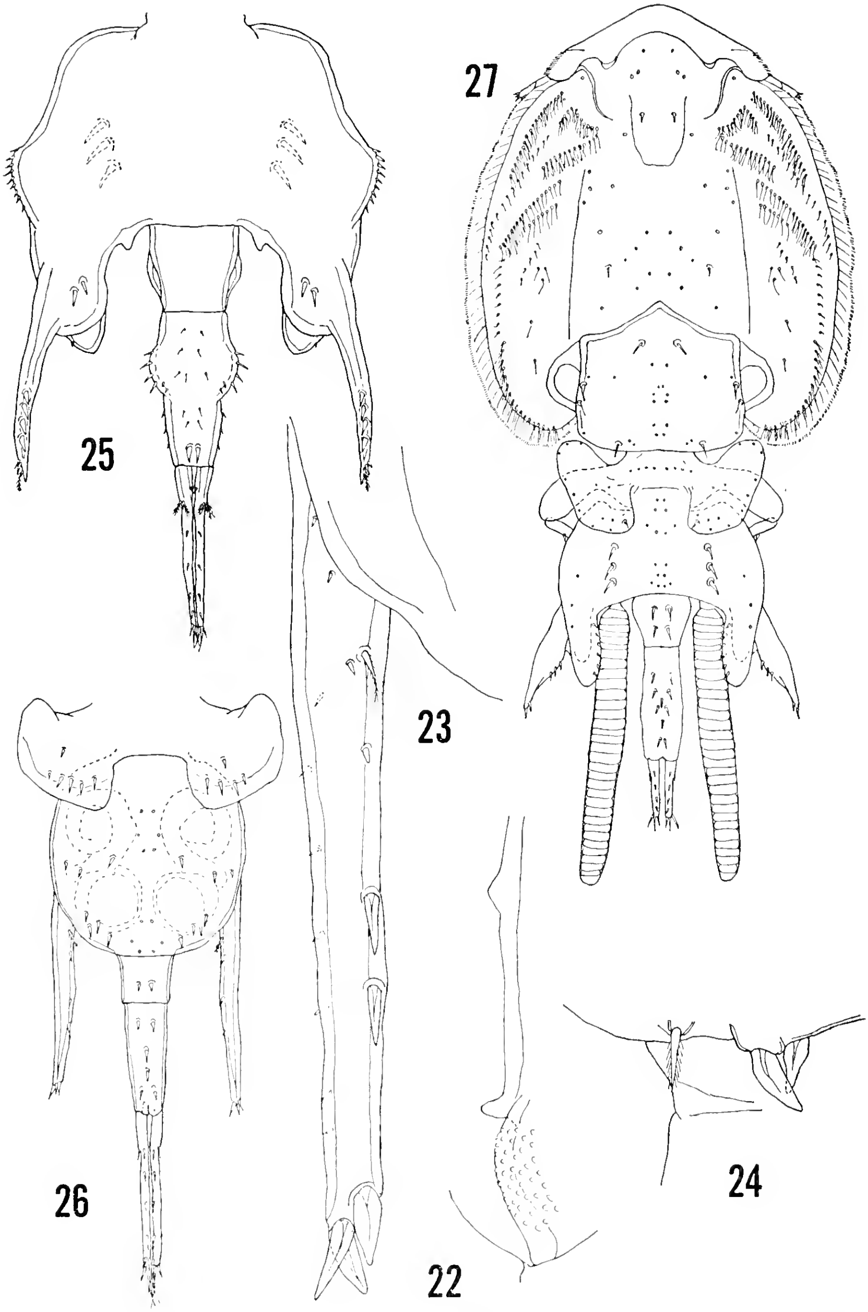
Figures 1–6.—*Gloiopotes americanus*, new species, female: 1, dorsal; 2, genital segment and abdomen, ventral; 3, caudal ramus; 4, postantennal area; 5, postantennal process; 6, first antenna.



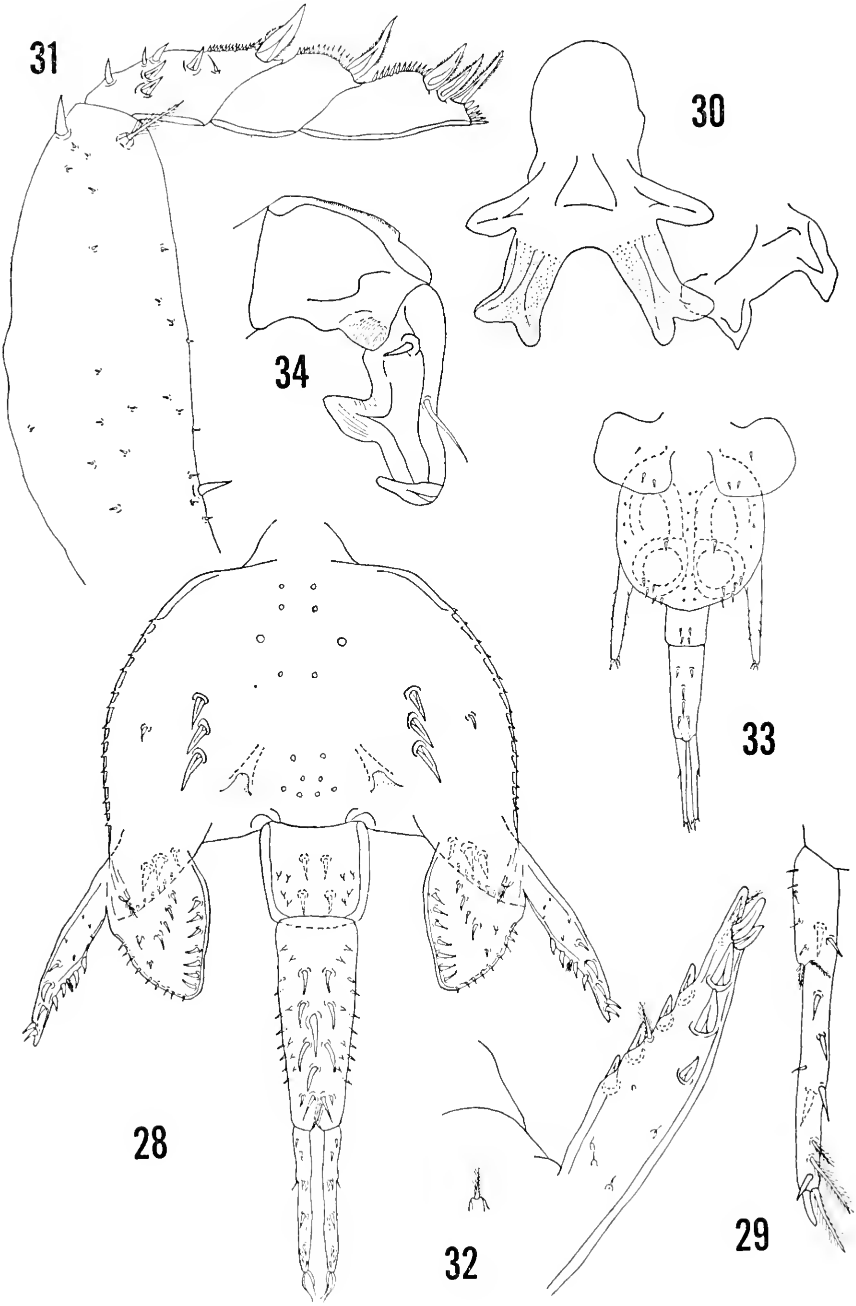
Figures 7–14.—*Gloiopotes americanus*, new species, female: 7, second antenna; 8, mouth tube; 9, second maxilla; 10, maxilliped; 11, sternal furca; 12, first leg; 13, bifid spine on first leg; 14, endopod of first leg.



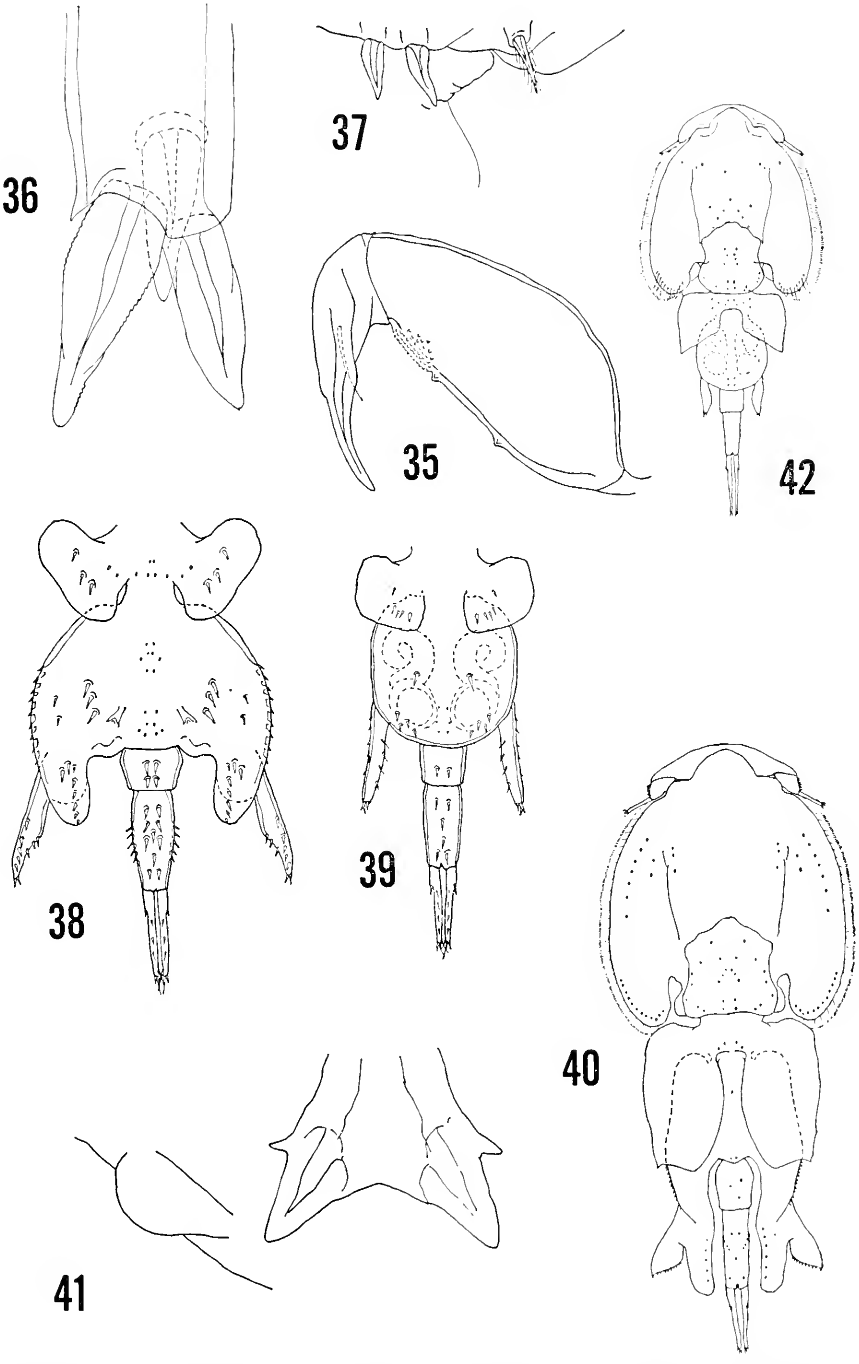
FIGURES 15–21.—*Gloiopotes americanus*, new species, female: 15, second leg; 16, third leg; 17, fourth leg; 18, end of fifth leg. Same, male: 19, dorsal; 20, genital segment and abdomen, dorsal; 21, second antenna.



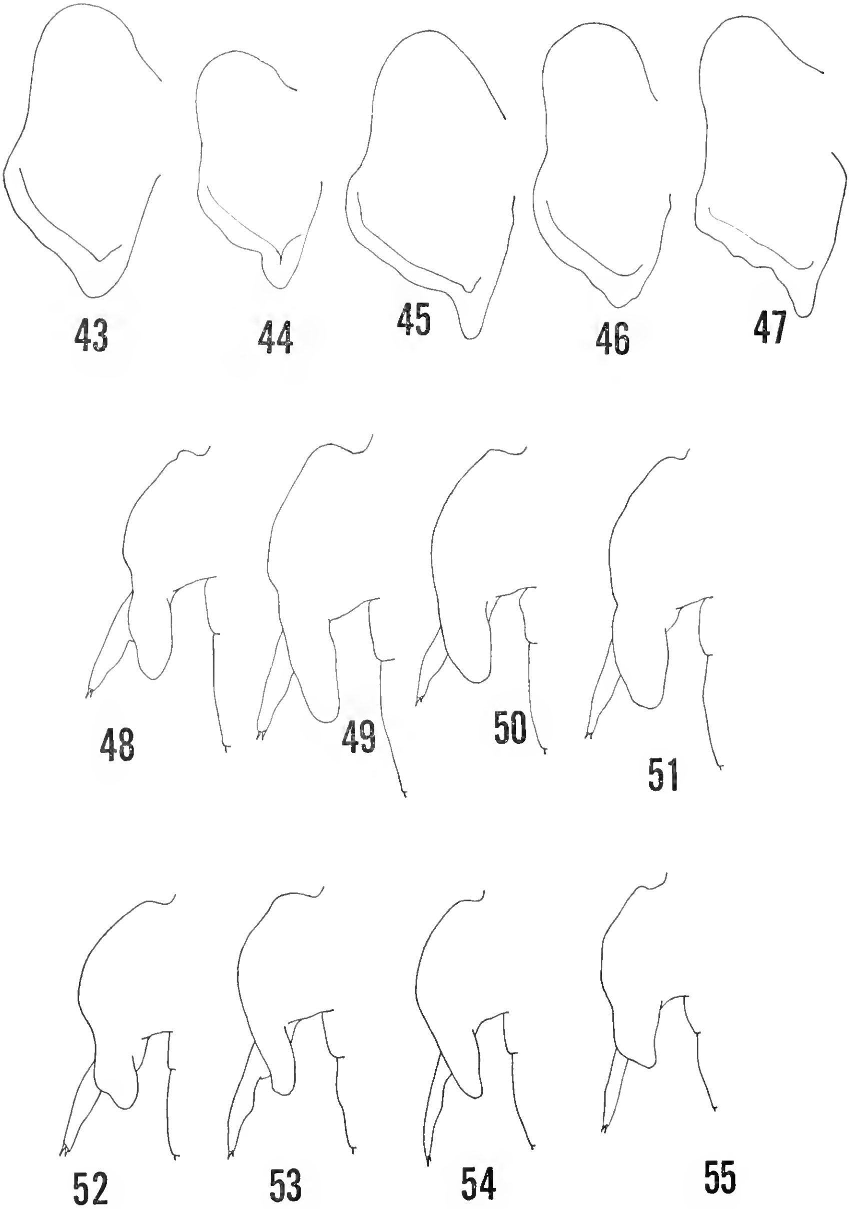
FIGURES 22–27.—*Gloiopotes americanus*, new species, male: 22, inner edge of maxilliped; 23, fifth leg; 24, sixth leg. *Gloiopotes ornatus*, female: 25, genital segment and abdomen, ventral. Same, male: 26, genital segment and abdomen, dorsal. *Gloiopotes huttoni*, female: 27, dorsal.



Figures 28–34.—*Gloiopotes huttoni*, female: 28, genital segment and abdomen, dorsal; 29, caudal ramus; 30, sternal furca; 31, fourth leg; 32, fifth leg. Same, male: 33, genital segment and abdomen, dorsal; 34, second antenna.



FIGURES 35–42.—*Gloiopotes huttoni*, male: 35, maxilliped; 36, end of fifth leg; 37, sixth leg. *Gloiopotes watsoni*, female: 38, genital segment and abdomen, dorsal. Same, male 39, genital segment and abdomen, dorsal. *Gloiopotes hygomianus*, female: 40, dorsal; 41, sternal furca. Same, male: 42, dorsal.



Figures 43–55.—*Gloipotes huttoni*, female: 43–47, dorsal thoracic plate from 5 specimens showing variation in shape. Same, female: 48–51, one edge of genital segment from 4 specimens showing variation in shape. *Gloiopotes watsoni*, female: 52–55, one edge of genital segment from 4 specimens showing variation in shape.